THE FEEDING ECOLOGY OF THE CARABID BEETLE *AGONUM DORSALE* IN CEREAL CROPS

by

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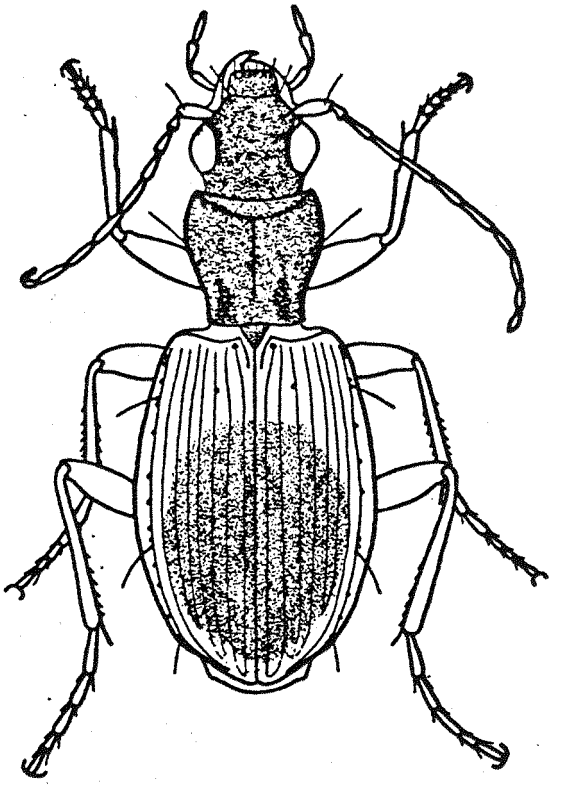
Thesis submitted for the Degree of
Doctor of Philosophy

UNIVERSITY OF SOUTHAMPTON

1983



Agonum dorsale (Pont.).

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

BIOLOGY

Doctor of Philosophy

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Previous field studies suggested that Agonum dorsale (Coleoptera:Carabidae) was the most promising polyphagous predator for the control of cereal aphids in Britain. The principal aim of this study was to assess this potential either for true biological or integrated control. In addition, the principles by which polyphagous invertebrates forage, and in particular how they select their prey, were studied.

A. dorsale was nocturnally active but observation of the beetle was possible under red light. A. dorsale was robust experimentally, e.g. adults could be maintained at an immature reproductive stage by restricting their food supply and they could be maintained for long periods in simple laboratory conditions.

Initial laboratory experiments suggested that A. dorsale had the attributes of an efficient cereal aphid predator; a type III functional response, area-restricted search, rapid passage of food through the gut. But both ambient temperature and reproductive maturity of the beetles were important in determining voracity.

However, A. dorsale showed no specific adaptations for the detection of aphids in the field and when confined with mature wheat, climbed only occasionally; climbs being mostly confined to the lower leaves and stem.

Of the prey selected by A. dorsale in wheat fields, micro-bomb calorimetry confirmed that cereal aphids had the highest calorific value. However, laboratory experiments showed that A. dorsale did not forage optimally. But differences between escape responses of the common prey types led to aphids being caught most easily for all likely field temperatures.

Fieldwork supported laboratory findings: gut analysis showed that aphids could form a large part of the diet but suggested that the beetles foraged on the ground. A. dorsale rarely climbed wheat plants in the field even when aphid densities were relatively high but the proportion of aphids in their diet increased as aphid density increased. This was because as aphid density increased on the wheat the number of aphids on the ground (and hence vulnerable to predation) also increased.

A computer model incorporating laboratory and field data was used to simulate the effect of predation by A. dorsale on a cereal aphid population. The simulations suggested that A. dorsale has little potential on its own, either in the biological, or the integrated control of cereal aphids. Aphid reproductive rate and the proportion of aphids reaching the ground mainly determined whether the beetles controlled the aphid population. Further simulations using predator density/voracity levels corresponding to the whole carabid population in a wheat field suggested that collectively they have an important role to play in the integrated control of cereal aphids.

CONTENTS

ACKNOWLEDGEMENTS

This research was funded by a N.E.R.C. / C.A.S.E. award between the Biology Department, University of Southampton and The Game Conservancy, Fordingbridge, Hampshire.

I would like to thank my parents for their support throughout my time at Southampton University. I would also like to thank my two supervisors, Dr. S.D. Wratten (University of Southampton) and Dr. G.P. Vickerman (Game Conservancy), for support and advice from the start to the finish of this study.

I would like to thank all the staff who have helped me during my postgraduate studies, but particularly John Allen, John Bailey, William Handley-Garland, Owen Jones, Bert Moody, Rory Putman, Rick Trenchard and Allan Watt who went out of their way to be of assistance.

Thanks to Mr. R. Sheppard of South Allenford Farm for allowing me to roam unfettered across his land both night and day during the course of my fieldwork.

Finally I am indebted to Margaret Newton for typing this thesis.

"It's been a hard days night"

- The Beatles

C H A P T E R 1

CHAPTER 1

INTRODUCTION

1.1 Control of pests by specific natural enemies in perennial, glasshouse and annual crop systems

Introduced Natural Enemies

The concept of establishing a low level equilibrium between a pest species and a specific natural enemy has been successfully put into practice in controlling pests of perennial and glasshouse crops (van den Bosch & Messenger 1973; Debach 1974; Huffaker & Messenger 1976). The stability of a perennial crop means that the starting numbers of the natural enemy are not as critical as in a glasshouse or annual crop because there is enough time, both economically and biologically, for them to achieve the desired equilibrium with the pest. Alternatively, the limited size of a glasshouse means that it is possible to apply either sufficient numbers of the natural enemy to the crop to quickly wipe out the pest, or just the right numbers to achieve the desired equilibrium well within the growing period of the crop (Hussey & Bravenboer 1971; Wyatt 1972).

By contrast, such control has not been possible for pests of annual field crops (Southwood 1977) where the growing period is too short and the area too large for either of the above situations to be applicable.

Further, where biological control has been successful, the natural enemies have been mostly parasitoids. A reason given for this is that the so called specific predators[1], are a poor half-way house between parasitoids and truly polyphagous predators. They are sufficiently polyphagous to prevent the closely coupled interaction necessary for control of the pest but not so polyphagous that they can reproduce in areas of very low prey density (Hassell 1978). Since pests

[1] Whenever the words predator and parasitoid are used in future they are used in the sense of a natural enemy unless otherwise specified.

of annual crops are often at low density and only sporadically attain high densities, the usefulness of specific predators to control them may be severely limited.

Resident Natural Enemies

Similar arguments apply to specific natural enemies "resident" in perennial crops. The annual crop, however, is standing for only a short period so control of the pest must be rapid, i.e. at the vulnerable stages of colonisation and early growth. Specific natural enemies are unlikely to be effective because they would have to be active in the crop at a period when pest density would be too low to support "control-effective" numbers of them. Immigration of specific natural enemies in sufficient numbers for control would be likely to occur after the pest had reached yield reducing levels while control by those specific natural enemies already in the crop would require an inappropriately long-term reproductive response because of their low density (Southwood & Comins 1976; Southwood 1977; Vickerman & Wratten 1979).

1.2 Polyphagous natural enemies

Biological control in annual crops, whether by introduced or resident natural enemies, has requirements that specific natural enemies are unlikely to meet.

The natural enemy should be capable of rapidly colonising and surviving in the crop until the pest arrives. It must be sufficiently polyphagous to survive in the absence of the pest but should have the ability to switch to and feed preferentially on the pest when it arrives in the crop. Control by such natural enemies is likely to result from a behavioural rather than a reproductive response because a polyphagous predator probably cannot adjust its reproductive rate to that of any one of its prey. If this is so, the density of polyphagous predators will impose a lower pest density threshold at which control of pest populations can occur than when compared with specific predators.

Switching will tend to make the natural enemies' overall response to the pest sigmoid (even if the functional response is the Type II of Holling 1959) and so more likely to suppress pest numbers (Hassell 1978). Preference may enhance this effect. Again, because these are behavioural responses they will only be effective at an early stage of infestation when pest populations are small.

The identification of the potential importance of polyphagy has led to interest in the role of such indigenous natural enemies in controlling pests of annual crops. Debach (1951) speculated that polyphagous predators may act as a "balance wheel" by feeding on any pests that become abundant. He considered that their action would at least slow down the increase in numbers of pests in such crops. Van den Bosch et al. (1971) and Ehler & van den Bosch (1974) went further and related the recent increase of noctuid moth pests of cotton directly to the killing by insecticides of resident polyphagous predators. This potential role was given further weight when Potts & Vickerman (1974, 1975) demonstrated a significant negative correlation between numbers of cereal aphids and the proportion of arthropods that are predatory in different fields. As aphid-specific predators were scarce the relationship was thought to be due to polyphagous predators. This was supported by later work (Sunderland 1975; Vickerman & Sunderland 1975; Sunderland & Vickerman 1980) which showed that many of these predators had fed on aphids.

The complexities of a polyphagous predator's interactions with its prey have caused there to be few theoretical publications on the subject. The potential of these predators has, however, been acknowledged (Southwood & Comins 1976; Hassell 1978), if not explored.

1.3 The Carabidae as polyphagous biological control agents in annual crops

Estimates of the number of species of Carabidae in the world vary from 25,000-40,000, making this one of the largest insect families in the world. The majority of them live in successional rather than climax habitats (Thiele 1977) and this may be the reason for their successful colonisation of crops throughout the world. The more complex

ground zone structure and spatial and temporal instability of successional stages may provide more niches for carabids, with less competition from other families, e.g. Formicidae. Crops may be widely colonised because they provide a varied, unstable habitat whose regular distribution of plants allows the carobids to penetrate them rapidly (Thiele 1977).

Many carabid species are thought to be evolutionarily preadapted to the annual crop cycle by their littoral origins (Tischler 1958). Both habitats are subject to great seasonal disturbances, both structurally and climatically. Of the 36 field crop-dwelling species that Tischler found in Schleswig-Holstein, 35 also occurred in littoral areas on rivers and the coast. Similar overlaps have been found by other workers (see Thiele 1977 for summary).

Since many of the Carabidae are both voracious and polyphagous predators (Thiele 1977; Allen 1979) increasing interest has been shown in them as important biological control agents.

1.4 Carabid Beetles in cereal crops

The discovery in the 1950s that cereal aphids could be vectors of barley yellow dwarf virus suggested that they may be economically important pests. In the late 1960s and through the 1970s spasmodic but severe outbreaks of the grain aphid, Sitobion avenae (F), caused direct damage to cereal crops in many European countries. As a result of these outbreaks research on cereal aphids has expanded rapidly, the effect of both monophagous and polyphagous predators on aphid populations having been an important part of these studies (see Vickerman & Wratten 1979; Carter et al. 1980 for full reviews of the cereal aphid system).

Initial work by Potts & Vickerman (1974, 1975) showed that the proportion of predatory arthropods (mostly polyphagous) in different fields could be negatively correlated with cereal aphid numbers. Further findings that these polyphagous predators fed on cereal aphids (Sunderland 1975; Vickerman & Sunderland 1975) supported their potential as natural enemies. Field experiments using barriers,

pitfall traps and insecticides to manipulate predator population size (Edwards, Sunderland & George 1979) also showed negative correlations between numbers of cereal aphids and polyphagous predators.

Many of these polyphagous predators have been carabids (about 30 species) and of these Agonum dorsale in particular has shown promise. A. dorsale feeds on aphids even when the aphids are at low field density (Sunderland 1975; Sunderland & Vickerman 1980); aphids can form a high proportion of the beetle's diet (Vickerman & Sunderland 1975; Sunderland & Vickerman 1980) and strong inverse correlations have been found between the numbers of cereal aphids and those of A. dorsale (Edwards et al. 1978).

This potential may be short-lived because the widespread use of broad spectrum insecticides, such as dimethoate, can cause severe reductions (76%) in carabid populations in the field within days of application (Vickerman & Sunderland 1977). Survey work by Vickerman (in litt.) on West Sussex farm sites has shown that populations of A. dorsale have decreased dramatically during the 1970's (Fig. 1.1). This is in contrast to the increasing use of herbicides, fungicides and insecticides, during this period (Fig. 1.2). These three groups of pesticides may severely affect field populations of carabids (Thiele 1977).

The lack of knowledge of the feeding ecology of carabids, even of those species considered to have the greatest potential as cereal aphid predators, caused concern in view of their continued reduction in numbers during the 1970s, and was the stimulus for the current project.

1.5 The life cycle of A. dorsale

The following is a brief summary of the life cycle of A. dorsale to provide a background for the subsequent chapters.

A. dorsale is a common carabid species in cereal crops throughout Europe and is particularly associated with winter-sown cereals (Pauer 1975; Basedow et al. 1976; Kvamme 1977; Thiele 1977). The species

Fig. 1.1 Mean numbers ($/m^2$) of A. dorsale found in cereal crops in June, West Sussex, 1970-80 (Vickerman, unpubl.)

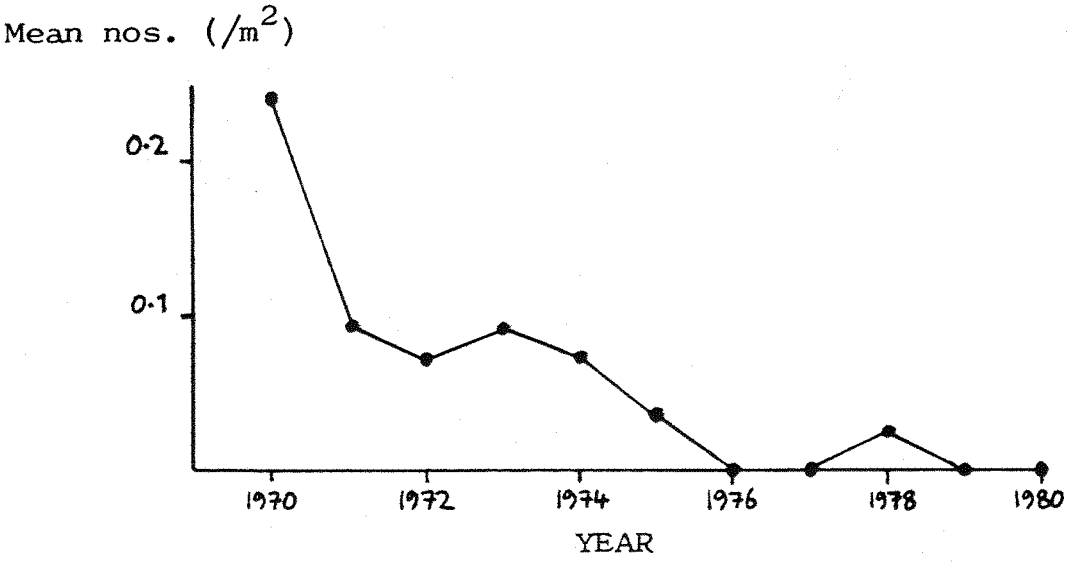
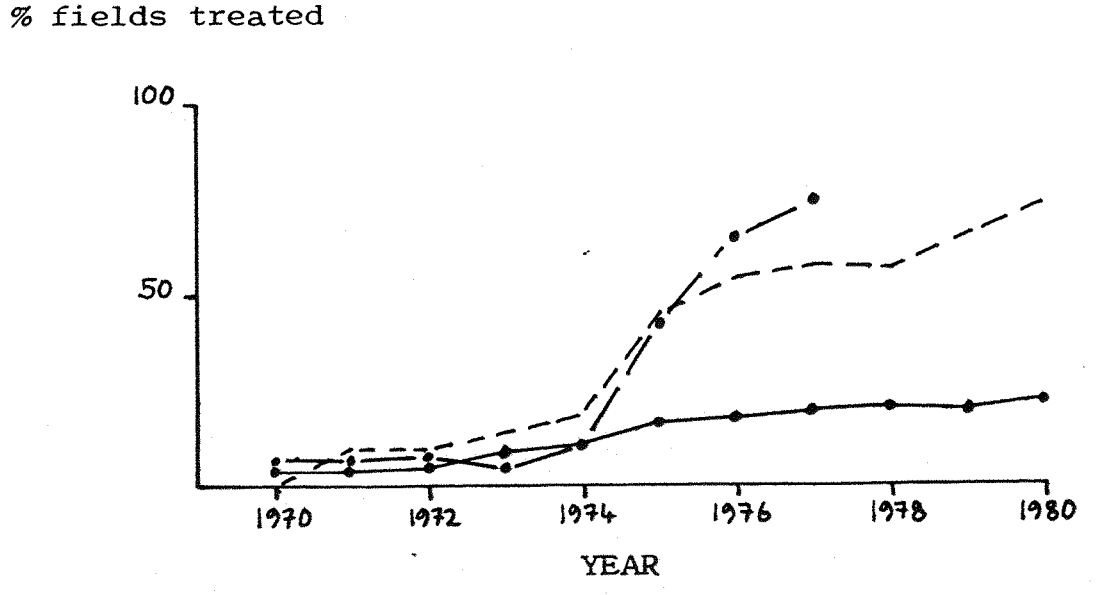


Fig. 1.2 Percentage of cereal fields treated with insecticides, fungicides or herbicides in the 1970's (Vickerman, unpubl.)



= insecticides (U.K.)

= foliar fungicides (Sussex study area)

= herbicides for controlling grass weeds (Sussex study area)

goes through the familiar coleopteran life cycle of

Adults mate → Eggs laid → Larvae mature → Larvae pupate → Adults emerge

with three larval instars (Evans 1975). The life cycle is completed in the crop from mid May to late August (Pollard 1968; Pauer 1975; Jones 1979; Brown pers. comm.). For the rest of the year the adults are aggregated and inactive in overwintering sites along fence lines and hedgerows adjoining the crops (Pollard 1968; Thiele 1977).

The adults become active in the overwintering sites in late April, moving rapidly out to colonise the crop in mid May (Pollard 1968; Jones 1979; Sotherton pers. comm.). Exact timing of mating and later events in the reproductive cycle in the field are not known. Laboratory work on the rearing of larvae (Dicker 1951) and dissection of field-sampled adults (Jones 1979) would suggest the following timetable:

Mating occurs before or soon after the adults move into the field. The eggs are laid singly in earth packages on plant stems and leaves (Dicker 1951) from mid May to probably late July. The eggs take about 7-10 days to hatch (June onwards) and about 20-25 days are required to go through the three larval instars and enter pupation. Emergence of adults occurs about 8-10 days later (August onwards) with the new generation adults moving straight out of the crop into overwintering sites where they can be found in sizeable aggregations (Pollard 1968). Few adults seem to live long enough to overwinter for a second year (Jones 1979).

A. dorsale is unusual in having this seasonal migration to and from the crop (Pollard 1968); both increased chance of mating and better defence (Larochelle & Lariviere 1978) have been invoked to explain this. An alternative hypothesis is that this is a relic of the species' evolutionary history (see also Section 1.3). Most British (and hence European) species in the genus are "hygrophilous and occur near water" (Lindroth 1974); see Table 1.1. The genus may have had

Table 1.1 The habitat of species of the genus Agonum native to the British Isles (after Lindroth 1974)

Specific name	Hygrophilous ?	Habitat
albipes	√	open damp soils near water/seashore
assimile	√	shady deciduous forests
dorsale	X	open meadows/grassland
ericeti	√	peat bogs, moist spots
fuliginosum	√	moist shady places
gracile	√	v. damp places - quagmires
gracilipes	√	on the coast
livens	√	marshy deciduous forests
marginatum	√	soft, wet soil, seashore, lake margins
micans	√	lake shores, river banks
moestum	√	margins of fresh water
muelleri	X	open cultivated soil
nigrum	√	marshy places, river banks
obscurum	√	damp forests, densely vegetated marsh
piceum	√	clayish muddy shores
sahlbergi	√	riparian
scitulum	√	marshy ground
sexpunctatum	√	v. damp/marshy soils
thoregi	√	damp soil near water, reed beds
versulum	√	margins of fresh water
vidnum	√	margins of fresh water

its origins in a species which inhabited environments liable to flood in winter (fenlands, shorelines etc.) and adapted to this by retreating to refuges above the water (grass tussocks, logs and so on). In partial support of this Kreckwitz (1980) has shown that adult A. dorsale prefer warmer, drier conditions during the winter than in summer. Hence perhaps by coincidence A. dorsale is well adapted to life in the similarly seasonally disturbed annual crop system.

While in the crop A. dorsale is known to be nocturnally active (Greenslade 1963; Luff 1978) with some evidence to suggest that this activity includes climbing of plants (Dicker 1951; Dunning, Baker & Windley 1975; Vickerman & Sunderland 1975). Whether this climbing was solely for egg laying (Dicker 1951), or included predatory behaviour as well, is not known. This is the limit of information on the detailed day-to-day behaviours of A. dorsale.

Both the known seasonal and day-to-day behaviour of A. dorsale suggests that it is well adapted to the annual crop system; this thesis assesses whether A. dorsale is an important predator of cereal aphids and hence its potential as a component in the integrated control of these pests.

C H A P T E R 2

CHAPTER 2

MATERIALS AND METHODS

2.1 Culturing of *A. dorsale* and prey species

i) Culturing *A. dorsale*

Adult *A. dorsale* were collected during the winter from large aggregations found along farmland hedgerows and fence lines. They were kept in the culture room (see below) in long daylength conditions and became sexually mature and entered the reproductive cycle with the successful production of new generation adults (see also Kreckwitz 1980).

Adults were kept as a continuously breeding culture in perspex cages in an environmentally controlled room based on the design of Scopes, Randall & Biggerstaff (1975) (in future this will be referred to simply as the culture room). The substrate in the cages was damp sand and a wooden, earth-filled seed tray was provided as a refuge. Food was provided by placing pots of wheat seedlings infested with cereal aphids (see below) in the boxes every 3 - 4 days. The mean temperature was $20^{o}C$ with a range of $2^{o}C$; daylength was 16 h and light intensity (white fluorescent tubes) was 6030 lux.

ii) Maintenance of sexually mature and immature laboratory populations of *A. dorsale*

Adult *A. dorsale* kept in the culture room reproduced continuously, providing a constant source of sexually maturing beetles. These could be dissected after use in experiments to determine the exact reproductive stage. Reproductive development can affect diet qualitatively and quantitatively (Sunderland

1975; Hengeveld 1980) and a separate laboratory population of sexually immature adults was maintained to examine such effects. Adults were kept at an immature stage by keeping them on a 3 days starved : 3 days fed rota. Their immaturity was checked by periodic dissection of samples of five individuals from the population. These immature adults were kept in standard sandwich boxes (Section 2.2) with a piece of damp cardboard as a refuge and their diet was strictly controlled. They were kept in the growth room or the dark room (Section 2.2), where the L:D ratio and temperature were the same as the culture room.

iii) Culturing of prey species

All cereal aphid species used were cultured on seedlings of winter wheat (cv. Hobbit). The wheat was grown in a glasshouse at 15°C with a range of 4°C, with a daylength of 16 h maintained by high-pressure sodium lamps. Wheat seed was sown in John Innes No. 2 potting compost in 10 cm diameter pots at sufficient density to produce a dense growth of seedlings.

The cereal aphid species used were Metopolophium dirhodum (Walker), Rhopalosiphum padi (L.) and Sitobion avenae (F.) and were cultured separately in perspex cages in the culture room.

Collembola and Mycetophilidae also survived well in the aphid cultures, provided the sand substrate and soil in the wheat pots were kept moist.

The aphid cultures could thus provide the three main prey types used in subsequent experiments, although they were supplemented with Collembola, Mycetophilidae and other invertebrate prey from the field as needed.

2.2 Laboratory facilities and preparation of *A. dorsale* for experiments

i) Standard facilities used in laboratory experiments

All the laboratory experiments were conducted in one of three controlled environment facilities.

The incubator

A L.E.E.C. incubator of internal dimensions 60 x 70 x 50 cm, was used where differing temperatures were required over long periods. The temperature could be varied between 5 and 20°C, with a 1°C range. Daylength was 16 h and light intensity was 3230 lux.

The Growth Room and Experimental Dark Room

When continuous observation of *A. dorsale* was necessary either of these rooms could be put on a reverse light:dark cycle to allow observation of this nocturnal beetle during normal working hours. The temperature in both rooms was 19°C with a 1°C range and daylength was 16 h. Light intensity was 8240 lux. in the growth room and 860 lux. in the dark room.

Subsequently, these facilities will be referred to only as the incubator, growth room or dark room. Temperature and light conditions were as indicated here, unless otherwise stated.

Clear polystyrene sandwich boxes (17 x 11 x 6 cm deep) were used in many of the laboratory experiments, and these were prepared in a standard way. The inside of the lid and walls was coated with poly-tetra-fluoroethylene as a suspension in water (abbreviated to the trade name of "Fluon" from now on). This forms an inert, slippery coat which restricted both *A. dorsale* and its prey to the arena floor.

The bottom of the sandwich box was filled to a depth of 1-2 cm with damp silver sand to provide humidity and a less slippery substrate than the polystyrene.

When mature wheat was required for use in arenas it was dug up from the Damerham field site (Section 2.7) and replanted in pots or arenas where it continued to grow successfully. The growth stages are described according to the Feekes scale (Large 1954). The cultivar was Maris Huntsman.

(ii) Preparation of A. dorsale for laboratory experiments

Unless otherwise stated, adult A. dorsale to be used in experiments were fed on cereal aphids. Individuals were, however, starved for three days before an experiment to standardise their voracity; by the end of this period the gut should have been empty (see Chapter 4.6 and Hengeveld 1980).

Where it was necessary to keep individuals on a reverse light:dark cycle in the growth or dark rooms, at least 2 wk were allowed for adjustment of their circadian rhythm. Previous studies would suggest that this is sufficient time for resynchronisation to the L:D phase reversal (Thiele 1977). To check this, observations were made of the number of beetles active at 3 or 4 h intervals before and after the L:D reversal (Section 2.3). Thiele (1977) suggested that light intensities as low as 1 to 10 lux. were sufficient to act as a zeitgober in the carabid L:D activity cycle; the minimum light intensity that laboratory animals were exposed to was 860 lux. (darkroom).

(iii) Sexing of live adult A. dorsale

The sexes are easy to tell apart in the later stages of reproductive development, when the enormously swollen abdomen and the extended cerci of the gravid female are clear markers. Immature beetles cannot easily be separated unless dissected.

Numbers of A. dorsale were examined for obvious morphological characteristics which would provide a quick means of identifying the

sex of live beetles (size, elytral patterns, skeletal characteristics) while in the field or laboratory. Unfortunately no sex-linked morphological characteristics were discovered which could be used to identify the sex of immature beetles.

2.3 Preliminary experiments with A. dorsale

(See Chapter 3 for results and discussion)

Initial experiments were designed to investigate the basic parameters of the activity period and searching behaviour of A. dorsale, with the particular purpose of designing later experiments.

(i) The Activity Period of A. dorsale

In the field many predators, including A. dorsale, may be most active at night (Vickerman & Sunderland 1975). The numbers of A. dorsale active in the culture-room, growth-room and dark-room cultures (Section 2.1) were recorded at 3 to 4 h intervals over 24 h to determine their periodicity under laboratory conditions. During the hours of darkness, numbers were recorded by observing the cultures for a few minutes under dim white light; this was not ideal as it caused some beetles to retreat to their refuges.

Individuals were counted as "active" when they had emerged from refuges (plant pots, seed trays) to move around the culture box. When no individuals could be seen the refuges were examined to assess activity and numbers there.

In order to observe the nocturnally active A. dorsale during normal working hours the growth- and dark-room cultures were put on a reverse light:dark cycle. Their activity cycle was assessed (as above) one day before, and three days after, this diel period reversal to see how quickly the beetles adjusted to the new cycle.

(ii) The Sensitivity of A. dorsale to Red Light

Many beetles are sensitive to light in the green to ultra-violet range only (Evans 1975), making nocturnal observation of them possible

under lights in the red range of the spectrum. To test this, the negatively phototactic behaviour (retreating under refuges) of A. dorsale was compared when suddenly illuminated with red or white light during the dark phase of the light cycle in the dark-room. The trials were replicated 10 times under the two types of lighting. The reaction of individuals to a shadow moved across them and a human hand waved at 10-20 cm under red and white light was also compared, with 10 replicates for each set of lighting. White light was from an ordinary 60 Watt bulb and red light from an ordinary 40 Watt red coloured bulb.

(iii) The behaviours shown by A. dorsale in the present or absence of prey

Trials were conducted in the sandwich box arenas in the growth-room. The behaviour of A. dorsale was observed for 30 min periods under red light during the dark phase of the diurnal light cycle as results (Chapter 3.2) showed them to be nocturnally active. Behaviour was recorded descriptively on a tape recorder with emphasis on searching behaviour. The behaviour of single individuals in an arena containing no cereal aphid prey (S. avenae) was compared with that of those in an arena containing a high density of cereal aphids (100 per arena).

(iv) The effect of handling on the subsequent behaviour of A. dorsale

Trials were carried out in sandwich box arenas in the growth-room.

The easiest method of transferring A. dorsale from cultures to experimental arenas was to use a pooter (Southwood 1978). This involved considerable disturbance of individuals which could have affected subsequent behaviour. To measure disturbance two parameters were recorded; the time taken to detect the first cereal aphid (S. avenae) in the arena and the total number of prey eaten over the trial. Trials were 30 min long and of two types:

"Control" - single A. dorsale were placed in arenas containing no prey and left for 2 h to "settle down". 30 cereal aphids (apterous adults) were then placed in the arena without disturbing the beetle. The above two parameters were then recorded.

"Experiment" - 30 cereal aphids (apterous adults) were placed in each arena. Single A. dorsale were then removed by pooter from a culture and placed in the arena. The two parameters were then recorded.

The starting of trials was staggered so that the first parameter could be recorded by separate observation of each beetle. Each type of trial was replicated ten times.

(v) The effect of satiation on A. dorsale with respect to trial length

Trials were carried out in sandwich box arenas in the growth-room.

Satiation can greatly affect a predator's response to its prey (Hassell 1978). This is especially important when determining a predator's functional response where both handling times and satiation may have similar affects. Satiation was determined by observing single A. dorsale in arenas containing 100 opterous adult cereal aphids (S. avenae). The following parameters were recorded.

Time to cessation of feeding: time from the start of the trial to when the individual ceased to feed for 15 min. After they had ceased to feed, the beetles were left in their respective arenas and any further predation recorded by counting the number of aphids prey left after another 24 h.

Handling time: the time from when the beetle detected the prey item to the time when the beetle continued hunting or moved off. (In consequence the total number of aphids eaten was also recorded).

Time between consumption of prey items: the time intervals between the periods of handling time.

This was repeated with 15 A. dorsale.

(vi) Close-range detection of aphid prey by A. dorsale

Casual observation suggested that searching behaviour was triggered when individuals made physical contact with prey; this was tested in two ways.

The sandwich box arena was used, but without sand in the bottom. Instead, a piece of graph paper was placed underneath the box so that the distance between a beetle and its prey could be recorded. Trials were carried out in the growth-room.

In the first set of trials a single beetle was placed in an arena with four adult apterous cereal aphids (S. avenae) spaced as in Figure 2.1 . The beetle's path of movement during a 15 min period was traced on a sheet of glass suspended over the sandwich box. This was repeated with 20 A. dorsale.

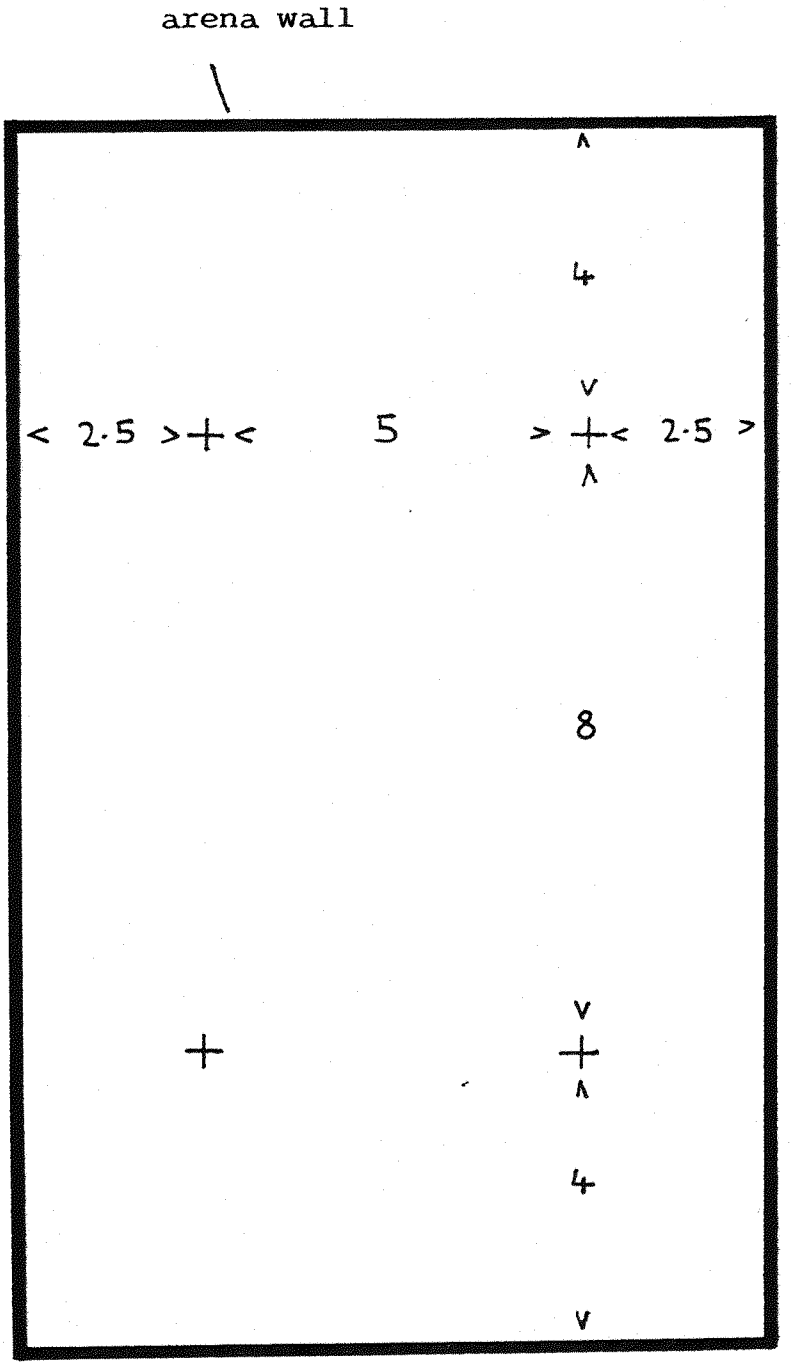
The distance from a prey item at which the beetle changed direction to move in a straight line towards that prey item was recorded. A "change of direction" was only recorded if the beetle successfully came into contact with the aphid as a result of the turn.

In the second set of trials, a single A. dorsale was placed in the arena and then a single apterous adult aphid was placed five times at each of the following distances directly in front of the beetle; 5, 4, 3, 2, 1 and 0 cm (for the last distance the aphid was placed as close to the beetle's mouth parts as possible without disturbance). This was replicated with 20 A. dorsale and the distances at which the aphid elicited searching behaviour from the beetles recorded (no contact occurred between beetle and aphid until distance 0 cm).

(vii) Close-range capture of prey by A. dorsale

Observation of A. dorsale when it came into contact with cereal aphid prey suggested that the part of the beetle's body that touched the prey determined whether the prey was caught. This was tested by placing the beetles in an arena with large numbers of aphids and

Fig. 2.1 The spatial distribution of cereal aphids, on the floor of the sandwich box arena, in trials to investigate the close range detection of prey by A. dorsale



+ = adult apterous cereal aphid

Scale 1:1

(figures are in cm)

observing the outcome of contacts between prey and predator.

Trials were carried out in sandwich box arenas in the growth-room. 100 apterous cereal aphids (S. avenae of size/age range instar III to adult) were placed in the arena and a single A. dorsale introduced and observed for 30 min. The section of the beetle's body (see Fig. 2.2) that contacted an aphid was recorded, and the outcome of the encounter noted. This was repeated for 20 A. dorsale.

2.4 The predatory potential of A. dorsale

(See Chapter 4 for results and discussion)

(i) Larval vs adult A. dorsale feeding rates

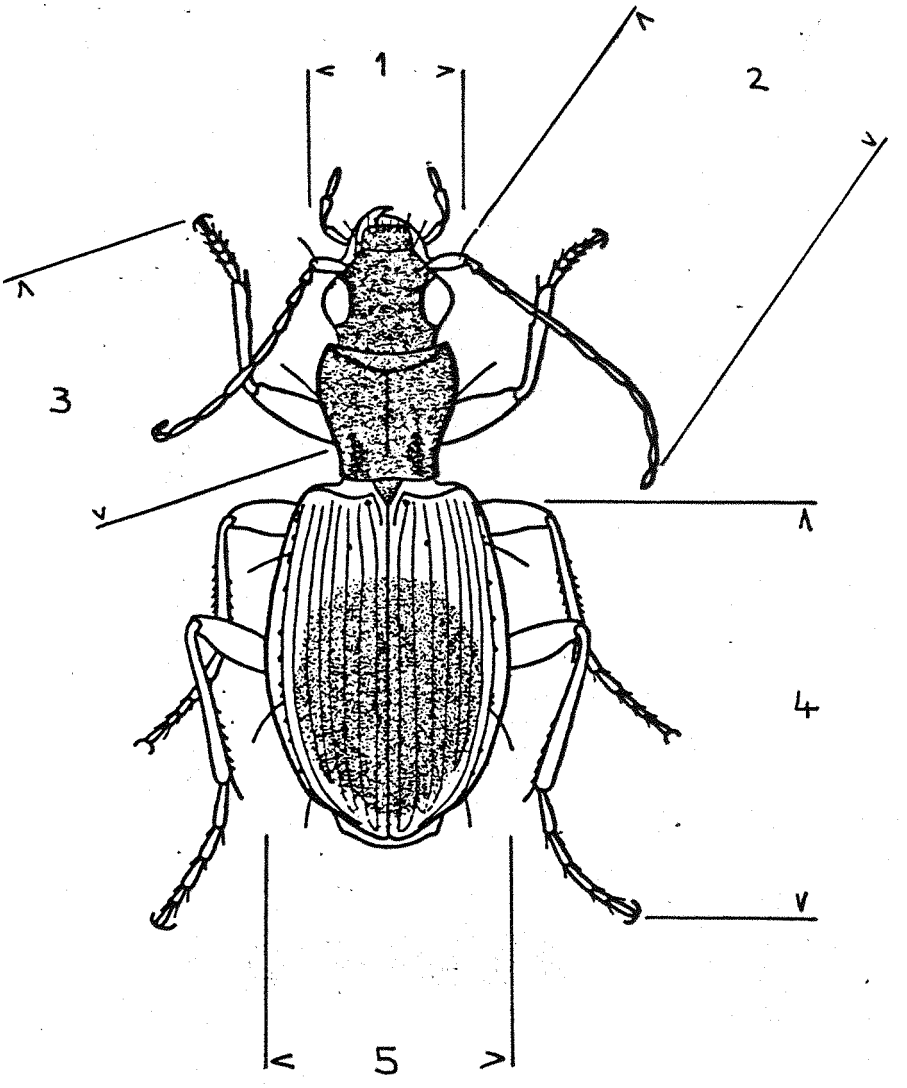
The experiment was performed in the dark-room. The three larval instars of A. dorsale were obtained by rearing from eggs (Section 2.9). Larvae were confined individually in polystyrene petri dishes (diameter 5 cm) with moist sand in the base. 15 cereal aphids (I/II instar, S. avenae) were placed in each dish and the number eaten recorded after 1, 2 and 3 h. There were at least five replicates for each A. dorsale instar.

The same experiment was repeated over 24 h with the A. dorsale third-instar larvae. The numbers of aphids consumed were recorded after 1, 18 and 24 h. There were ten replicates. In addition the number of aphids consumed by 10 reproductively immature adult A. dorsale in sandwich boxes was also recorded at these times (60 S. avenae per sandwich box were used because adult consumption was known to be higher).

(ii) The fecundity, site of egg laying and percentage egg hatch of A. dorsale

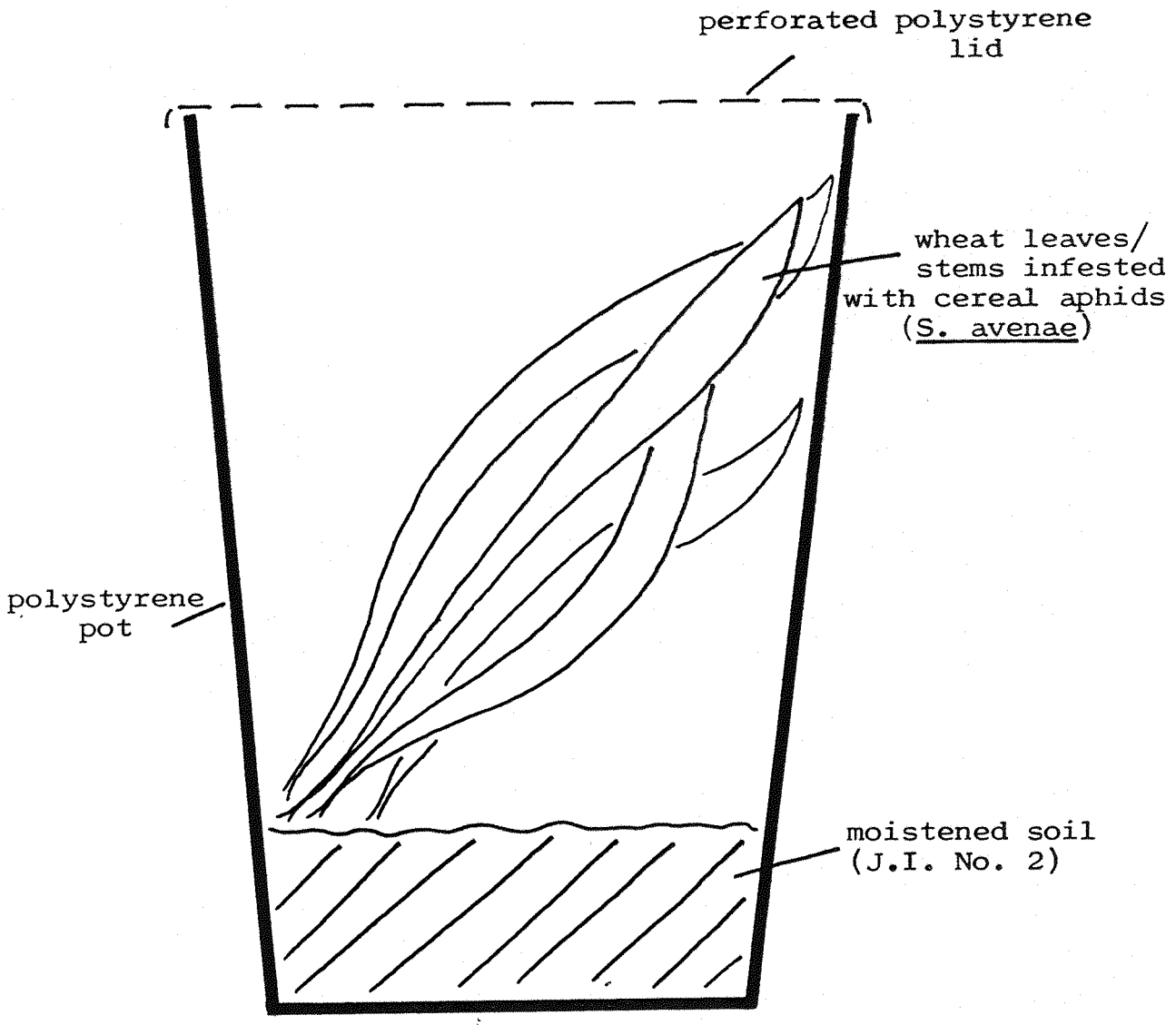
Ten gravid female A. dorsale which had not yet begun to lay eggs were removed from the culture room and placed individually in polystyrene pots (Fig. 2.3). The aphids on the wheat leaves provided food for the beetles and were replaced every day with freshly-cut

Fig. 2.2 Sections of Agonum dorsale body used to record predator/prey contacts



1. Head, mandibles, palps
2. Antennae
3. Fore legs
4. Mid and hind legs
5. Rear of abdomen

Fig. 2.3 Polystyrene pot used to assess fecundity and site of egg laying of A. dorsale



Scale 1:1

wheat leaves infested with aphids (S. avenae).

Every day, any eggs found on the leaves were placed on moistened filter paper in petri dishes until they hatched. Some of the larvae were then used in the predation experiments. The remaining larvae were raised through to adults to measure the survival rate, live larvae being closely monitored to measure the development times of each stage of the life cycle. When oviposition ceased, females were removed and dissected to record their reproductive state and the number of unlaid eggs. The soil in the pots was sorted under a low power binocular microscope for eggs not laid on the wheat.

(iii) Changes in path and speed of movement of A. dorsale as a result of encountering prey items

Trials were carried out in the dark-room. The sandwich box arena was used with 100 cereal aphids (S. avenae) per box, or with no prey present. Reproductively immature A. dorsale were introduced singly into the arena and, during a 10 min period, the path of the beetle was traced, using a fine-tipped felt pen, on a sheet of glass suspended above the sandwich box.

The length of the path was measured, using an ipsometer, and the number of turns greater than 45^{o} made within a distance travelled of 2 cm recorded. The speed of movement was recorded separately by tracing the path of the beetle for intervals of 10 s. At least ten replicates were carried out.

A clean box was used for each beetle to avoid the possibility of pheromone produced by the previous individual altering the behaviour of the next.

(iv) The functional response of a A. dorsale to different sizes of cereal aphid prey

Experiments were carried out in the dark-room. Apterous aphids (S. avenae) were grouped into four size classes:

I	0.8 mm	(body length)
II	0.8 - 1.1 mm	
III	1.1 - 1.4 mm	
IV	1.4 - 1.7 mm	

Each size class of aphids was presented to reproductively immature A. dorsale in the standard sandwich box arena at densities from 5 - 50 per box. Single beetles were placed in each box and the number of aphids eaten after 1 h recorded. During the highest and the lowest density trials handling times and % successful encounters were recorded. Each combination of aphid size and density was replicated ten times.

The "handling time" was recorded as the time from when the beetle first detected the prey item (Chapter 3.4) to the time when the beetle continued hunting or moved off after consuming the prey.

An "encounter" was recorded when an individual beetle detected a prey item, a "successful encounter" being when the detection resulted in the death and/or consumption of the prey.

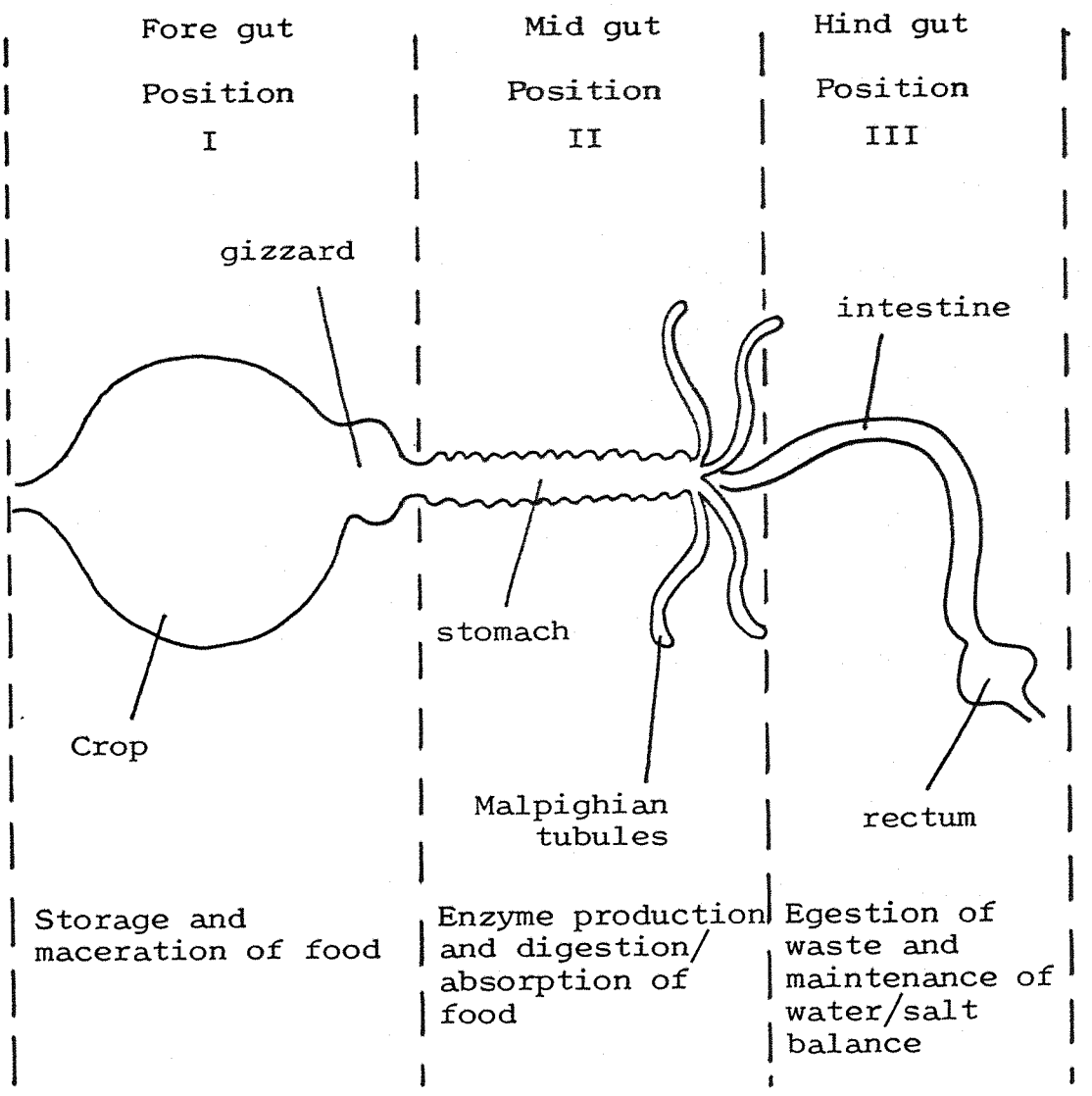
(v) The length of time food is retained in the gut by A. dorsale

The experiment was conducted in the dark-room. 35 sexually immature A. dorsale were put in a sandwich box with large numbers of cereal aphids (S. avenae) and allowed to feed for 24 h. The beetles were then removed from the food source and placed individually in polystyrene pots (13 cm high x 9 cm diameter) with moist tissue paper as a refuge. Five beetles were then dissected at each of the following times after they were removed from the food source; 1½, 3, 6, 9, 21, 24 and 27 h. Aphid remains were recorded as present or absent in one of three sections of the gut. The gut was divided into three sections on the basis of their different functions (Fig. 2.4). The sex and reproductive state of the beetles were also recorded.

(vi) The effect of temperature on the voracity of A. dorsale

The incubator was used to maintain test groups of beetles at temperatures of 5, 10, 15 or 20°C. Ten reproductively immature

Fig. 2.4 The three functional divisions of the gut (Barnes 1974; Evans 1975) in which the presence/absence of aphid remains were recorded



A. dorsale were used at each temperature. Each beetle was placed in a sandwich box arena with 40 apterous cereal aphids (S. avenae of size class III instar to adult) as prey. Numbers of aphids eaten per day were recorded for at least 10 days at each temperature, the total number of aphids being made up to 40 again each day. Adults were acclimated for 1 wk at each temperature before commencement of trials. This period was chosen because reviews suggest (Wieser 1973) that acclimation takes place in the short term over a few days or in the long term over a few weeks. For acclimation to be adaptive for A. dorsale within its short field-active period it would have to occur over a few days.

(vii) The effect of reproductive development on the voracity of A. dorsale

Three groups of A. dorsale were compared:

1. Males and females maintained at a reproductively immature stage in laboratory cultures.
2. Reproductively immature males and females, recently collected from the field during their winter diapause.
3. Reproductively mature males and females, from laboratory cultures.

Comparisons between groups 1 and 3 were made to assess whether voracity changed with reproductive development. Groups 1 and 2 were compared to see if voracity altered when adults were kept in culture conditions for long periods.

Ten individuals in groups 1 and 2 and 20 in group 3 were tested (as the stage of reproductive development can be variable, 20 individuals gave a better sample size).

A. dorsale were placed individually into sandwich box arenas with 40 cereal aphids (S. avenae, size/age range III instar to adult). The boxes were placed in an incubator at 10°C.

Numbers of aphids eaten by each individual were recorded every day, for 3 wks, the numbers of aphids being made up to 40 each day. At the end of this period the beetles were dissected to assess their reproductive state.

2.5 Does A. dorsale show a prey-searching adaptation specific to cereal aphids?

(See Chapter 5 for results and discussion)

(i) The role of kairomones in the detection of cereal aphids by A. dorsale

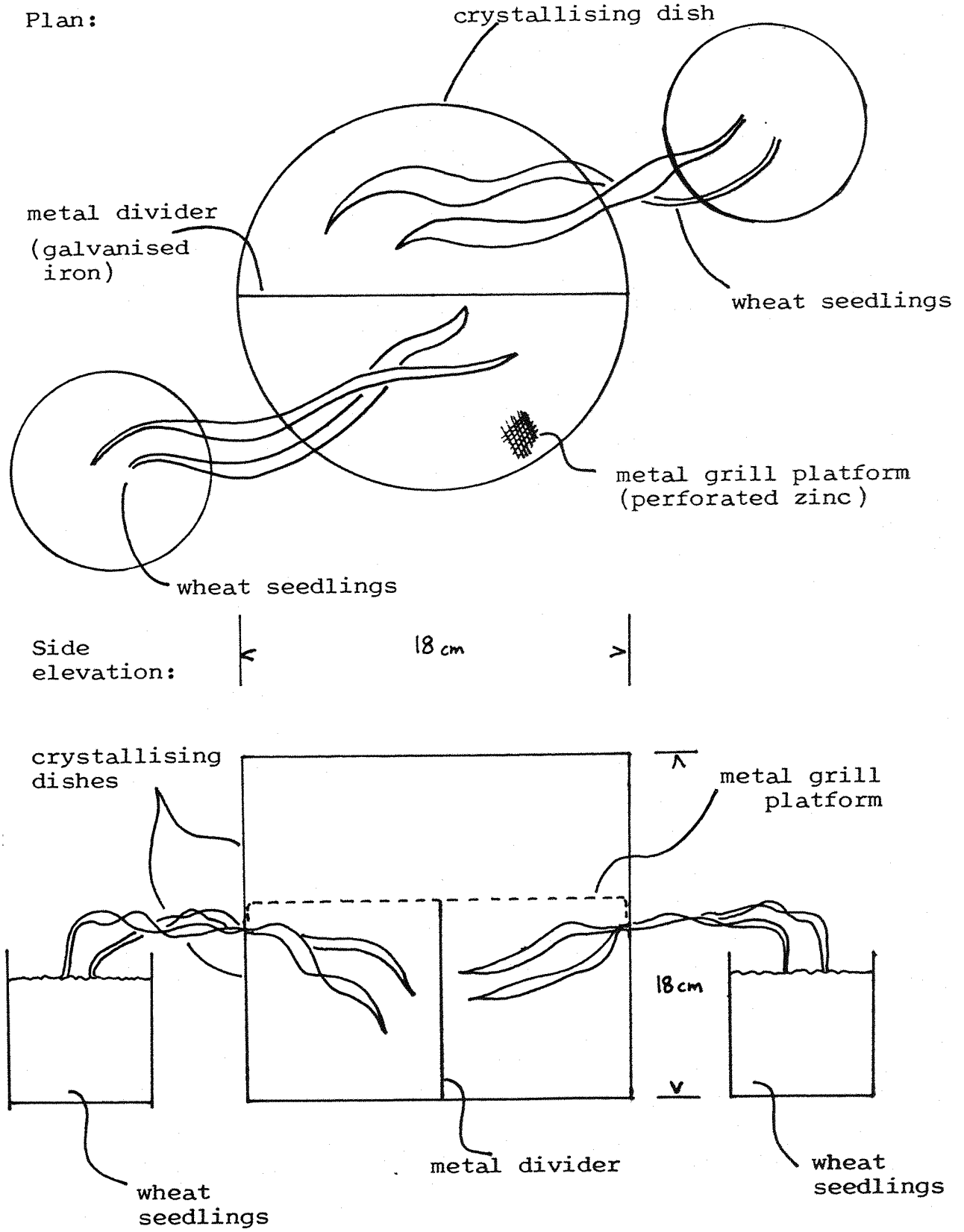
Trials were carried out in the growth-room. The arena used was essentially a choice chamber consisting of two glass crystallising dishes with a metal divider and platform (Fig. 2.5). No plastics were used as these can become contaminated by kairomones and confuse results. The leaves of the wheat seedlings (height 20 cm) were inserted into the chamber beneath the metal grid platform (Fig. 2.5). The leaves were either aphid free, or had heavy infestations of the cereal aphid S. avenae.

At the start of a trial the upper crystallising dish was removed and a single A. dorsale adult placed in the centre of the grill. The crystallising dish was then quickly replaced. Trials were of 5 min duration only, to avoid saturating the arena with kairomone. After each trial the air in the chamber was flushed out with a hairdryer set to blow cold air.

Two types of trial were carried out on each choice chamber arrangement. In the first, the average speed of movement of A. dorsale was recorded by measuring the distance moved by an individual over 5 s intervals. The individual's path was traced with a felt tip pen on the upper crystallising dish and measured with an ipsometer. In the second, the number and length of times that searching behaviour was shown for and also the position of the individual in the chamber was recorded every 6 s.

Three arrangements of the choice chamber were used:

Fig. 2.5 The Choice Chamber used to assess the role of kairomones in the detection of cereal aphid prey by A. dorsale



1. Wheat with no aphids in both sides of the chamber.

2. As for 1. but with the whole apparatus turned through 180°.

3. Wheat with no aphids on one side of the chamber and wheat infested with aphids on the other.

Results from 1 and 2 were compared to show whether there was inherent bias in the chamber or the growth-room, causing individuals to spend more time on one side of the arena than the other. The results of 1 and 2 were then compared with 3 to show any effects caused by the aphids.

(ii) The role of honeydew and exuviae in the detection of cereal aphid prey by A. dorsale

Trials were conducted in the dark room. The arenas consisted of large flower pots (diameter 23 cm) into which 10 wheat plants (G.S. 8-10) from the Damerham field site (Section 2.7) had been transplanted. One set of arenas was kept aphid-free while the others were allowed to develop a large cereal aphid infestation (S. avenae). At the beginning of the trial the aphids (but notthe honeydew or exuviae) were removed from the infested arenas. A trans-superglaze barrier, height 5 cm, was embedded in the soil round the edge of the pot to present A. dorsale individuals from escaping.

Individual A. dorsale were placed in one or other type of arena and their behaviour recorded for 30 min with a stop watch and tape recorder. Ten replicates were carried out for each type of arena. In between trials the sand and wheat surfaces were moistened with water, from an atomiser, to simulate the condensation that nocturnal animals would be exposed to.

(iii) The effect of wheat stem structure close to the ground on the climbing frequency of A. dorsale in the absence of prey

Trials were carried out in the dark-room. The arena was a large flower pot (diameter 23 cm) planted with three wheat stems (G.S. 8), taken from the Damerham field site (Section 2.7), in one of three

positions (see Fig. 2.6). Both sand[1] and stems were kept moist with water from an atomiser to simulate the condensation that occurs at night in a wheat field.

The A. dorsale used were sexual immatures from laboratory cultures. Individuals were introduced singly into the arena and their climbing behaviour noted for 30 min. with a taperecorder and stopwatch. Trials were replicated 20 times for each stem position.

(iv) The effect of aphid distribution between the ground and wheat seedlings on the climbing frequency and searching behaviour of A. dorsale

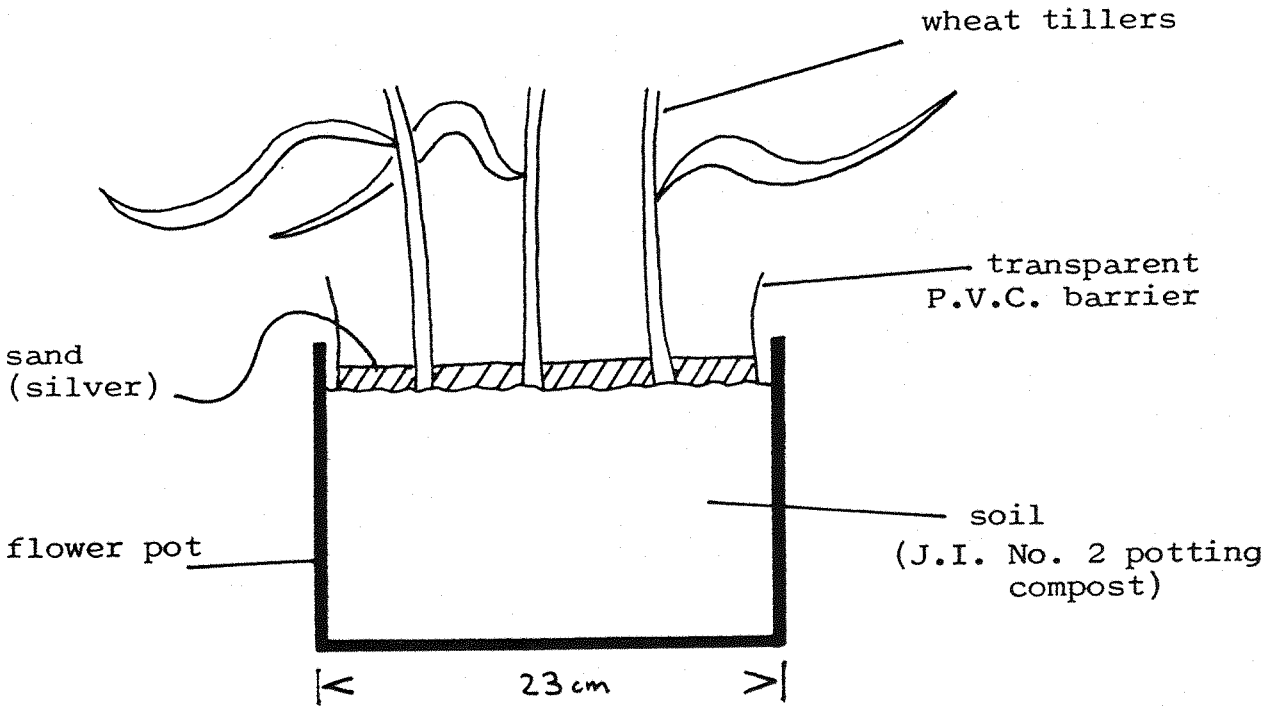
Trials were carried out in sandwich box arenas in the dark-room. The boxes were part-filled (2-3 cm) with J.I. No. 2 potting compost soil into which were planted 15,2 cm-high, wheat seedlings (c.v. Hobbit), in a regular 5 x 3 arrangement. Seedlings were not used in the trials until they were 6-8 cm in height and were replaced when taller than 12 cm. The soil was covered with a layer of silver sand to make the beetles and aphids more easily seen. Apterous adult cereal aphids (S. avenae) were placed in the arena at the equivalent densities, per unit surface area of plant or ground, of one per seedling and 20 on the arena floor (i.e. one aphid per 10 cm^2). Four arrangements of aphids were used:

1. No aphids on wheat or soil.
2. Aphids on soil only.
3. Aphids on wheat only.
4. Aphids on wheat and soil.

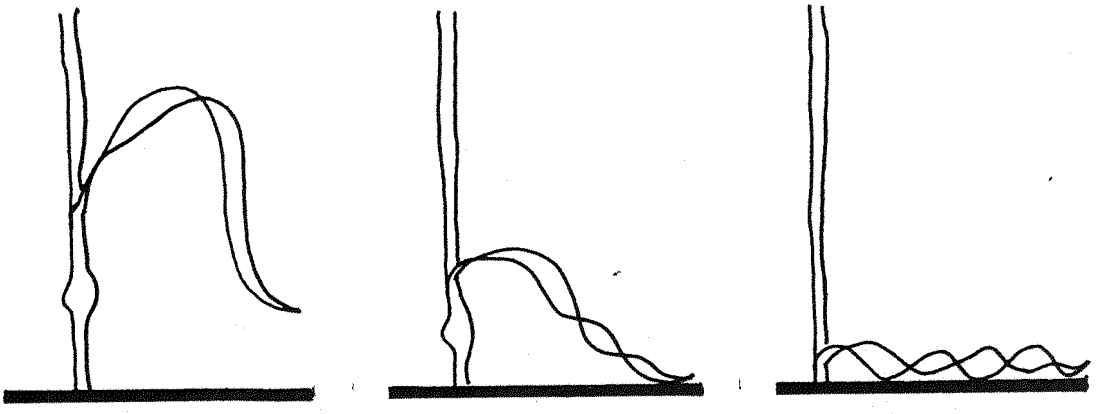
Single A. dorsale were introduced into the arena, observed for 30 min and their movements and behaviour recorded using a taperecorder and stop watch. Ten replicates per prey arrangement were recorded.

[1] A layer of silver sand was placed over the soil to form an even, light-coloured background against which A. dorsale could easily be seen.

Fig. 2.6 Arrangement of wheat used in the investigation of the effect of tiller structure on climbing frequency of A. dorsale



The three lower leaf positions used, achieved by replanting tillers at different depths.



No leaves touching ground

Tips of leaves touching ground

Whole of leaf touching ground

(v) The effect of aphid distribution between ground and plant on the searching behaviour of A. dorsale using mature, field-grown wheat

Trials were conducted in the dark-room using reproductively immature A. dorsale. Wheat (c.v. Maris Huntsman) was transplanted (at G.S. 8-10) from the Damerham field site to laboratory arenas. Where wheat was infested with aphids the species used was S. avenae.

The arena was a seed propagator base (57 x 28 cm) and was set up as shown in Fig. 2.7. Trans-superglaze (P.V.C. double-glazing sheeting) was used as a barrier to keep beetles in the arena; the layer of silver sand made observation of the aphid prey and the beetles easier. Wheat was planted in the same density and pattern as that found at the Damerham field site, six rows/m and about 100 tillers/row metre.

Six different distributions of aphids were used in the trials (Fig. 2.8). Adult A. dorsale did not migrate into the crop until mid May (Chapter 7.2) when the crop was at G.S. 7. By this stage lower leaves on the stems have senesced so an aphid distribution with the aphids close to the ground was achieved by using a deeper propagator base (15 cm) and burying the wheat up to the fourth leaf (which still carried aphids). Distributions remained constant through the trials because the aphids remained immobile under the red lights used for observation in the night period.

Trials were conducted by introducing single A. dorsale into the arena and recording their behaviour for 30 min with a stop watch and tape recorder. There were at least 10 replicates per distribution.

2.6 The basis of prey choice by A. dorsale

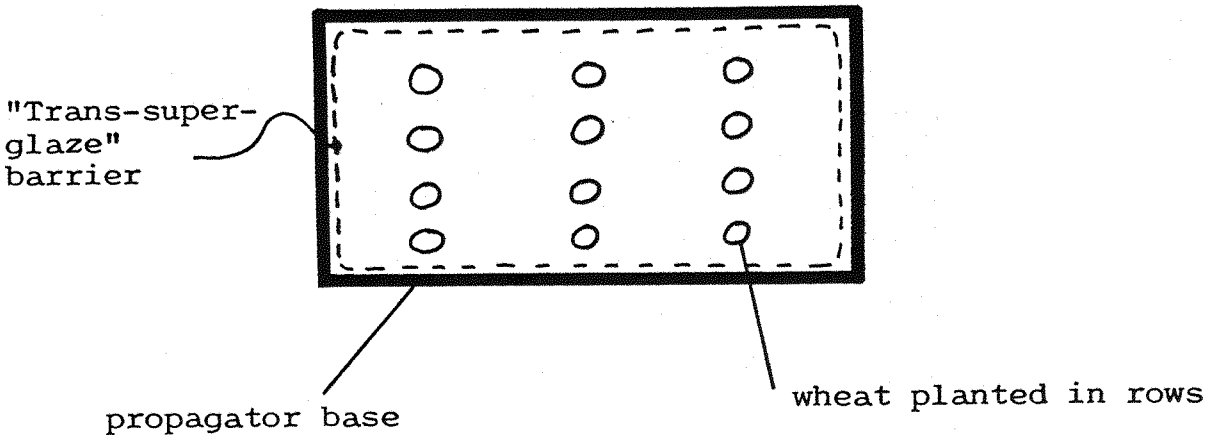
(See Chapter 6 for results and discussion)

(i) Micro-bomb calorimetry of prey types commonly found in wheat fields

Prey known to be eaten by A. dorsale (Section 7.3) were collected from field study areas with a D-vac (Section 2.7). Cereal aphids

Fig. 2.7 Arena used for wheat climbing experiments

Plan:



Side elevation:

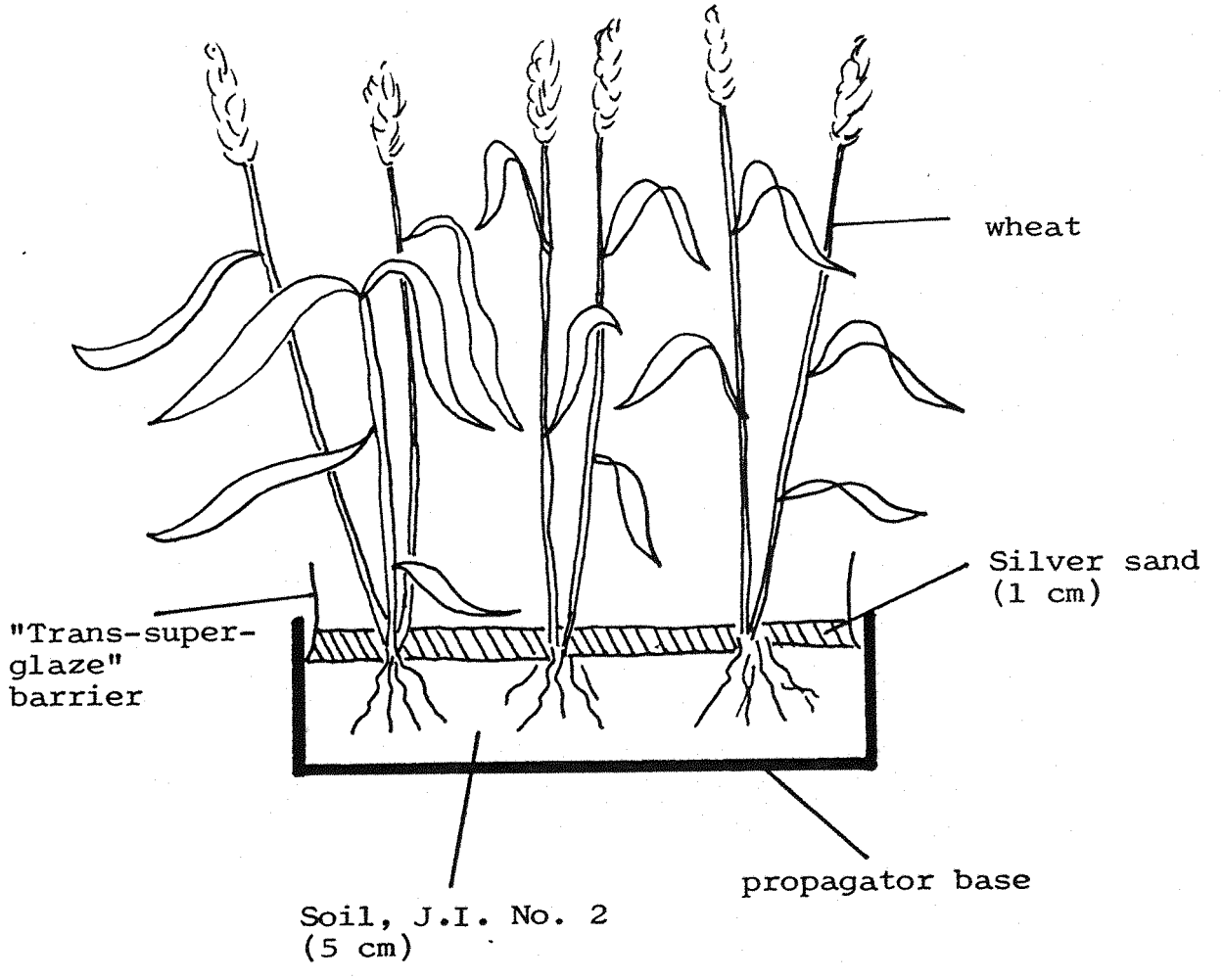
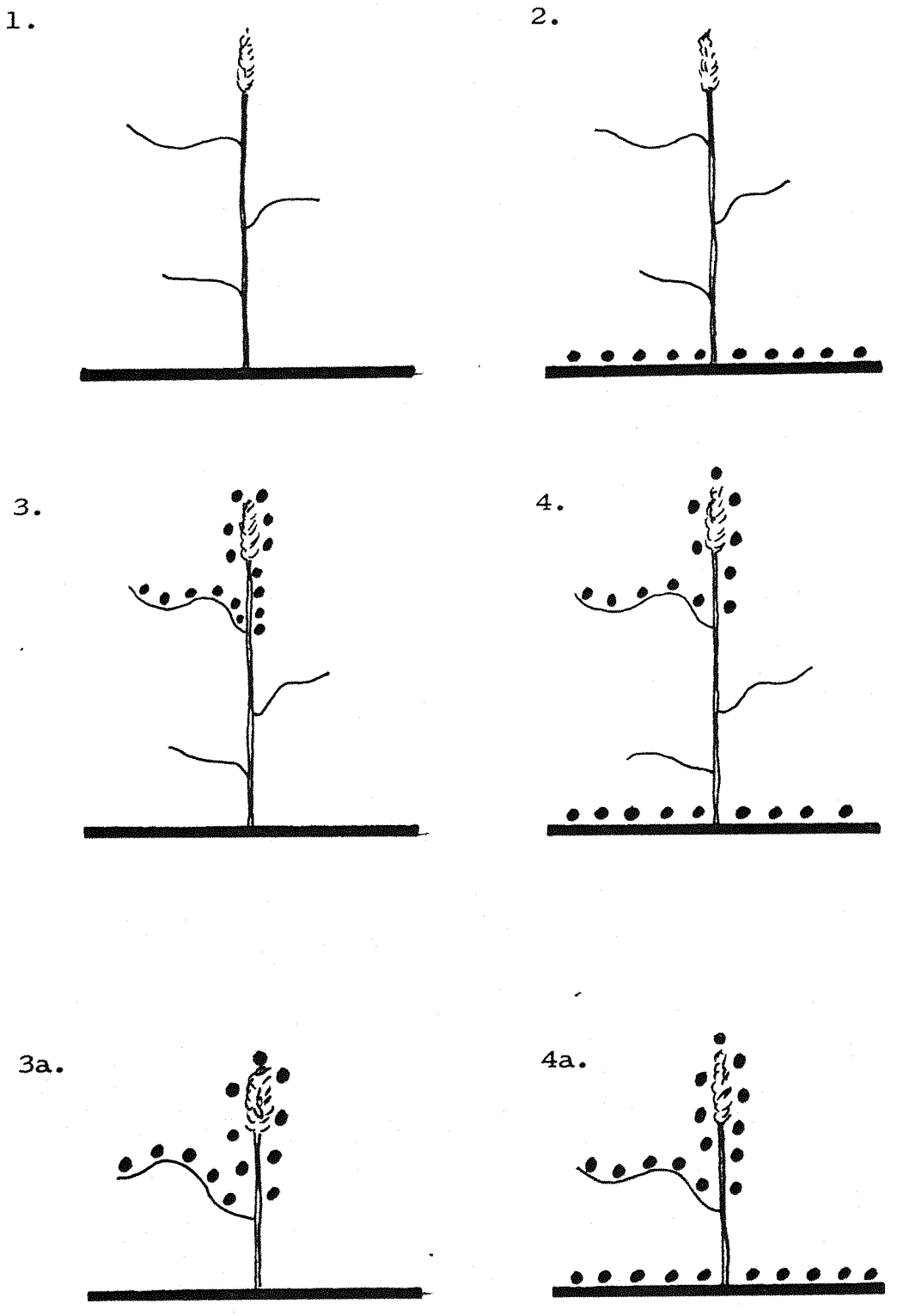


Fig. 2.8 Aphid distributions used for the wheat climbing experiments



● = distribution of cereal aphids in the arena

(S. avenae) were sorted into the size classes used for the functional response experiments (Section 2.4). Other prey were sorted into the more crude size classes used in the preference experiments (see later). The sized prey samples were freeze-dried and individual prey weighed on a V.D.F. Torsion microbalance[1]. (Sensitivity: 5μg). Each prey class was then separately ground to powder and compressed into a pellet to be fired in a phillips micro-bomb calorimeter (Figs. 2.9 & 2.10). Only a few replicates of each prey type were possible as each firing required the sizing and sorting of large numbers of prey. (See Phillipson, 1964 for general methodology of calibrating and operating a micro-bomb calorimeter).

(ii) The selection of dead and live prey commonly found in cereal crops by A. dorsale

The experiments were carried out in the dark-room. Prey were presented to the beetles for 24 h periods in sandwich box arenas and the number of prey attacked or eaten recorded. The A. dorsale individuals were reproductive immatures from laboratory cultures.

Prey were sorted into orders or families and then into approximate size categories. The resulting groups of prey were presented one at a time to the beetles. This was repeated with similarly sorted prey which had been freeze-killed. There were at least five replicates for each prey class.

(iii) Selection between the cereal aphid species Sitobion avenae and Metopolophium dirhodum by A. dorsale.

Experiments were conducted in the dark-room using reproductively immature adult A. dorsale. Apterous aphids of the two species were divided into two approximate size classes:

[1] Marketed by S. Garcia Sales Ltd., U.K.

Fig. 2.9 Sequence of prey treatment for micro-bomb calorimetry

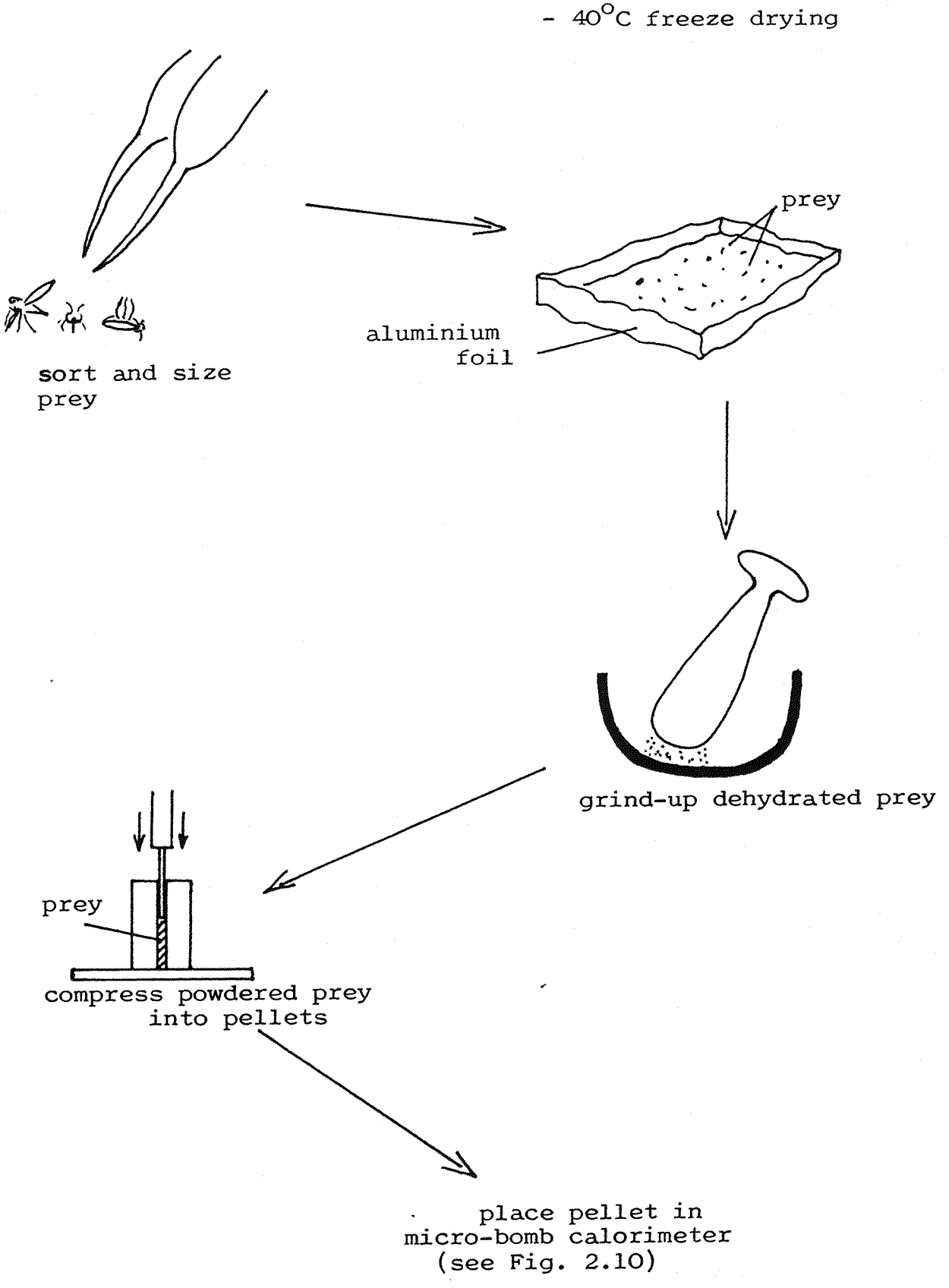
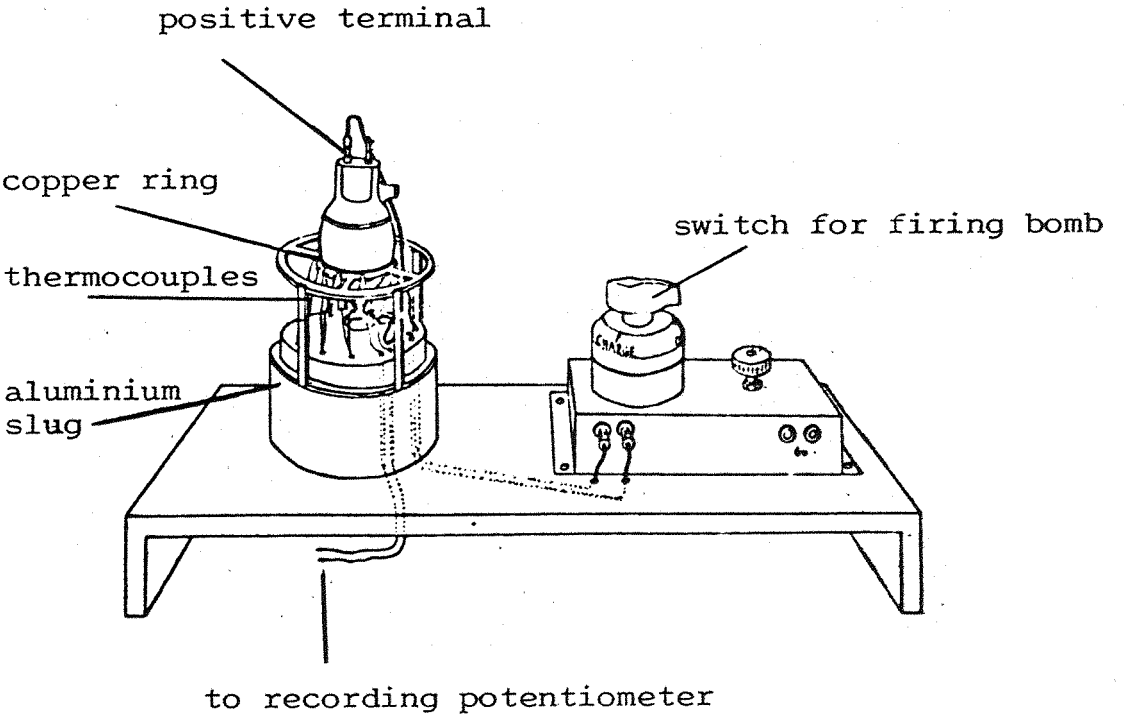
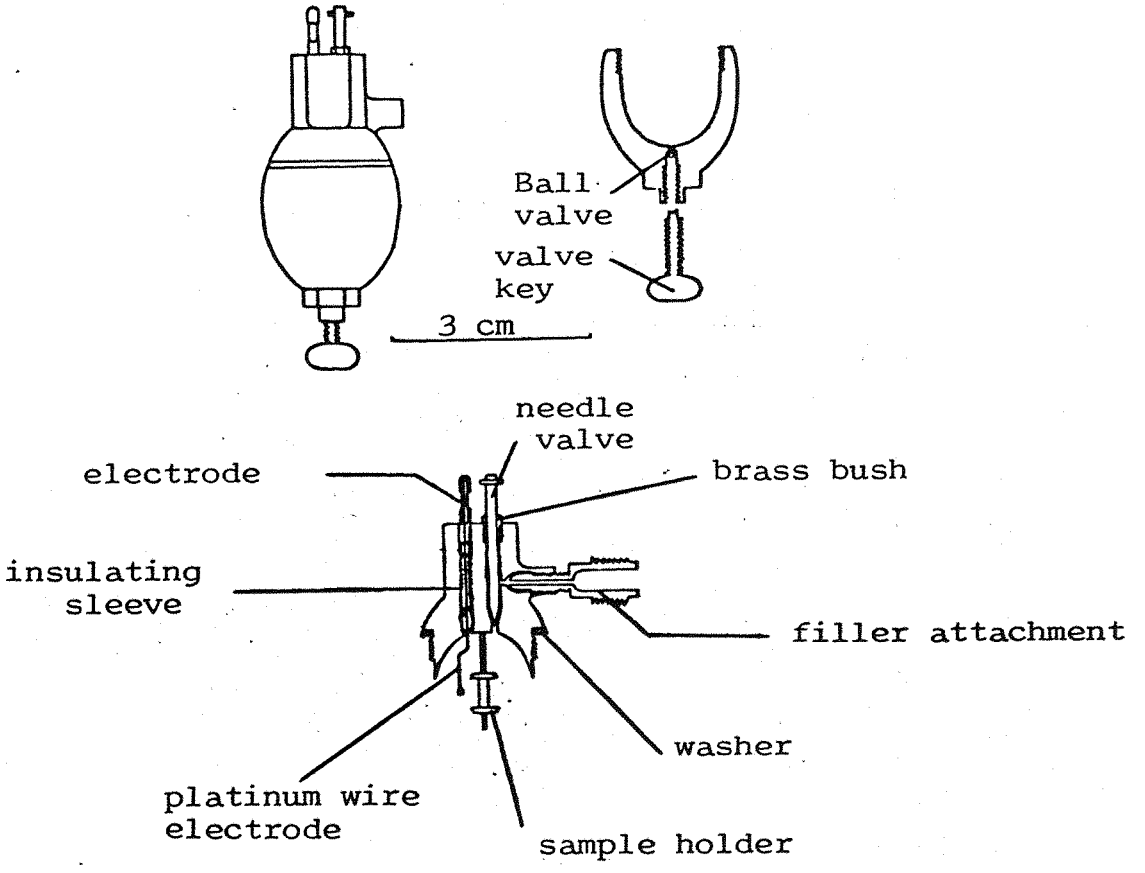


Fig. 2.10 The Phillipson micro-bomb calorimeter (after Phillipson 1964)





"Small" = I & II instars

"Large" = IV instar adults

(N.B. "Middle size" aphids were discarded)

Each size class/aphid species combination was presented to A. dorsale at densities of 10, 20, 30 and 40 aphids per sandwich box arena. Single A. dorsale were placed in each arena and the number of aphids eaten after 1 h recorded. Some trials were continuously observed to record handling times and percentage successful encounters (see Section 2.4). Each combination of size class, species and density was replicated five times.

In the second part of the experiment single A. dorsale were presented with a choice between the two cereal aphid species. The two aphid species were presented in four different ratios:

S. avenae	:	M. dirhodum
1		4
2		3
3		2
4		1

In all cases a total of 100 aphids per sandwich box arena were presented to beetles, to ensure that depletion of prey was minimal within the 1 h duration of the trials. At the end of the trial the remaining number of each aphid species was recorded. Trials used either "Nymph" or "Adult" aphids (see above) and 10 replicates were carried out with each aphid size for each of the four prey ratios above.

(iv) The effect of previous prey experience on prey choice

Trials were conducted in the dark-room. 20 A. dorsale were fed on either cereal aphids (S. avenae) of size/age range third instar to adult or Collembola (Entomobryoidea) of length 3-4 mm. The 20 beetles were placed singly in sandwich box arenas. Ten beetles were presented with 40 aphids each and 10 with 40 Collembola each and the numbers of both prey eaten counted each day and replaced. Individual

beetles were observed to record handling times and percentage successful encounters (Section 2.4) for the two prey types.

A period of 2 wks was allowed for the beetles to "adjust" to their particular prey type (see Lawton, Beddington & Bonser 1974), then all 20 A. dorsale were presented with a mixture of aphids and Collembola (20 aphids:20 Collembola).

The numbers of prey eaten over the next 10 days were recorded, with the original ratio of prey being maintained by replacing those eaten. In addition the beetles were observed to record handling times and percentage successful encounters for both aphids and Collembola over the 10 day period of the trial. At the end of the 10 day trial the 20 A. dorsale were dissected to assess their sex and reproductive state.

(v) The preference of A. dorsale for cereal aphids versus other common wheat-field prey types

Trials were carried out in the growth-room; A. dorsale used were reproductive immatures. For 2 wks before the trials all beetles were fed on raw ham to avoid biases due to previous diet.

Prey were freeze-killed and divided into orders or families and into approximate size classes (see Table 2.1). Prey classes were presented pair-wise with 10 of each prey being presented at a time. The total of 20 prey items were laid out in a random pattern on moist sand in sandwich box arenas. The A. dorsale were then placed singly in the boxes and left for 1½ h, after which time the numbers of each prey class remaining were recorded. There were 10 replicates of each pair-wise comparison.

(vi) The effect of temperature on the capture efficiency of common prey types by A. dorsale

The apparatus (Fig. 2.11) was used in the growth-room. The water bath could be controlled to produce temperatures from 2-15°C with a range of 1°C in the arena. The temperature profile in the arena

Table 2.1 Taxa and size-classes of prey used in "preference" experiments

Order or Family	SMALL "Type" & length[1]	LARGE "Type & length
Aphididae	S. avenae 1 - 1.5 mm	S. avenae 2.0 mm
Collembola	Entomobryoidea 2 - 3 mm	
Diptera	Mycetophilidae 2.5 - 3 mm	Lonchopteridae 4 - 6 mm
Acari	Mesotigmatid 0.5 - 1.0 mm	
Araneae	Linyphiidae 2.5 - 5 mm	
Thysanoptera	Thripidae 1 - 1.5 mm	

[1] Families are given to indicate the body form of the prey used, e.g. elongate rather than globular Collembola.

Fig. 2.11 Apparatus for testing the effect of temperature on the capture of prey by A. dorsale

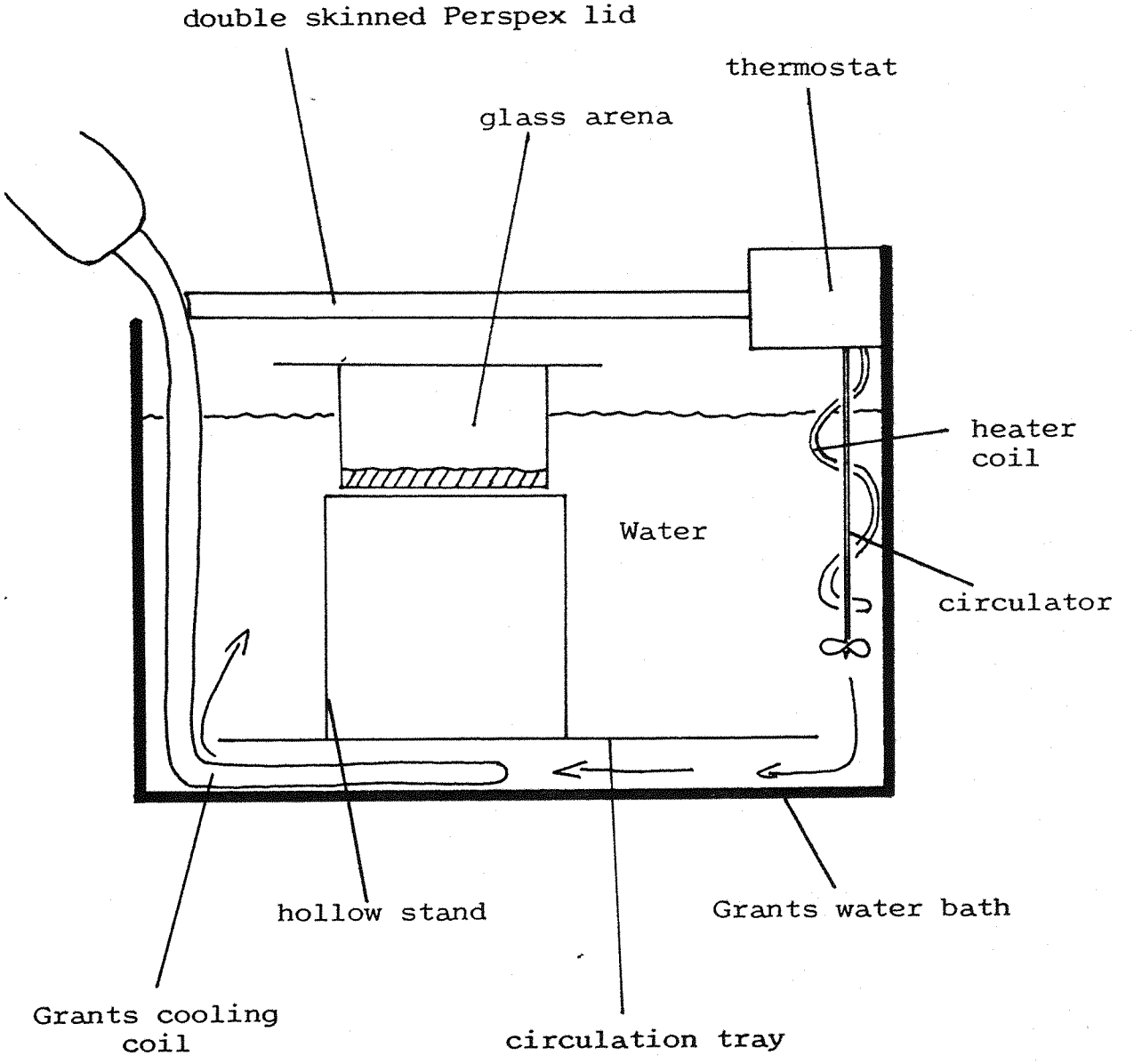
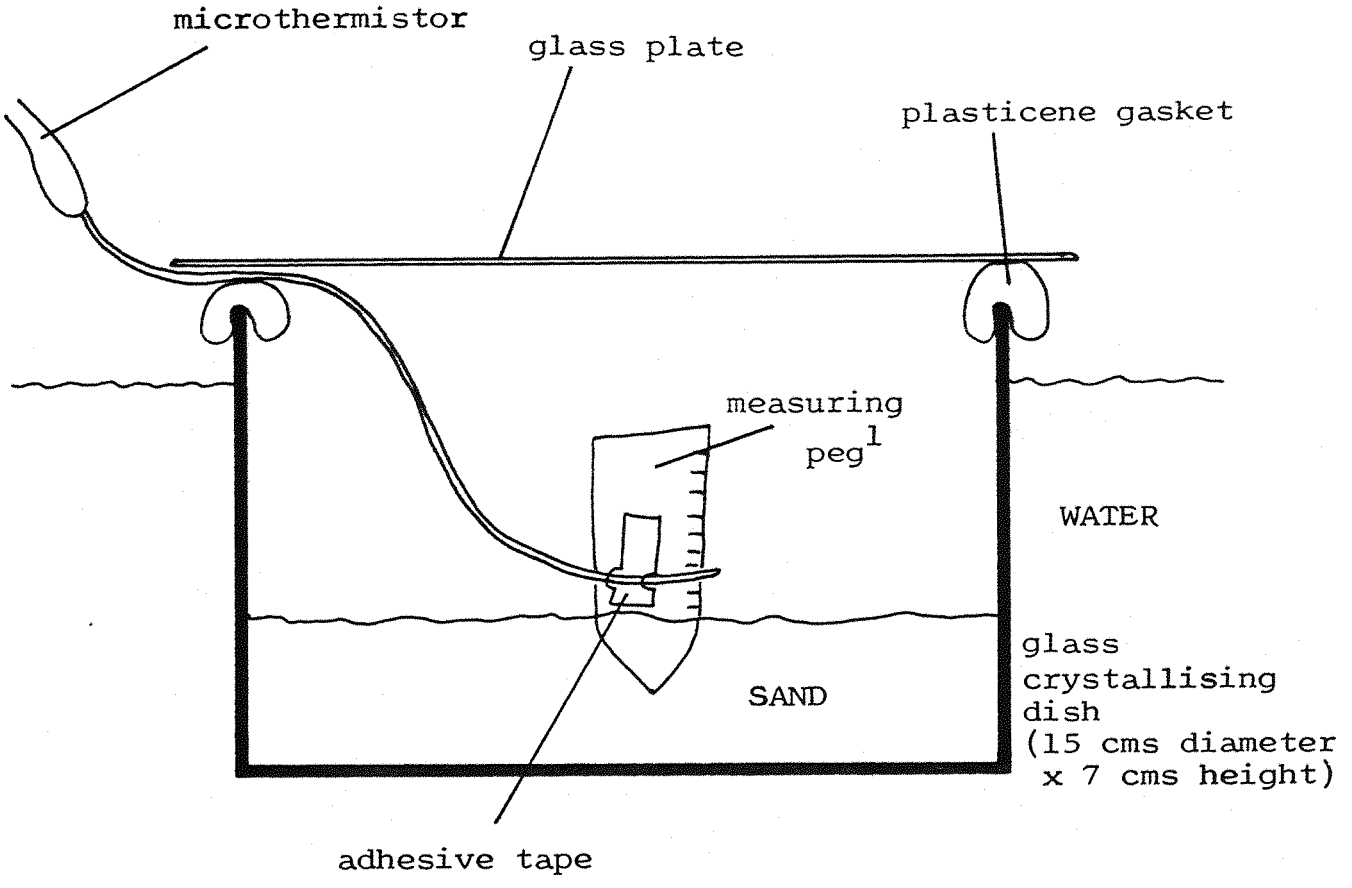


Fig. 2.12 Capture rate arena in detail



[1] N.B. The microthermistor and measuring peg were removed during trials.

was checked using a Y.S.I. microthermistor[1] (511 series probe) connected to a Y.S.I. telethermometer[1] (Fig. 2.12). This was done each time a new trial temperature was set to ensure that the beetles were exposed to the temperature. The thermistor was also used to check that the temperature in the arena had returned to the trial level after the lids had been removed to place prey or beetles in the arena.

The three prey types used (cereal aphids, Mycetophilidae and Collembola) were all obtained from laboratory cultures and were acclimated to the trial temperature in an incubator for 3-4 days (see Weiser 1973) prior to the trial run. The A. darsale were reproductively immature, taken from laboratory cultures and were similarly acclimated prior to the trial.

To start a trial the required prey type was placed in the arena at high density (about one prey per 2-3 cm^2). A. dorsale were then introduced singly into the arena and interactions between them and prey recorded for 30 min with a tape recorder and stop watch. There were at least 10 replicates for each temperature and prey type.

2.7 The South Allenford Farm Fieldwork

(See Chapter 7 for results and discussion)

(i) The field sites

Field work during the first two years of the project was carried out on a study farm near the Game Conservancy, Fordingbridge. The final year's field work required detailed observation of A. dorsale and was carried out at the Biology Department's experimental grounds in Southampton.

The Study Farm

The Game Conservancy, Fordingbridge has established links with local farmers in the Avon valley and this enabled field work in this project to be carried out on commercially farmed land. The work was

[1] Both marketed by Yellow Springs Instruments Co., Yellow Springs, Illinois, U.S.A.

carried out on the 8 km^2 mixed arable-livestock farm of South Allenford. The farm is sited on chalk downland near the village of Damerham on the Hampshire-Dorset border. A crop rotation is used with either oilseed rape or grass being sown as break crops between cereals (barley and wheat), more fertile fields often being sown with cereals for several years in a row. Grass fields are harvested for seed in their first year. In the second year the grass is grazed by cattle and sheep and cut for hay and silage. In the last year they are grazed by pigs and then ploughed up and sown with winter cereals. Fodder turnip crops are grown in some fields after harvest of the cereal crop, these are grazed by sheep and then sown with spring barley.

The Study Fields

Collections of A. dorsale for laboratory work were made from many fields on the study farm, but detailed field work in 1979 and 1980 was carried out in three fields. The location of these fields on the farm is shown in Figure 2.13. Details of crops and cultural practices in these fields for 1979 and 1980 are given in Table 2.2.

(ii) Field Sampling Techniques

Five techniques were used:

Surface searching	for sampling A. dorsale
Pitfall traps	
Dietrick vacuum insect net (D vac)	for sampling prey
Plant clipping	
Soil scraping	

Surface searching and pitfall traps

Searches for A. dorsale were made, within $1m^2$ quadrats, during the 1978/79 winter (on the bare field surfaces and during the summer 1980. Stones and organic debres were moved and the soil surface disturbed to a depth 1-2 cm; any A. dorsale discovered were collected with a pooter.

Fig. 2.13 The Study Farm

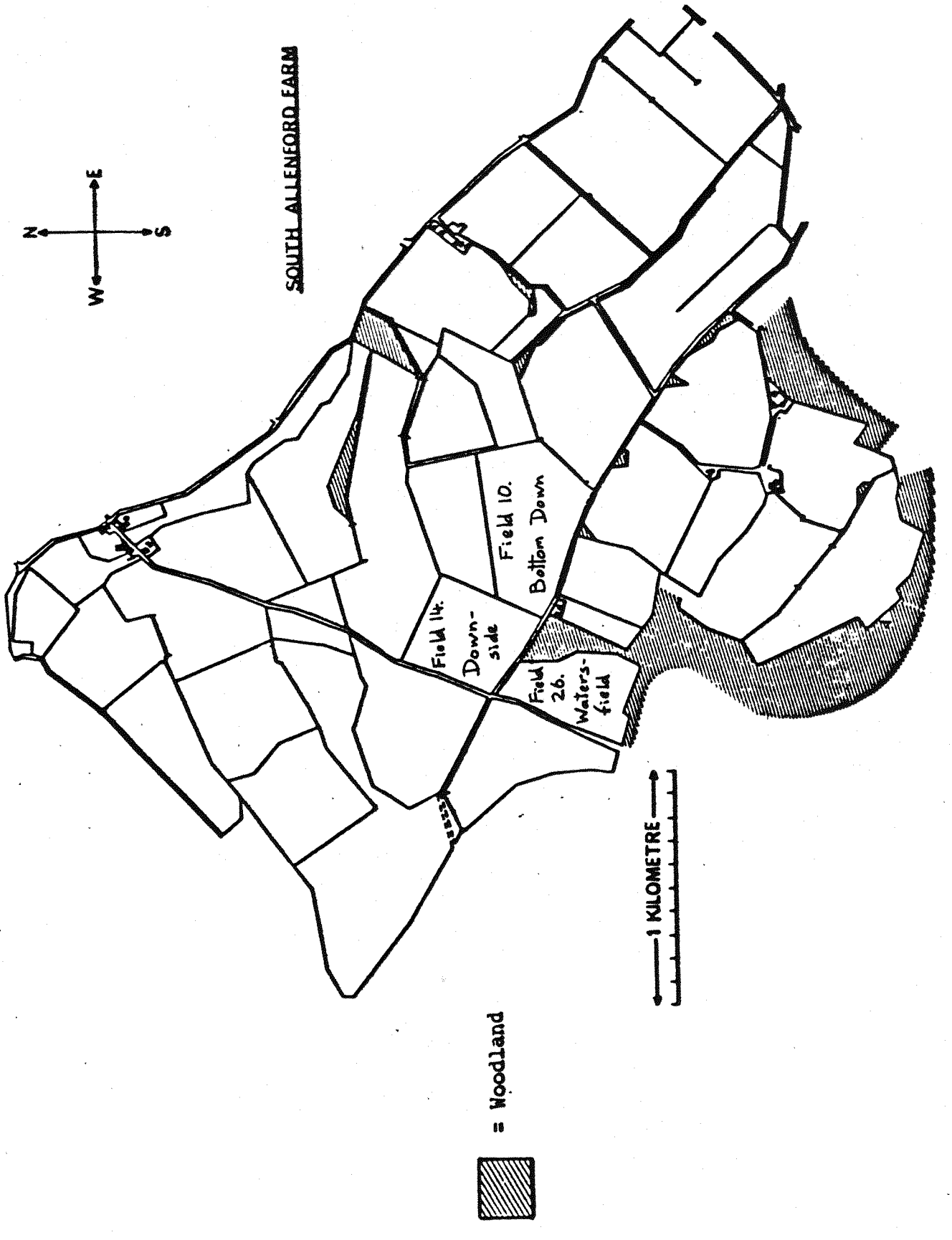


Table 2.2 Details of the agricultural treatments of the study fields

	1979	1979	1980
Field name	Downside	Bottom Down	Watersfield
Field number	14	10	26
Field size (ha)	18	25	15
Crop	Spring Barley	Winter Wheat	Winter Wheat
Variety	Golden Promise	Maris Huntsman	Maris Huntsman
Drilling date	26 February	20 October	2 November
Fertilizers (date of application)	N_2 (not known)	N_2 (23.3. & 9.5.)	N_2 (not known)
Herbicides	C.M.P.P. + Dicambra + Mecoprop	C.M.P.P.	
(date of application)	(9.5.)	(4.5.)	
Fungicide	Triadimelon	Benomyl; Triadimelon + Thiophanate methyl	
(date of application)	(4.6.)	(4.5.); (16.6.)	(not known)
Harvest date	Early August	26 August	Early September

Pitfall traps consisted of white plastic beakers (9 cm diameter and 13 cm depth) which fitted exactly into "Trocal" rain water pipe (10.2 cm outside diameter). Collars cut from the rain water pipe were sunk into the ground and then the pitfalls could be removed and replaced without disturbing the important soil-trap boundary (Mitchell 1963). Pitfalls used for weekly samples contained a 4% formalin solution with detergent to drown and preserve beetles caught. Those used for overnight sampling contained water only. The water prevented the carabids from eating each other and the traps were emptied after sufficiently short a time to prevent the beetles dying and decomposing.

Pitfalls containing samples were taken back to the laboratory for sorting.

The D-vac, plant clippings and soil scrapings

The D-vac, plant clipping and soil scraping samples were taken in the grid area formed by the field pitfall traps, (see later). The site of each sample being decided in a cartesian coordinate grid system where the sample coordinates were extracted from random number tables.

The D-vac has a nozzle area of 0.09 m^2 which allows the calculation of densities of prey sampled (but see Southwood 1978 for correction factors and effects of habitat type). Each sample was taken by pressing the nozzle of the D-vac over the crop and on to the ground and holding for 10 s. Each sample was then bagged separately.

Each plant clipping sample was taken by carefully cutting five wheat stems at their bases, from an area of 0.25 m^2, and placing them into a large polythene bag containing filter paper soaked in ethyl acetate (to kill the arthoropods collected). The wheat stems were stored in a deep freeze before sorting in the laboratory.

A soil scraping sample was taken by removing the top 3 cm of the soil from a 0.02 m^2 quadrat and placing it quickly in a bag with filter papers soaked in ethyl acetate. The soil was stored in a deep freeze until ready for sorting. Organic matter was floated off from the soil with a saturated Sodium Chloride solution and then removed with a fine sieve to a petri dish for identification of prey (Edwards & Fletcher 1971).

(iii) Dissection of A. dorsale to investigate diet and reproductive development

A. dorsale were caught in pitfall traps, containing 4% solution as a preservative, at the Damerham field sites. The beetles were then stored in 70% aqueous alcohol prior to dissection.

Dissection was performed under a binocular microscope in a staining block filled with 70% alcohol solution. The entire gut was removed and placed on a microscope slide in a drop of polyvinyl lactophenol (Oldroyd 1970). This chemical is both sufficiently clear and viscous to make dissection and sorting of gut fragments easy. The slides were made semi-permanent by ringing with clear nail varnish.

Fragments could usually be identified to order, and at best family; cereal aphids could sometimes be identified to species.

(iv) Analysis of A. dorsale diet by gel slab electrophoresis

A. dorsale were caught alive over night during the 1980 Damerham field season. These individuals were then freeze-killed and stored in a freezer as soon as possible to prevent digestion or excretion of gut contents.

Individuals were dissected in staining blocks filled with distilled water. The gut was removed in one piece and transferred to a small capillary tube sealed at one end. A small plunger was then used to macerate the gut with buffer solution in the capillary tube. The buffer used was Tris/EDTA/borate pH 8.3 (Margolis & Kenrick 1968). Each gut was macerated and stored in a separate capillary tube to avoid cross contamination.

Electrophoresis was carried out on vertical polyacrylamide concentration gradient slab gels with a total gel gradient of 5-28%. The essential methodology and equipment are described in Margolis & Kenrick (1968) and Margolis & Wrigley (1975). The polyacrlyamide gels were supplied by Universal Scientific Ltd. The following is a brief description of the method.

The gels were suspended in the electrophoresis tank which contained the Tris/EDTA/borate buffer. The sample spacer applied to the top of the gel allowed the running of 14 beetle guts on each slab. The macerated gut solutions were applied to the sample spacer with a micro-syringe which was washed out with alcohol followed by distilled water between each application. Electrophoresis took place overnight since the method relies on proteins migrating along the gel until physically stopped by the decreasing pore size of the gel matrix. The gels were then stained for proteins possessing esterase activity with a solution of napthyl acetate and Fast Blue in dim light conditions (Shaw & Prasad 1970). This usually required 3-4 h before the bands on the gel could be seen clearly.

Visual comparisons between control guts (i.e. laboratory-starved A. dorsale) and field-sampled guts showed diet composition on a qualitative basis.

(v) 1979 Damerham Field Season

Field work in 1979 took place on South Allenford farm near the village of Damerham, Hampshire (N.G.R. SU103158). The area chosen was a field of winter wheat (cv. Maris Huntsman) separated from a field of spring barley (cv. Golden Promise) by a fence line (fields 10 and 14 in Fig. 2.13).

Pitfall trap grids were in position in both fields and down the dividing fence line from late March until mid May. After this date, trapping had to be abandoned in these areas as an insecticide trial was set up in them. A new pitfall trap grid was set up on the far side of the winter wheat field (Fig. 2.14) and in the fence line there. These field pitfall traps were left in place until the stubble was burnt off in late September. Fence line pitfalls remained in place until early October.

Prey were sampled during the day with a D-vac, from mid May until mid August, in the area of the pitfall grid. A standard sample consisted of five sub-samples, each of three 10 s "sucks" with the

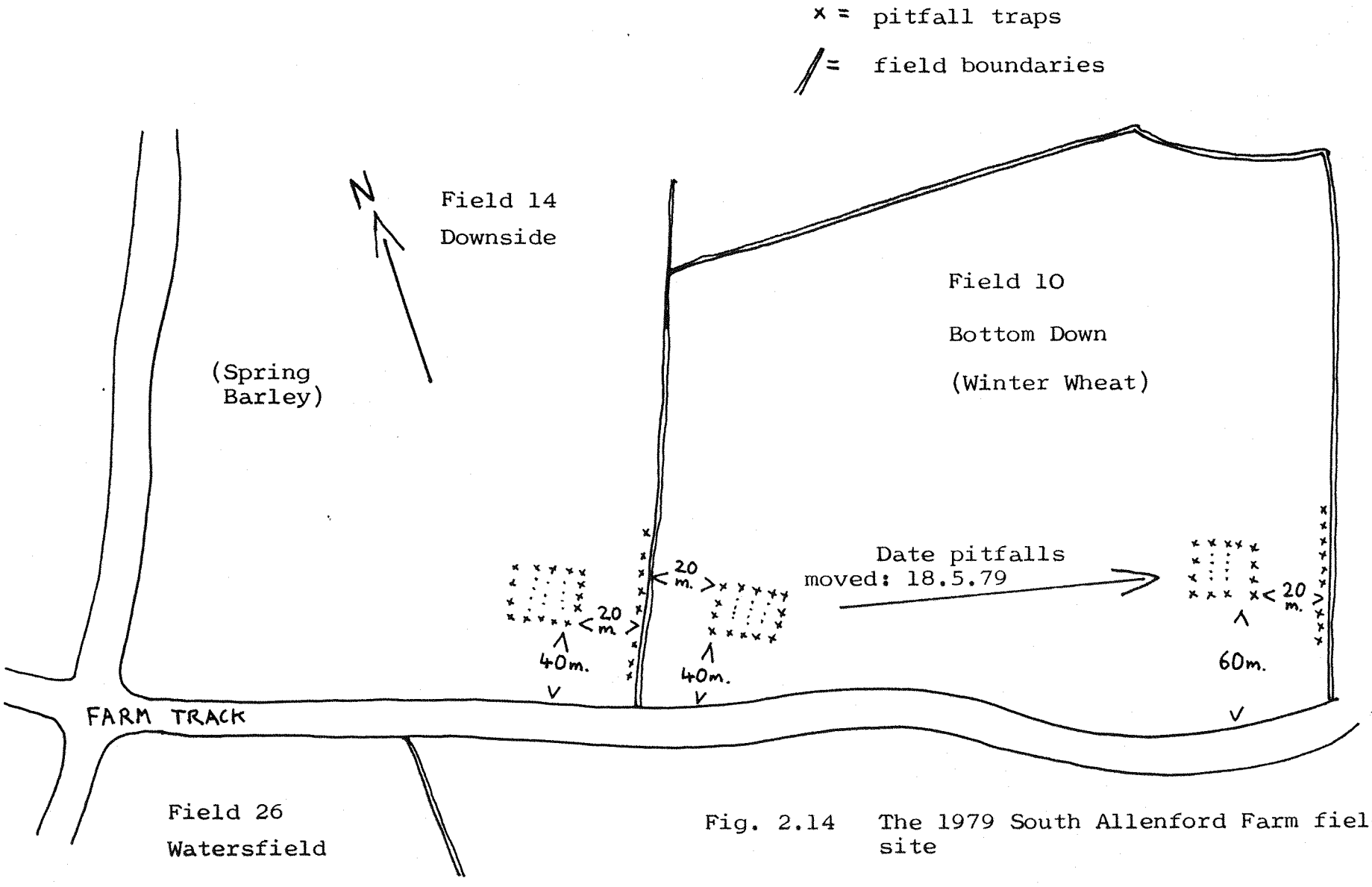


Fig. 2.14 The 1979 South Allenford Farm field site

Not to scale

D-vac. Each sub-sample covered an area of 0.27 m^2, the entire sample being 1.35 m^2.

During the winter periods, surface searching was carried out in the field with a 1 m^2 quadrat for overwintering A. dorsale. Searching consisted of disturbing stones, organic debris and soil to a depth of 2-3 cm.

(vi) 1980 Damerham Field Season

Field work was again carried out on South Allenford farm near Damerham, Hampshire. All work was carried out in a single field of winter wheat (cv. Maris Huntsman)(see 26 in Fig. 2.13). The field was chosen because a survey during the spring of 1980 had shown adjoining hedgerows to contain aggregations of overwintering A. dorsale (Chapters 1 & 7).

Two types of pitfall grid were put out in the field, one for weekly sampling (20 pitfalls in a 4 x 5 grid) and one for overnight sampling (120 pitfalls in a 4 x 30 grid) (Fig. 2.15).

Weekly sampling pitfalls were taken back to the laboratory for sorting, fresh pitfalls being put out as the old ones were collected. Overnight sampling pitfalls were left in the ground with plastic lids on throughout the week. The lids were removed at 17.00 hours on the night of sampling and the following morning at 05.00 hours the traps were emptied of their catch and the lids replaced.

During the night of the pitfall sampling, further samples were taken with a D-vac and the plant clipping and soil scraping techniques. Samples were taken between 24.00 and 01.00 hours. Usually three D-vac and 10 each of the plant clipping and soil scraping samples were taken.

At the time of sampling, temperature and humidity profiles in the wheat crop were also recorded. At first this was done at several sites in the field but data were so similar that measurements at one

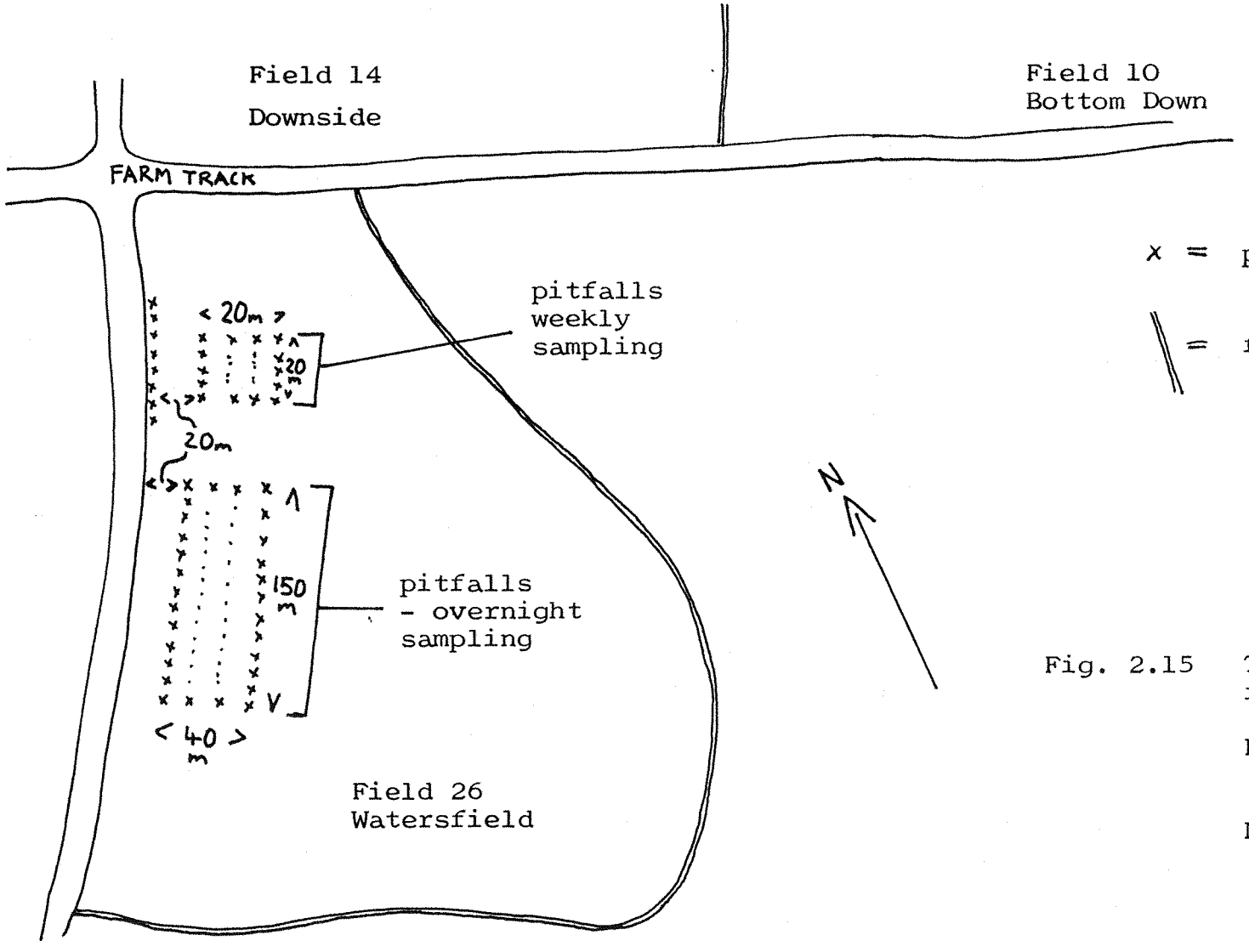


Fig. 2.15 The 1980 South Allenford farm field site

Pitfalls are marked by x

Not to scale

site only were sufficient. Temperature was measured by attaching Y.S.I. Thermistors to a stand (made from a bamboo cane) at the following heights, 0, 1, 2.5, 5, 10, 20, 30, 40, 50, 60, 70, 80 and 90 cm above ground level. The thermistors were linked to a multi-channel Y.S.I. telethermometer. Humidity was recorded with cobalt thiocyanate paper at the same heights as the thermistors on a second stand.

Sampling was continued until field populations of A. dorsale had declined to zero (from mid May until late July).

A rechargeable torch with a red filter was used as many insects cannot see red light (Imms 1973). This torch was also used while ground searches were made for active A. dorsale using a 1 m^2 quadrat.

In late May an arena 1 m x 1 m with a wall height of 40 cm was dug into the field near its centre. The arena was stocked with A. dorsale from laboratory cultures and observation of these adults was attempted during the day and night to assess activity periods and climbing frequency.

The nightly routine for field work is summarized in Table 2.3.

2.8 Field observation of the foraging behaviour of A. dorsale

(See Chapter 8 for results and discussion)

(i) The field site

The field site used in 1981 was at Chilworth Manor, a large local house with extensive gardens used as an experimental station by the University of Southampton. Plots of winter wheat have been grown there for some years and although broadcast-sown, have a similar shoot density to commercially grown wheat. Some plots have also received fertiliser and herbicide treatments, as would commercial crops. This site was used rather than the Damerham fields as an electricity supply was needed close at hand to power red lights for all-night observations of beetle activity.

Table 2.3 Nightly routine for Damerham 1980 field work

17.00	Arrive field site, replace weekly sample pitfall traps, open overnight sample pitfall traps.
23.00	Start field work (full darkness).
	Humidity and temperature monitored. D-vac, plant clipping and soil scraping prey samples taken. Soil searches/arena observation of A. dorsale
05.00	Overnight pitfall traps emptied.

Previous work at this site had shown that while there was some natural input of cereal aphids (C. Williams pers. comm.), there was no natural population of A. dorsale (J. Dover pers. comm.). All beetles had to be introduced to the site, having been collected the previous autumn and kept in a state of diapause in an outside insectary.

(ii) The experimental plot

The plot of winter wheat (cv. Hobbit) used measured 5 x 5 m. A total of 24 arenas (0.5 x 0.5 m) were dug into this plot in early May with minimum disturbance to the wheat crop (Fig. 2.16). Each arena consisted of four pieces of hardboard (25 cm high x 50 cm across) held together by wooden stakes at each corner. The hardboard was sunk 10 cm into the ground to prevent the majority of the introduced A. dorsale escaping. In addition the hardboard was painted with Fluon just above soil level to prevent arthropods (particularly potential items) climbing out of the arenas.

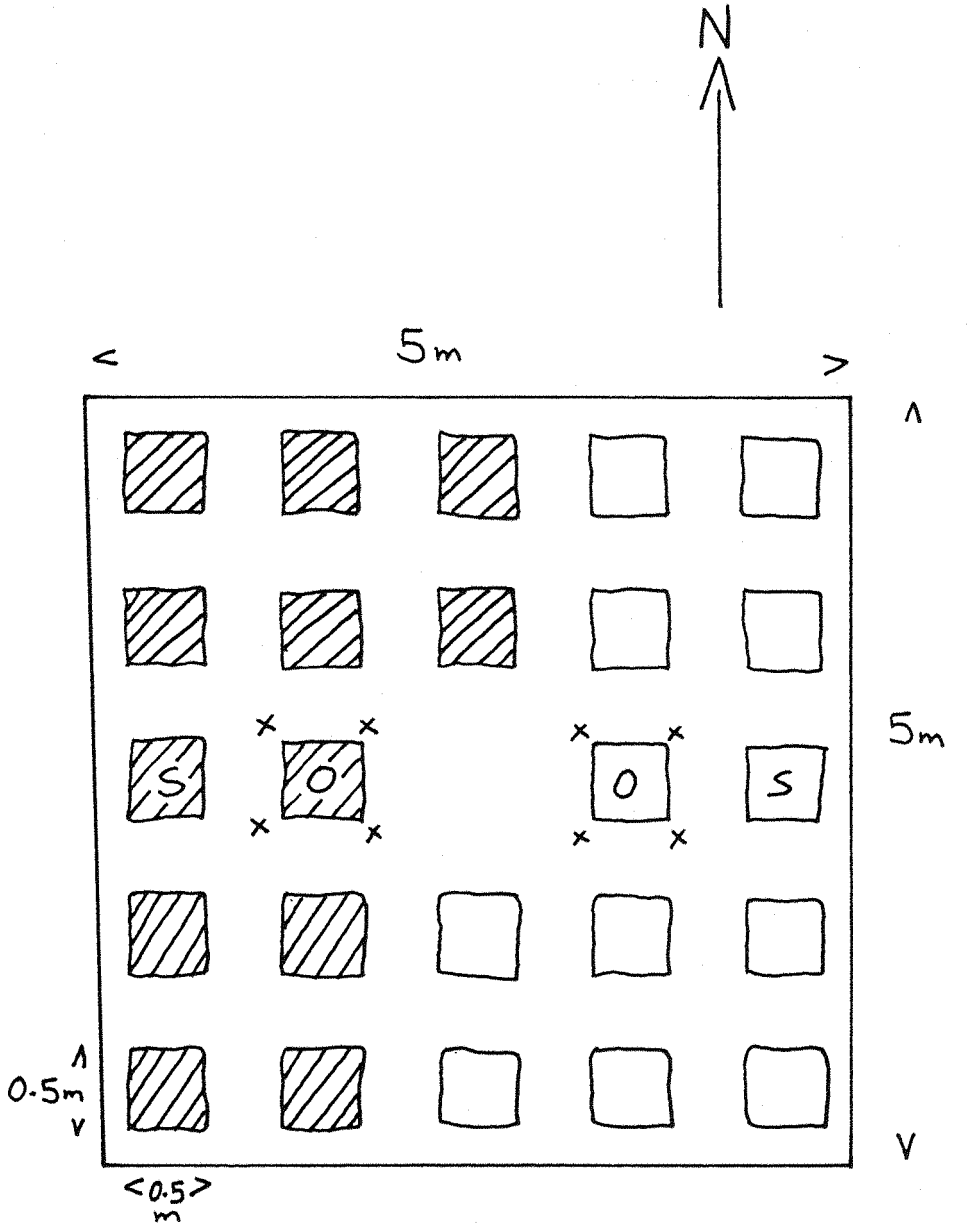
Twelve of the arenas were covered with Terylene netting cages (0.5 m diameter x 1.5 m tall) so that large populations of aphids could be built up in them (Vickerman & Wratten 1979). The other 12 arenas were left exposed so that aphid populations would be low. Of each set of 12 arenas, A. dorsale were introduced into two of them, one being used for observation, the other for removal of adults for gut dissection. The remaining cages were used for prey sampling (Fig. 2.16).

(iii) Stocking and sampling of arenas

A. dorsale introduced into arenas gradually escaped; this necessitated the restocking of arenas with the beetles on a weekly basis. Caged arenas were stocked with aphids (S. avenae) from early May and by the time the trials started (21 May) aphid populations were large enough to require no further introductions.

A. dorsale introduced into arenas so that they could be sampled subsequently for gut dissection were collected after 3 days, when most

Fig. 2.16 The Chilworth wheat plot arrangement for the 1981 field season



= arenas with cages

O = A. dorsale observation arenas

× = Red lights around observation arena

S = A. dorsale sampling arenas

All other arenas were for prey sampling

had fed. They were then dissected in the laboratory as before (Section 2.7). This was done at 2 wk intervals throughout the period of field observation of A. dorsale.

Prey samples were not taken from the two arenas containing A. dorsale because this may have disturbed the beetles e.g. the sampling required removal of soil from the arena. Samples were taken weekly from the other arenas by removing from each arena, the soil to a depth of 2-3 cm from a 0.0025 m^2 quadrat and 10 wheat stems. These samples were collected and sorted in the same way as the Damerham samples (Section 2.7).

On each observation night (see below) notes were made of weather conditions, changing day length and general condition of the crop. Temperature and humidity recordings were also made; see Section 2.7 for methods. Humidity recordings were stopped because even on dry nights humidity was close to 100 percent in the crop. Daily maximum and minimum temperatures were also recorded using two Max/Min thermometers, one each on the ground in the uncaged and caged observation arenas.

(iv) Fieldobservation of A. dorsale

Observation of A. dorsale in both uncaged and caged arenas on the same night was not possible because there were not enough beetles to keep both arenas fully stocked. Accordingly, observations were carried out for several weeks in the uncaged arena first and then switched to the caged arena. The observation period dates were:

Uncaged arena:	Initial trials	21-23 May
	Full trials (see below)	26-28 May
		1-3 June
		8-10 June
		15-17 June
Caged arena:	Full trials	22-23 June
		29- 1 June/July

i.e. observation was carried out on three nights per week over the field active period of A. dorsale (Chapter 7.2). Table 2.4 summarizes the usual nightly routine of the field work.

Observation of A. dorsale in the arenas was made possible by the use of red lights (see also Chapter 3.3) spaced around the observation arenas (Fig. 2.16). To record the beetles' behaviour it was necessary to lie on the ground in the centre of the experimental plot (Fig. 2.16) to obtain a "ground-level" view. The behaviours were divided into the categories used in previous chapters (see Chapters 3 and 5) and were recorded using a stop watch and taperecorder as before. In any one arena the actual surface area of the wheat is much greater (from 10 to 20 x) than the surface area of the ground (see Section 7.3). This meant that a special searching sequence had to be used when looking for beetles to ensure that both ground and wheat were searched equally well and that the complex surface of the wheat was searched adequately. The observation arena was mentally divided into eight "Observation areas"; four ground quarters and four wheat quarters (Fig. 2.17). These quarters were searched in the random order indicated in Figure 2.17, with plant quarters being searched for five times as long (10 min) as ground quarters (2 min) to allow for the difference in surface area. It was felt that these times allowed both the ground and plant "Observation areas" to be searched adequately.

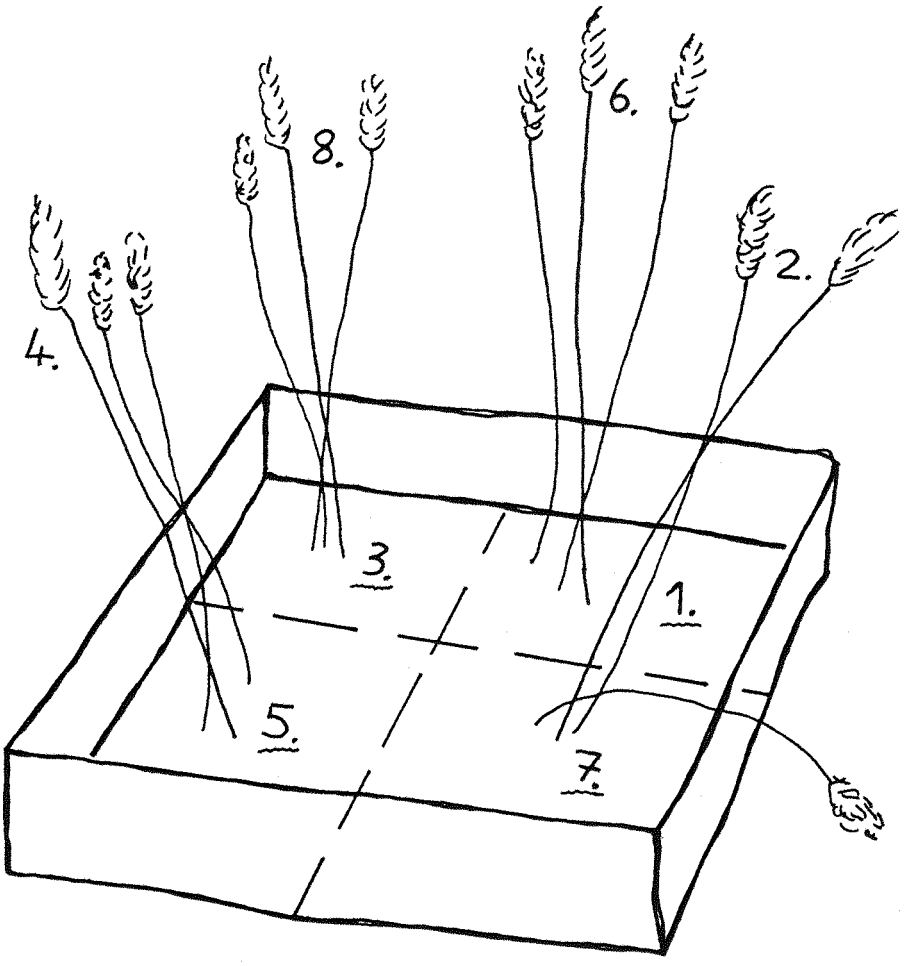
For the initial trials the behaviour of individuals when they were first seen was recorded at intervals throughout the day. These trials were used to assess how easily individuals could be followed in the arena and whether the beetles were strictly nocturnal. After these initial trials, individuals were followed for as long as possible to record detailed behavioural data as had been done in the laboratory (Chapter 5.6). Each beetle was followed for a maximum of 30 min to ensure that nightly observations were taken from a representive sample of individuals in the arena.

Observation of A. dorsale finished at the end of the beetle's field active period. The caged prey sampling arenas were then used

Table 2.4 The nightly routine for the Chilworth 1981 field work

21.00	Arrive at field site, switch on red observation lights, prepare prey sampling equipment.
22.00	Start observation of beetles.
24.30	Prey sampoing and break.
01.30	Continue observations.
03.00	Break
03.30	Continue observation.
04.30	Finish - dawn.

Fig. 2.17 The "Observation areas" used to eliminate observer bias in searching the arena for beetles



Numbers indicate the order in which the observation areas were searched by the observer.

to assess the fate of aphids moving or falling on to the ground in the absence of A. dorsale. Aphids were knocked off wheat plants by tapping stems, any remaining aphids being carefully removed with a soft paint brush. The numbers of aphids returning to the stems were then recorded after 24 and 48 h.

C H A P T E R 3

CHAPTER 3

PRELIMINARY EXPERIMENTS WITH *A. DORSALE*

(See Chapter 2.3 for materials and methods)

3.1 Introduction

Most field and laboratory studies on the Carabidae have not involved direct observation of the beetles hunting. Instead, indirect techniques, such as gut dissection and serology, have been used in the field while laboratory experiments have measured simple consumption rates (Thiele 1977). The exceptions to this (Swiecimski 1957; Bauer 1977; Wilson 1978; Dreisig 1981) concerned diurnally active species. Many carabids, however, are known to be nocturnal (Thiele 1977).

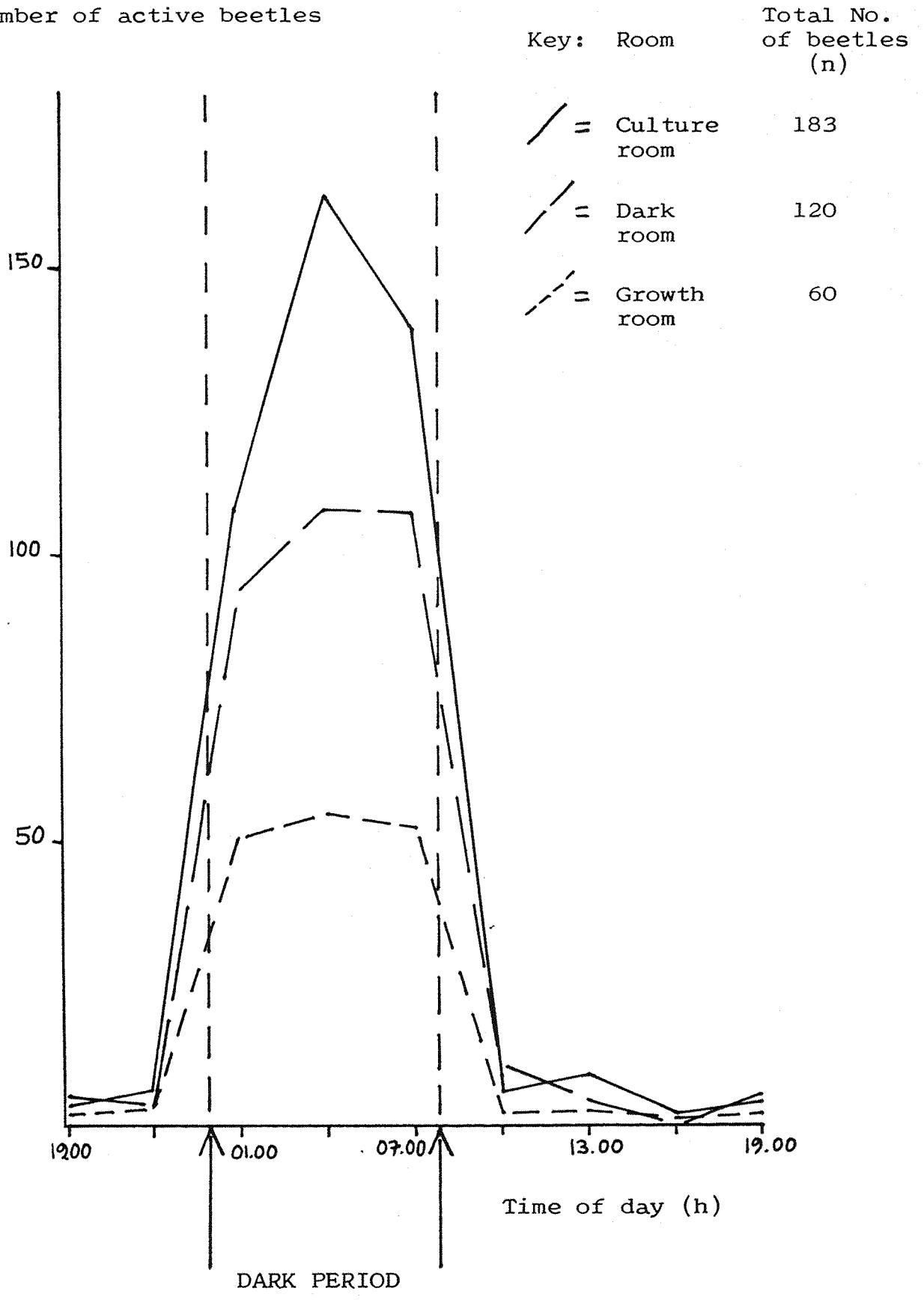
This chapter shows that *A. dorsale* is nocturnal but that it can be observed in the dark by use of red light. The range of basic behaviours was also recorded with particular reference to those which showed that the beetle was searching for prey. The important components of close-range detection and handling of prey were also examined.

3.2 The activity period of *A. dorsale*

Observation over a period of 24 h of numbers of *A. dorsale* active in the culture, growth and dark rooms gave frequency distributions of active beetles (Fig. 3.1). Individuals were counted as active when they were seen moving about in the culture boxes. Most individuals aggregated under refuges and did not move far from them during the light period.

A. dorsale was strongly nocturnally active with the onset and decline of activity closely linked to the beginning and end of the dark period of the diel cycle (Fig. 3.1).

Fig. 3.1 The total numbers of A. dorsale active in three laboratory cultures throughout the 24 h cycle



In order to observe this nocturnally-active beetle during normal working hours, the growth or dark rooms were changed to a reverse light:dark cycle. Observations over a 24 h period 3 days after the reversal of the diel cycle showed that there was a complete reversal of activity, even after this short period (Fig. 3.2). However, as an additional precaution the beetles were allowed to adjust for 1-2 wk before beginning experimentation.

3.3 The sensitivity of A. dorsale to red light

A. dorsale retreated under refuges in the cultures during the light period and this negatively phototactic behaviour was used to assay their sensitivity to red light. The proportion of beetles that retreated under a refuge when suddenly exposed to red or white light during the dark period was recorded.

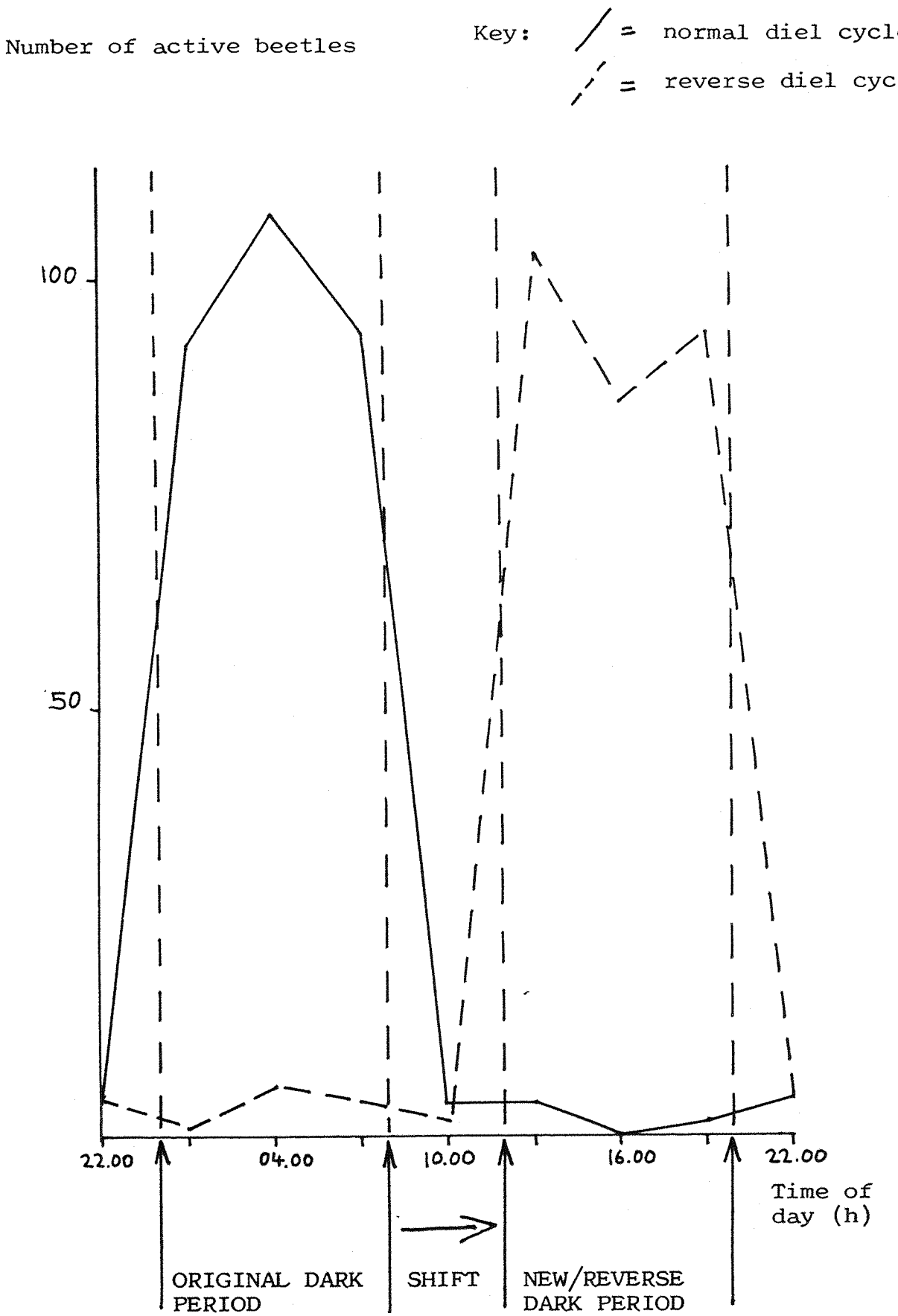
A. dorsale reacted to sudden white light with an abrupt halt of activity followed by immediate retreat under a refuge. None of the beetles tested reacted to red light in any discernible way. In addition, under white light A. dorsale reacted to large objects (human hand) moving at distances of 20 cm or closer to it and also to shadows passing over it. This did not happen under red light.

It was concluded that A. dorsale could not perceive red light sufficiently to alter its behaviour or diurnal rhythm. During experimental periods the red lights were left permanently on so that they would form a constant background that A. dorsale would become habituated to. Observation of cultures under constant red light confirmed that they had the same natural activity period as that observed in Section 3.2 for beetles without red light.

3.4 The behaviours shown by A. dorsale in the presence or absence of prey

It is particularly useful in work on predators to be able to identify behaviours which indicate that the predator is searching for prey. Comparison of the behaviours shown by A. dorsale in the presence

Fig. 3.2 The total numbers of A. dorsale active before and 3 days after being placed on a reverse light:dark cycle



or absence of prey identified a style of movement that increased dramatically in frequency in the presence of prey. This behaviour was labelled "SEARCHING" for several reasons; it seemed to be triggered by A. dorsale bumping into prey items, A. dorsale seemed more receptive to prey that it bumped into while searching as compared to running (see below), the behaviour seems designed to bring A. dorsale into contact with prey because of its tight turns and the sweeping of the antennae over the ground. Descriptive summaries with a crude assessment of frequency shown are given for the five behavioural categories observed (Table 3.1).

The "SEARCHING" behaviour was examined in more detail and compared to the "RUN" behaviour, the only other behaviour that could bring A. dorsale into contact with prey. The total number of times each behaviour was shown in the presence/absence of prey was recorded for 15 beetles. The proportion of these total frequencies that occurred directly after attacking a prey item (whether the attack was successful or not) was also recorded. In addition, the proportion of all prey bumped into that were subsequently attacked during each behaviour was also recorded (Table 3.2).

"SEARCH" was most often shown when prey were present (Table 3.2) and this was because the behaviour was triggered by A. dorsale bumping into and attacking prey items. While in the "SEARCH" behaviour A. dorsale attacked most of the prey it bumped into. In contrast the "RUN" behaviour was shown with equal frequency in the presence or absence of prey and was not triggered by attacks on prey (Table 3.2). A. dorsale also made far fewer attacks on the prey that it bumped into while in the "RUN" behaviour than in the "SEARCH" behaviour.

In summary, A. dorsale runs around bumping into prey until one of these contacts stimulates it to attack. The beetle then shows searching behaviour which leads it to discover and attack more prey and so on. In the absence of prey, searching is only occasionally shown. The changes in antennal position and body movement that denoted the "SEARCH" behaviour were very characteristic (Fig. 3.3). In addition the clear difference in gait between "SEARCH" and "RUN"

Table 3.1 The characteristic behaviours shown by A. dorsale in the presence or absence of prey

Name assigned to behaviour	Description of behaviour	Prey present	Prey absent
STILL	Beetle stationary, antennae pointed forward and upward, no obvious activity.	√√	√√
RUN	Beetle moving rapidly (10 cms^{-1}), antennae pointed forward and upward. Movement mostly in straight lines or long shallow curves.	√√√	√√√
GROOM	Beetle stationary, varying combinations of legs/palps used to clean antennae, legs, mouthparts.	√√	√
SEARCH	Beetle moving slowly (2-3 cms^{-1}), antennae pointing forward but swept across ground in front of beetle. Movement in a series of tight curves (at least 90^{o} changes of direction in 2-5 cms).	√√√	√
EAT	Beetle stationary, antennae usually pointing back and up. Prey obviously visible in jaws or jaws obviously being used to chew.	√√	

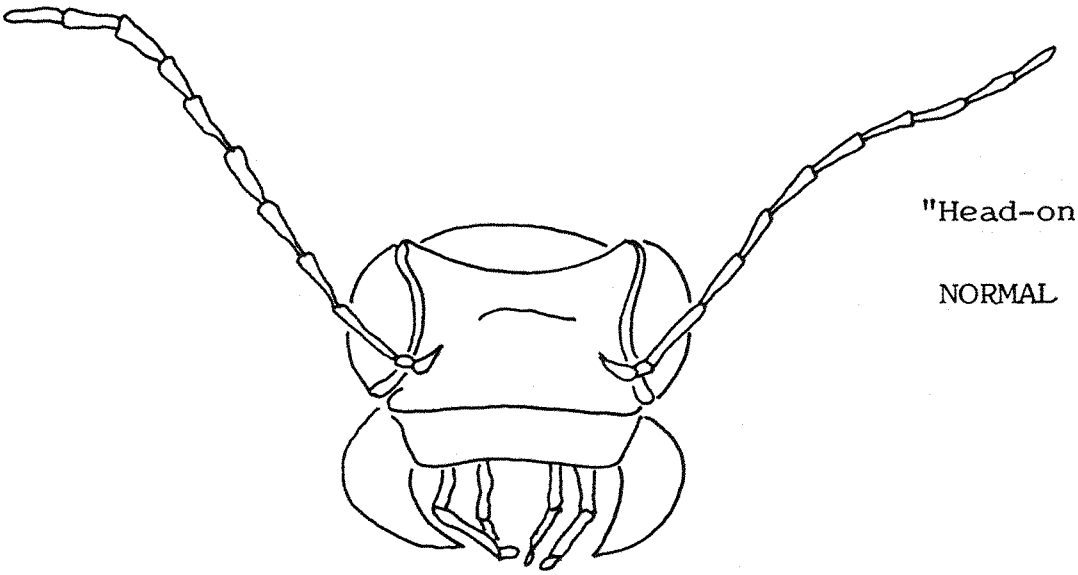
Key: √ = behaviour shown infrequently
√√ = behaviour shown frequently
√√√ = behaviour shown very frequently

Table 3.2 A comparison of the "SEARCH" and "RUN" behaviours in the presence/absence of prey.

Variable Recorded	BEHAVIOUR SHOWN	
	SEARCH	RUN
Total number of times behaviour shown, prey absent	2	311
Total number of times behaviour shown, prey present	135	297
Proportion of behaviour occurring directly after an attack on a prey item	0.93 (n = 135)	0.17 (n = 297)
Proportion of prey bumped into that were then attacked during the behaviour	0.89 (n = 145)	0.33 (n = 385)

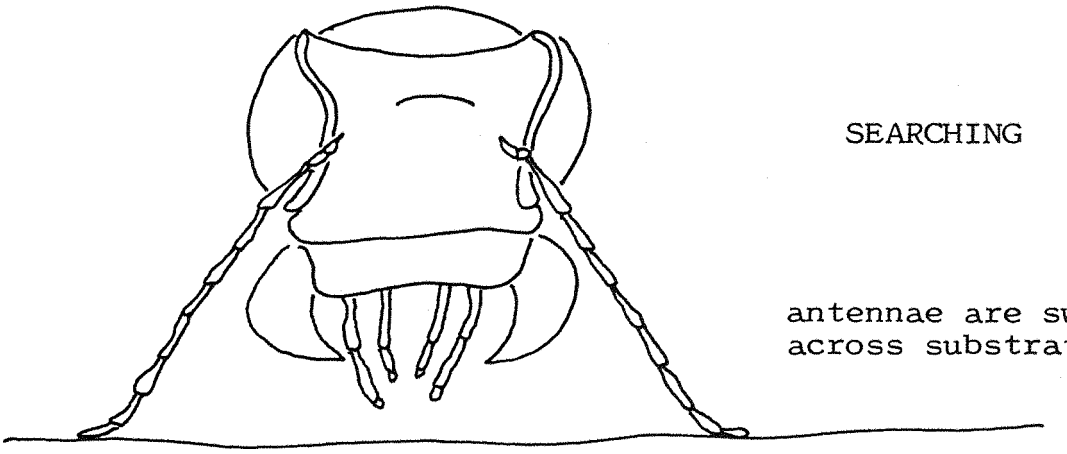
(Figures are cumulative totals for the 15 A. dorsale observed)

Fig. 3.3 The Searching Behaviour of A. dorsale



"Head-on" view

NORMAL

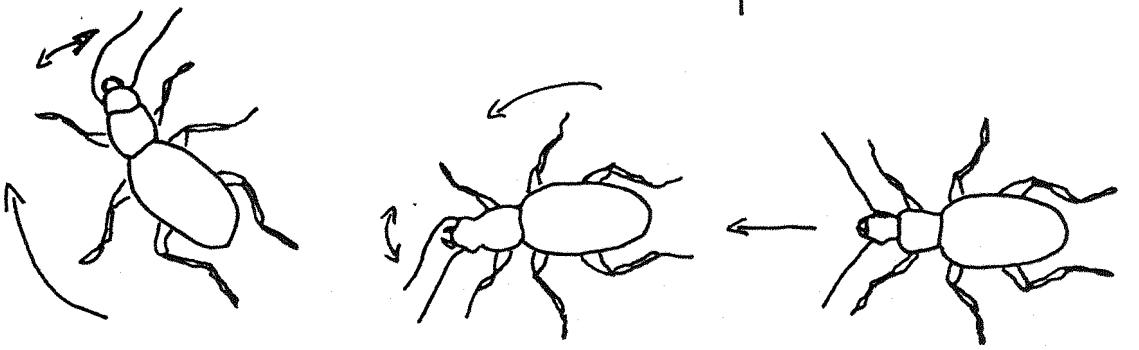


SEARCHING

antennae are swept across substrate

Plan view

Search | Normal



Arrows indicate flexing of body (particularly at thorax/ abdomen) and sweeping of antennae across substrate.

allowed the easy separation of these two behaviours. Differences in gait are a common and relatively inflexible characteristic of coleopteran movement (Crowson 1981) making them ideal behavioural markers.

3.5 The effect of handling on the subsequent behaviour of A. dorsale

A convenient way of handling many small invertebrates during experimentation is the insect-pooter (Southwood 1971), but disturbance of the animal caused by its use can lead to atypical behaviour during subsequent trials. The variables recorded to measure disturbance were those likely to be used in later experiments; searching behaviour and voracity. The time taken to detect the first prey item was used to measure the "settling-down" period of the beetle when first transferred from pooter to arena, while the number of prey eaten was used as measure of disturbance over the whole trial.

The "Control" used beetles placed in arenas at least one hour before the start of the test (prey were added at the start), these being very time consuming to prepare compared with those pootered directly into arenas. The values obtained of the two variables with disturbed and undisturbed A. dorsale are given in Table 3.3. Equality of variances was tested using the F-ratio test and the "Control" and "Experiment" trials were then compared with the appropriate form of the t-test (Bailey 1959).

Undisturbed beetles took significantly less time to find their first aphid than the disturbed beetles. Even disturbed beetles, however, took only about 1 min longer to find the first aphid, and this is unlikely to be significant in a 30 min or longer trial. In addition there was no significant difference between the total numbers of aphids eaten for the disturbed versus undisturbed A. dorsale over the subsequent 30 min of the trial (Table 3.3).

The results from Section 3.6 (the satiation trials) are included in Table 3.3 for comparison both of time taken to find the first prey item and number of aphids eaten over 30 min. For this experiment,

Table 3.3 The effect of disturbance due to handling with a pooter on the behaviour of A. dorsale as measured by the time taken to detect the first prey item and the total number of prey eaten during the trial period.

Parameter recorded	Trial type	$\bar{x}$	s.d.	n	t - test Comparisons
Time taken to detect the first aphid prey item (s)	Control	35	26.4	10	$p < 0.01$
	Experiment	109	65.9	10	$p < 0.05$
	Results from 3.6	71	49.8	15	$p < 0.05$
Total number of aphid prey eaten over the period of the trial	Control	4.1	2.51	10	$p > 0.1$
	Experiment	4.3	2.31	10	$p > 0.1$
	Results from 3.6 (first 30 mins. only)	5.1	0.88	15	$p > 0.1$

beetles were treated in the same way as the disturbed beetles. There was no significant difference between the disturbed beetles and the 3.6 trials. Beetles used in Section 3.6 also took significantly longer to find the first prey item than undisturbed beetles. This was despite the density of prey being approximately three times greater in the 3.6 trials. This suggests that the behaviour of A. dorsale is only initially altered when transferred rapidly by pooter into an experimental arena and that it quickly "settles down" to feed at a rate not significantly different from undisturbed beetles.

3.6 The effect of satiation on A. dorsale with respect to trial length

Laboratory experimentation cannot simulate fully the field situation, so it is often directed towards finding a maximum or minimum level of a given parameter. The functional response, searching efficiency and other variables of predation can be affected in a similar way by more than one factor. An example of this is the way in which either satiation or handling time can produce a Type II functional response (Hassell 1978). In order to ascertain the maximum/minimum levels of these variables the effects of these different factors must be separated out. Satiation will affect many aspects of a predator's performance whether in the field or in the laboratory. Accordingly, the number of cereal aphid prey eaten and the time taken for A. dorsale to stop feeding were recorded as discrete measures of satiation but also two continuous measures were used; the change in handling time and time between consumption of prey items, with increasing number of aphids eaten.

The means and standard deviations of time until satiation and number of aphids consumed before satiation are given in Table 3.4. Adult A. dorsale when starved for 3 days can eat between nine and 12 apterous adult aphids before becoming satiated and take significantly longer than an hour to become satiated. Any trial of 1 h or less should not be greatly affected by satiation; more detailed analysis (Fig. 3.4) confirms this. The cumulative plot of the number of beetles which had stopped feeding shows that most did so well after

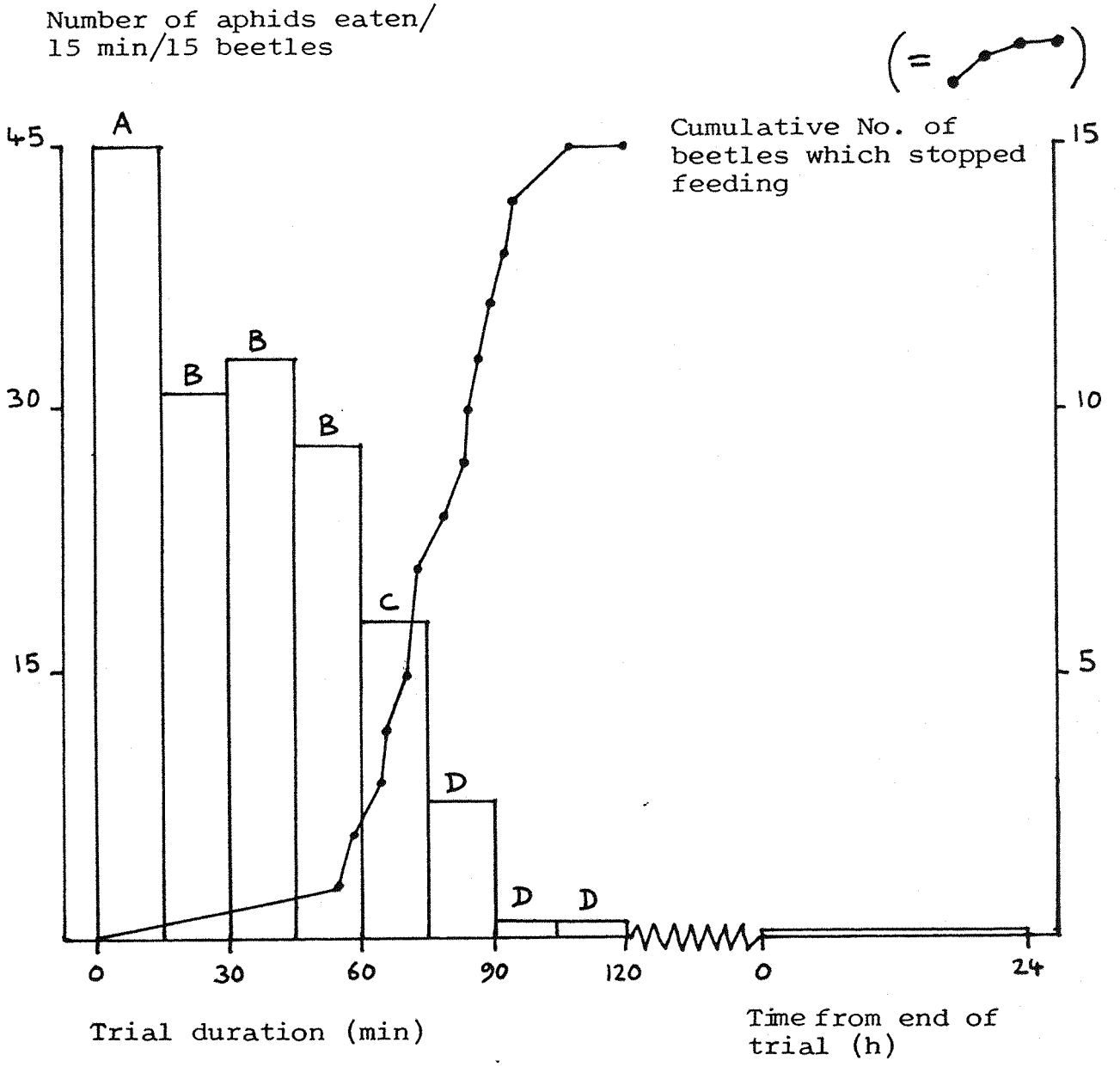
Table 3.4 The time taken and the number of aphid prey eaten for A. dorsale to become satiated

Parameter measured	$\bar{x}$	n	95% confidence limits	t - test null-hypothesis	P
Time taken to stop feeding (min.)	78.13	15	70.11 to 86.14	Individuals do not take longer than 60 min to stop feeding	< 0.001
Number of aphids eaten before satiation	11.0	15	9.5 to 12.5		

Table 3.5 The regression analyses of numbers of aphids eaten (X) against handling time and between-attack time (Y)

Y	Intercept a $\pm$ S.E.	Slope b $\pm$ S.E.	n	t - test (difference of slope from 0)
Handling time	319 $\pm$ 18.1	4.41 $\pm$ 2.5	165	NS
Between-attack time	59 $\pm$ 14.3	4.49 $\pm$ 2.1	150	$p < 0.05$

Fig. 3.4 Number of aphids eaten/15 min/15 A. dorsale and cumulative number of beetles which stopped feeding in relation to trial duration



$\bar{x}$
□ = Columns with the same letter are not significantly difference at the p = 0.02 level using the Wilcoxon matched pairs signed ranks test.

1 h. The histogram shows how the total number of aphids eaten per 15 min by the 15 trial beetles decreased with time. The feeding rate was high for 0-15 min and although it then dropped significantly it did not change significantly again until the 61-75 min period when it fell rapidly to nearly zero. Although individuals were watched for 15 min only after they had stopped feeding, counts of prey remaining after a further 24 h showed that the feeding rate had remained low indicating that this experiment had measured satiation as intended.

Although the feeding rate dropped after 0-15 min this is too short a period for experimental purposes and these results show that after 15 min the trial length can be extended for up to 1 h without further changes in feeding rate due to satiation.

Cessation of feeding due to satiation occurred over a restricted period of time prior to which there was little change in feeding rate but there may have been less obvious changes in other variables. The time spent handling prey and the time between attacks on prey were recorded throughout trials. The regression analysis of these data where X was the sequential number of prey attacked and Y was handling time or between-attack time, is given in Table 3.5. The t-test (Snedecor & Cochran 1967) was used to show whether the slopes differed significantly from zero. Handling time did not change significantly while between-attack times increased significantly with the number of aphids eaten.

This has important implications for predation work either in the laboratory or field. Handling time is a component of many insect models (Hassell 1978; 1982); these results show that for A. dorsale measurements of it will be robust because satiation does not significantly affect it.

3.7 Close-range detection of aphid prey by A. dorsale

Predators show a wide variety of adaptions to guide them to their prey. These can work from long range, e.g. parasitoids (Hassell 1978) to very short range, e.g. coccinellids (Stubbs 1980). Predators

that must search for patchily-distributed prey may show both adaptions. The first would enable them to find the patches of prey and the second to find prey within the patches (Waage 1979). Such adaptions may be shown by A. dorsale; cereal aphids form a large part of its diet and these are patchily distributed within the crop (Dean 1973).

Two approaches were adopted to test the close-range detection of aphids by A. dorsale; individuals were placed in an arena with a small number of aphids and the distances at which the beetles walked past without attacking prey were recorded or single aphid prey were presented at decreasing distances from the beetle until they elicited the "SEARCH" behaviour (Section 3.4) or an attack on the aphid.

For the first approach, aphids within the arena were divided into the "target" aphid (the aphid that the beetle happened to be walking towards at that moment) and "alternative" aphids (all other aphids in the arena). A. dorsale was assumed to be walking towards the target aphid by chance but in doing so passed close by alternative aphids which it ignored. If A. dorsale walked in a straight line towards the target aphid then it had presumably not detected the alternative aphids. A frequency distribution of the distances from which A. dorsale walked straight towards the target aphid was constructed (Fig. 3.5). This frequency distribution could then be compared with model distributions based on whether the beetle could detect aphids at distances of 4, 3, 2 or 1 cm. The assumption was made that walks towards the target aphid could start at random from anywhere in the area. So in each frequency class the number of walks starting at that range of distances away from the target aphid would be directly proportional to the corresponding area of the arena within that distance range from the aphid. The further away A. dorsale could detect aphids the smaller would be the frequency of long walks towards the target aphid because the beetle would more often be close enough to alternative aphids to detect them. Figure 3.6 shows how the model frequency distribution was constructed, in this case assuming that A. dorsale could detect aphids at a maximum of 1 cm away.

Fig. 3.5 The frequency distribution of straight line walks towards a target aphid in the sandwich box arena

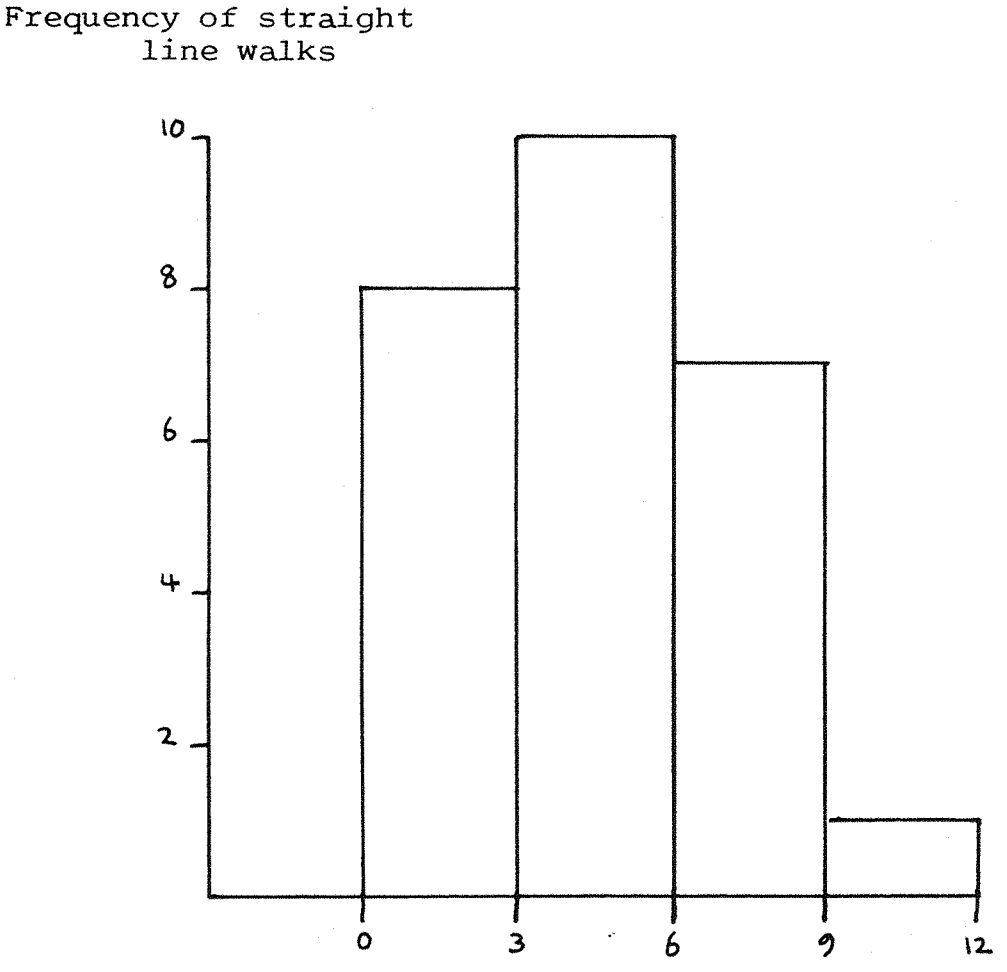
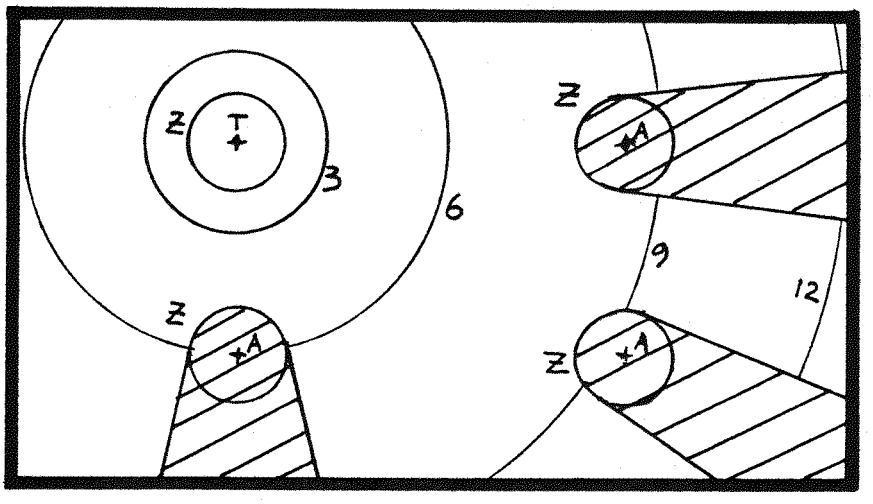


Fig. 3.6 The calculation in the 1cm perception model of the frequency distribution of straight line walks towards aphid prey in the sandwich box arena.

Plan view of arena:



T = Target aphid

3-12 = Distance (cm) from T.

A = Alternative aphid prey

Z = Boundary zone for 1cm perception model inside which the aphid prey is perceived.

= Shadow zone from which beetle cannot reach T in a straight line without perceiving A.

Calculation:

Frequency classes of distances from T (cm) (as in Figure 3.5)	Arena area corresponding to frequency class (minus the relevant shadow zone area) (cm^2)	Area frequency classes as proportions of: (Total arena area - total shadow zone area)	Predicted straight-line walk frequency = (Area proportions x total No. observed walks)
0 - 3	27.15	0.214	5.564
3 - 6	43.40	0.341	8.866
6 - 9	36.54	0.287	7.462
9 - 12	17.48	0.138	3.588
12	2.55	0.020	0.520

Model frequencies were calculated for detection distances of 1, 2, 3 and 4 cm and compared with the observed frequencies using the Kolmogorov-Smirnov test (Siegel 1956). Only the 4 cm perception distance model did not fit the data (Table 3.6) although the fit did improve considerably from the 3 cm to the 2 or 1 cm models. These results suggest that A. dorsale can detect aphids at a distance of 2 cm or less but that more detailed observations are needed to decide the exact distance.

The second experimental approach provided the more detailed observations required; the placing of single aphid prey at distances from 5 cm to 0 cm away from the beetle's head showed that searching behaviour or attacks on the prey were only elicited when the aphids were placed so as to touch the beetle's head (0 cm). This produced searching/attacks in 50% of presentations; all other distances produced no response. This suggests that A. dorsale must touch aphid prey to become aware of their presence within the range of distances possible (0-15 cm) in the sandwich box arena. This makes it probable that the beetle has no mechanism for detecting individual prey within a patch (other than by physical contact) but does not rule out the possibility that A. dorsale can detect patches of aphids over longer distances.

3.8 Close-range capture of prey by A. dorsale

As many carabids are nocturnal there has been little observation of the outcome of physical contact between the beetles and their prey. Work of this type has concentrated on the diurnal visually-hunting carabids (Swiecimski 1957; Bauer 1977; Wilson 1978; Dreisig 1981). These studies have shown that such beetles can usually detect moving prey only and that often if the beetle misses at the first attempt at capture, it has no second chance. Contact between prey and predator consists of the prey touching the beetle's jaws and immediately escaping or being caught.

A. dorsale is nocturnally active (Section 3.2, also Luff 1978) and nothing is known about the outcome of contacts between the beetle

Table 3.6 Observed and predicted frequency classes of straight line walks towards aphid prey in the sandwich box arena

		Frequency classes of straight line walk distances (cm) towards target aphid prey					Goodness of fit of model (see text)
		0-3	> 3-6	>6-9	> 9-12	> 12	
Observed	cm	8	10	7	1	0	
Predicted for x cm perception Model	1	5.56	8.87	7.46	3.59	0.52	$p > 0.20$
	2	7.7	10.61	6.14	1.3	0.18	$p > 0.20$
	3	11.34	12.77	1.79	0.10	0	$p < 0.10$
	4	15.21	10.79	0	0	0	$p < 0.05$

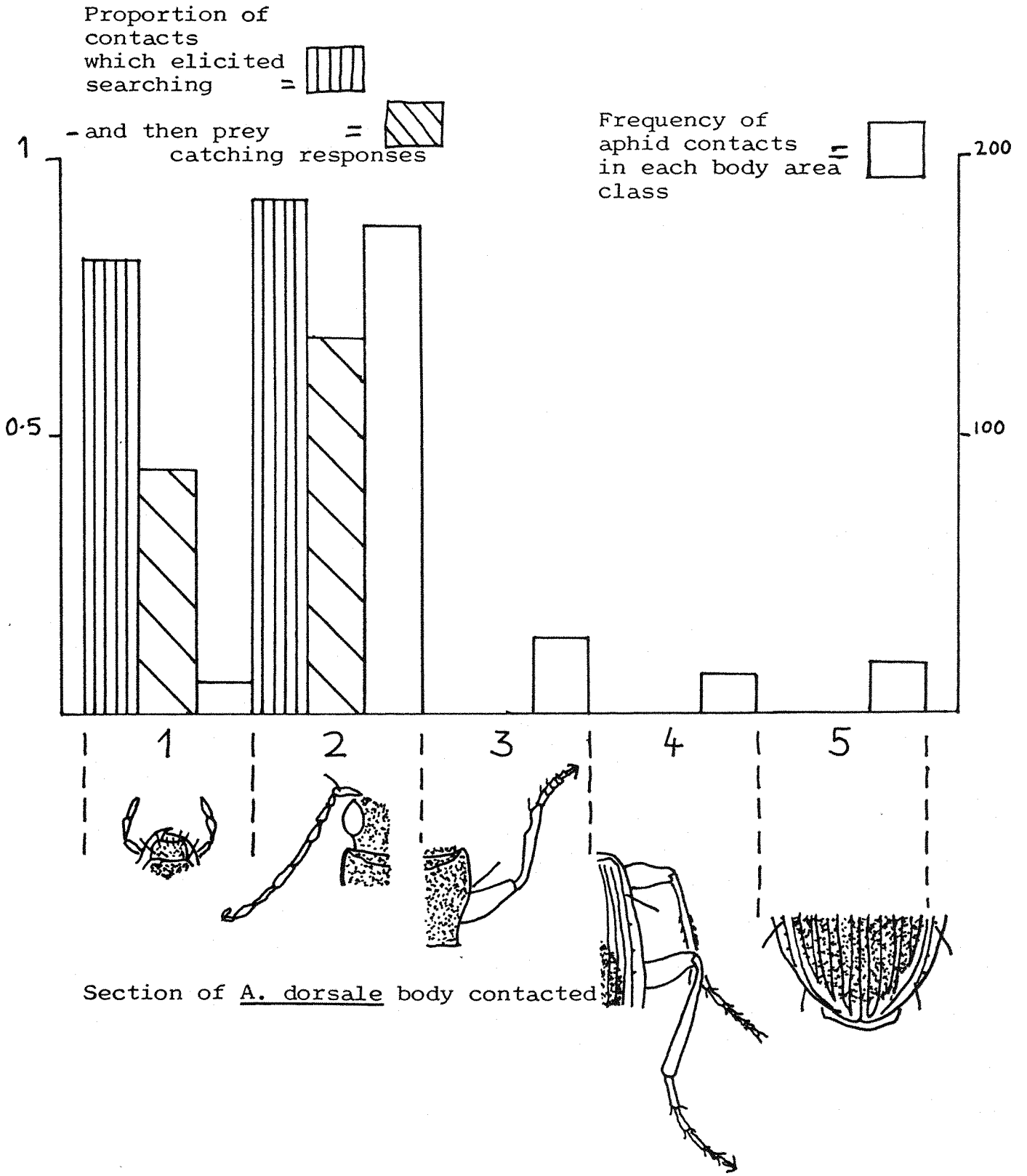
and its prey. Casual observation during earlier experiments suggested that prey was mostly captured when the beetle contacted it with the antennae and that even when this happened, capture was not certain. In this experiment the beetle's body was mentally divided into sections; mouthparts, antennae, fore-legs, mid/hind legs and rear of abdomen. The number of prey contacts made with these sections and whether they led to searching behaviour and prey capture by A. dorsale were recorded and are shown in Figure 3.7. Only contacts with the beetle's mouthparts or antennae elicited searching or capture behaviour. While contact with mouthparts or antennae elicited similar proportions of searching behaviour, capture of prey was higher when the initial contact was with the antennae. This was probably because the beetle was moving forwards when it contacted prey with the antennae or mouthparts; if the mouthparts were the initial point of contact the beetle missed prey because it had already moved over the aphid. Clearly contact between A. dorsale and prey is not sufficient, contact must be with the antennae or mouthparts for the beetle to respond with prey-searching or catching behaviour.

3.9 Discussion

Work by Greenslade (1963), Vickerman & Sunderland (1975) and Luff (1978) suggested that A. dorsale was predominantly nocturnally active. Observation of the beetles' activity period in three separate laboratory cultures showed A. dorsale to be strictly nocturnal. The diurnal rhythm could be entrained with even the relatively low light intensity provided by a single fluorescent strip light. Reversing the light:dark cycle so that A. dorsale would be active during normal working hours required only a few days before the beetles adjusted to the new regime.

The light wave sensitivity of many beetles is in the green to ultra-violet range (Evans 1975), producing the possibility of observing them nocturnally by using red light. A. dorsale did not retreat under refuges when exposed to red light nor did it react to the visual stimuli of large moving objects or shadows. In addition, the diel activity pattern was not altered by exposure to red light during the dark period

Fig. 3.7 The proportion of contacts which elicited searching and prey capture by A. dorsale when the aphid prey were contacted by different areas of the beetle's body



and nocturnal observation of A. dorsale was subsequently carried out under red light.

A. dorsale showed a number of recognisably distinct behavioural postures, one of which was termed "SEARCHING" and it was regularly elicited after the beetle had physically contacted an aphid and often led to the beetle encountering and successfully catching more aphid prey. This posture was rarely shown in the absence of prey. It seems that A. dorsale, even when starved, is not stimulated to search until it contacts prey. This implies that the beetle may discover prey by chance rather than directed searching.

As A. dorsale could withstand periods of starving (Chapter 2.2) and alteration of diel activity cycle it was likely to be a hardy experimental animal. This was confirmed by the way in which it took only about 1 min to recover from being moved from culture to experimental arena. The use of the pooter for this purpose should not be a source of error, even in tests only a few minutes long.

Trials showed that the feeding rate of beetles in experiments less than 1 h long was not affected by satiation. Measurements of handling time were also independent of satiation. The beetle appeared to suddenly stop feeding altogether rather than show a gradual increase in handling time or decrease in the amount eaten of each prey item. The mechanisms by which predators detect prey may work at several distinct distances; this causes methodological problems in that the size of experimental arena may determine which mechanism is noticed by the researcher. The very small sandwich box arena was used to determine only whether A. dorsale had a close-range mechanism for detecting prey. The first set of trials indicated that detection occurred at 2 cm or less but this conclusion was based on a hypothetical model and did not measure directly the detection distance. The second set of trials measured the detection distance directly and this was found to be 0 cm, i.e. the beetle had physically to contact prey before searching and catching behaviour was elicited.

The close range capture trials also demonstrated that A. dorsale has physically to contact prey before it shows searching behaviour

but also that the area of the body with which it makes the contact is crucial. The searching/capture response was only elicited if the beetle contacted prey with its antennae or mouthparts. Capture of prey was most successful if the antennae were contacted first, but this is unlikely unless the beetle shows the "SEARCHING" behaviour; only in this behaviour are the antennae brought close to the ground (Fig. 3.3).

Later chapters will consider in more detail the mechanisms by which A. dorsale finds aphids and also the interaction between the beetle and prey other than aphids. These results suggest that a close-range prey-finding mechanism does not exist for A. dorsale preying on cereal aphids and that any adaptions shown by the beetle to find this prey must function at distances greater than 15 cm (the maximum distance between beetle & prey in the sandwich box).

C H A P T E R 4

CHAPTER 4

THE PREDATORY POTENTIAL OF A. DORSALE

(See Chapter 2.4 for materials and methods)

4.1 Introduction

Arthropod natural enemies can be divided into the two classes of predators and parasitoids. Parasitoids present a more simple relationship with their prey both theoretically and experimentally. Firstly, only the adult female searches for prey and secondly successful "capture" of prey is directly linked to the reproductive fitness of the searching parasitoid. Predators by contrast often search for prey at all stages of the life cycle and there is no simple link between number of prey captured and reproductive success.

Despite the complex relationship between predator and prey, theoretical studies suggest that it has some important basic parameters. The magnitude of these parameters can greatly affect the dynamics of the predator and prey populations. Table 4.1 gives a summary of some parameters commonly used in predator-prey models (see Hassell 1978 for a discussion of the models) and indicates their relative magnitude for biological control.

The aforementioned parameters were developed for specific predators and parasitoids searching in stable environments. Consideration of polyphagous predators and annual crop systems produces different requirements. Stability is no longer a useful concept within the short life time of these crops. But stability-related parameters which also act to reduce the pest population at an early stage can still be important and the effect of some may be enhanced by the polyphagy of the predators. The total response (Hassell 1978) of the polyphagous predator is more likely to be sigmoid because the predator population size is not closely linked to that of the pest, so avoiding the delay that occurs while specific predators build up sufficient numbers to affect the pest population. The sigmoid functional response may also be more common

Table 4.1 Parameters from predator-prey models and their relationship to biological control

Reference	Parameter	Optimum for biological control	Effect of parameter
(Nicholson 1933) (Holling 1959) (Hassell and Varley 1969)	a, a', Q — attack rate, area of discovery etc.	High	Reduce average population levels
(Holling 1959)	a' attack rate; T_s search time	Increase disproportionately with density	Sigmoid functional response; increasing proportion of prey killed at lower prey densities and potential stability of pest population
(Holling 1959)	T total search/ feeding time	High	Reduce average population levels
(Holling 1959)	T_h handling time	Low (as a proportion of T_t)	Small increase in stability, but small increase in average population level
(Hassell & Varley 1969)	m mutual interference constant	0 - 1 (depending on prey reproductive rate)	Potential increase in stability

Table 4.1 Continued

Reference	Parameter	Optimum for biological control	Effect of parameter
(Hassell & May 1973)	μ predator aggregation index	High (depending on prey reproductive rate and proportion of prey in the large patch)	Potential increase in stability
(Hassell & May 1974)	k predator aggregation index	All values $k < 1$ (range $0 \rightarrow \infty$) Prey must show intra-specific DD.	Potential stability

in polyphagous predators; in addition to the predator directly varying a' or T_s in response to pest density (Table 4.1), it can do so indirectly either by simply switching from locally alternative prey to the pest or by switching from the alternative prey habitat to the pest habitat.

This chapter deals with those parameters which can act to reduce pest population levels within the framework of A. dorsale preying on cereal aphids and in the absence of habitat heterogeneity or prey choice. The object was to assess the maximum potential of A. dorsale to limit cereal aphid numbers.

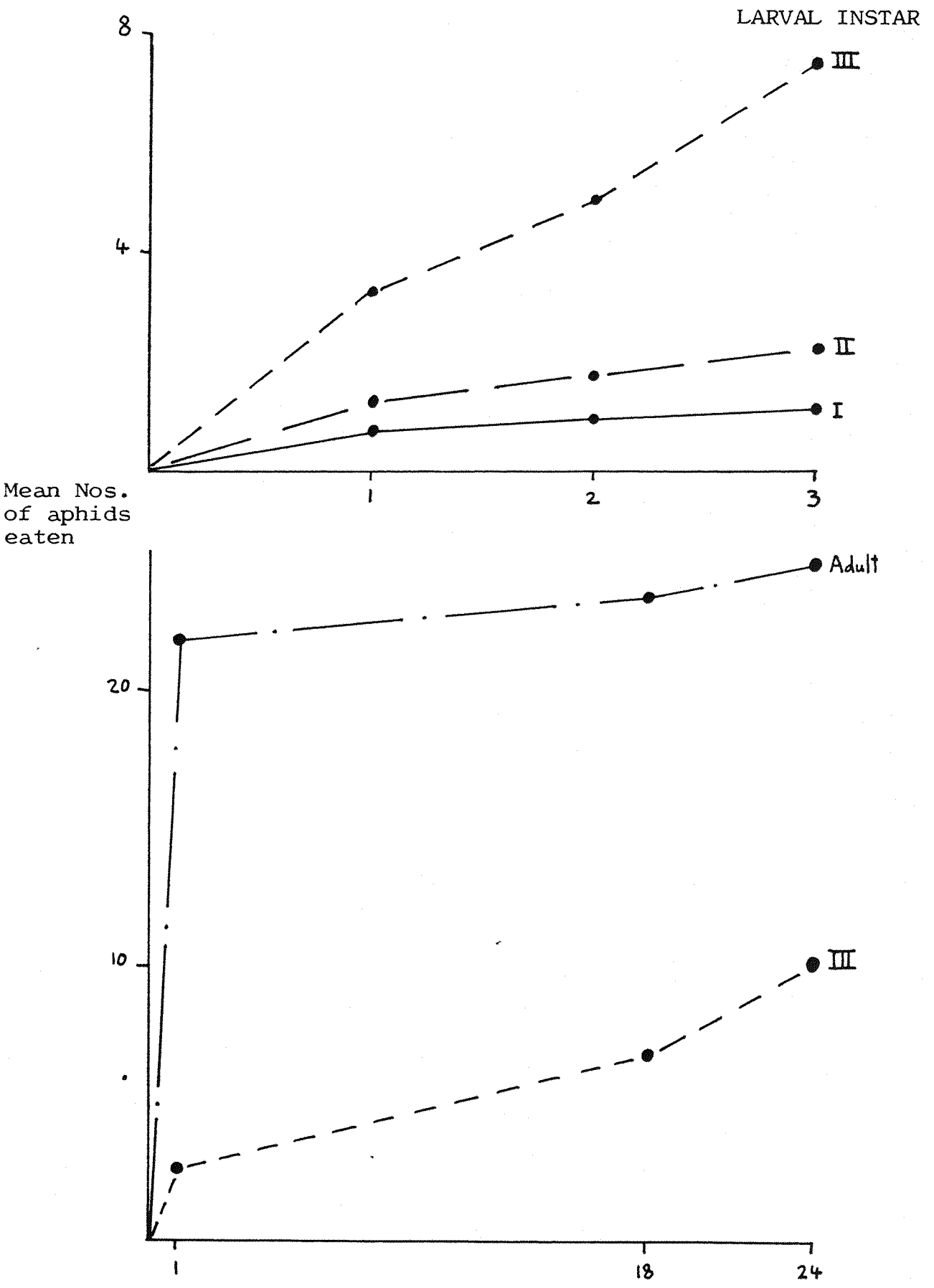
Larval voracity was compared with that of adults. Larval survival and adult fecundity were also assessed. The adults' capacity for area-restricted search and their functional response to different aphid size classes were recorded. Also the voracity of the adults was recorded over periods of several weeks at different temperatures and at different stages of reproductive development. These variables were used to show whether the parameters of the conventional predator-prey models control the predatory potential of A. dorsale or whether factors such as satiation or temperature are more important.

4.2 Larval vs. Adult A. dorsale feeding rates

The ratio of larval:adult voracity is extremely variable in the Coleoptera; while all larvae must feed to develop, some adult beetles do not feed at all (Crowson 1981) and others are extremely voracious (many Carabidae). This ratio was examined for A. dorsale to determine whether larvae or adults would be the larger cause of mortality in cereal aphid populations.

There was a general trend of increasing voracity with larval size (Fig. 4.1) over the 3 h period of the trial. The differences between the three instars after 3 h was tested using a Kruskal-Wallis one-way analysis of variance (Siegel 1956). The differences were significant at the $p = 0.01$ level ($n = 17$).

Fig. 4.1 The feeding rates of A. dorsale larvae over 3h, and, for third instar larvae compared with that of adults, over 24h.



The voracity of the third and largest larval instar was significantly less than that of the pre-reproductive adults with which it was compared (t-test; $p < 0.001$; $n = 20$) after 24 h (Fig. 4.1). The smaller larval instars were not compared as even over this short time their survival was unpredictable. Given that the complete larval stage lasts only about 25 days (Chapter 1.5) it seems unlikely that the total number of prey eaten by individuals of instars I and II ever exceeds that of instar III. As adults are active for much longer in the field than larvae, larval voracity is always likely to be lower than that of adults.

4.3 The fecundity, site of egg laying and percentage egg hatch of A. dorsale

The role of polyphagous predators in cereals has been envisaged as follows (after Southwood and Comins 1976): they would have most effect early in the season when the aphids first invade the crop. At this time their high attack rates and ability to switch preferentially to aphids would be at a premium. Their ability to control very high numbers of aphids would be poor because their numerical response would consist of local aggregation rather than large scale immigration or reproduction.

Much of this is conjecture but studies show (Barnes 1974; Huffaker & Messenger 1976; Thiele 1977; Crowson 1981) that most of these polyphagous predators have only one generation per year, so the fecundity of these predators will not directly affect their ability to control cereal aphid numbers. Conversely, aphid numbers will not affect the fecundity of these predators as they can make use of alternative food sources. Instead the importance of measuring their fecundity lies in the increasing use of pesticides in agriculture. The detrimental effect of these chemicals on the polyphagous predators' populations (Thiele 1977) may be greater than their potential rate of increase leading to a widespread decline of predator populations. Southwood & Comins (1976) state that "the outcome of a spring invasion" (of cereal aphids) will "often be determined by the balance between

numbers of the invaders, ..., and the size of the autochthonous population of polyphagous predators". They conceive that at low pest densities polyphagous predators could impose control but that at this level even a small pest increase would lead to the pest population "escaping" to cause outbreaks. This small increase could be caused either by pest reproduction or by predator numbers being reduced, as would happen after an application of pesticide.

In this experiment the survivorship of eggs and larvae was assessed in the laboratory in conditions of constant temperature high humidity and abundant food, with a suitable substrate for pupation. If larval survival was poor in these comparatively favourable conditions then survival in the field (where predation, dessication and disease will add to mortalities) is likely to be poor also. In this case the ability of the A. dorsale population to recover from the extra mortalities imposed by pesticide use will be poor.

Gravid female A. dorsale were given abundant food in the form of cereal aphids (S. avenae) and presented with the choice of soil or freshly cut wheat leaves (placed vertically in the arenas) on which to lay their eggs. Ten females were monitored for numbers of eggs laid but only the eggs from five females were kept for assessment of hatching and larval survival. Five larvae were monitored in detail to measure the length of development time.

On dissection all 10 females had reached stage 5 in the reproductive development scale (Chapter 7.2), that is they had laid nearly all their eggs (94%) and there were no new eggs developing. Examination of the soil and wheat leaves provided in the containers for the females showed that all eggs had been laid singly on the wheat, each in a package of soil (see Dicker 1951). The number of eggs laid (about 35 per female) is comparable with numbers laid by other carabids of similar size (Thiele 1977). Also, as no beetles dissected from the field (Section 7.2) contained even half this number of eggs this may be close to the maximum attainable by A. dorsale.

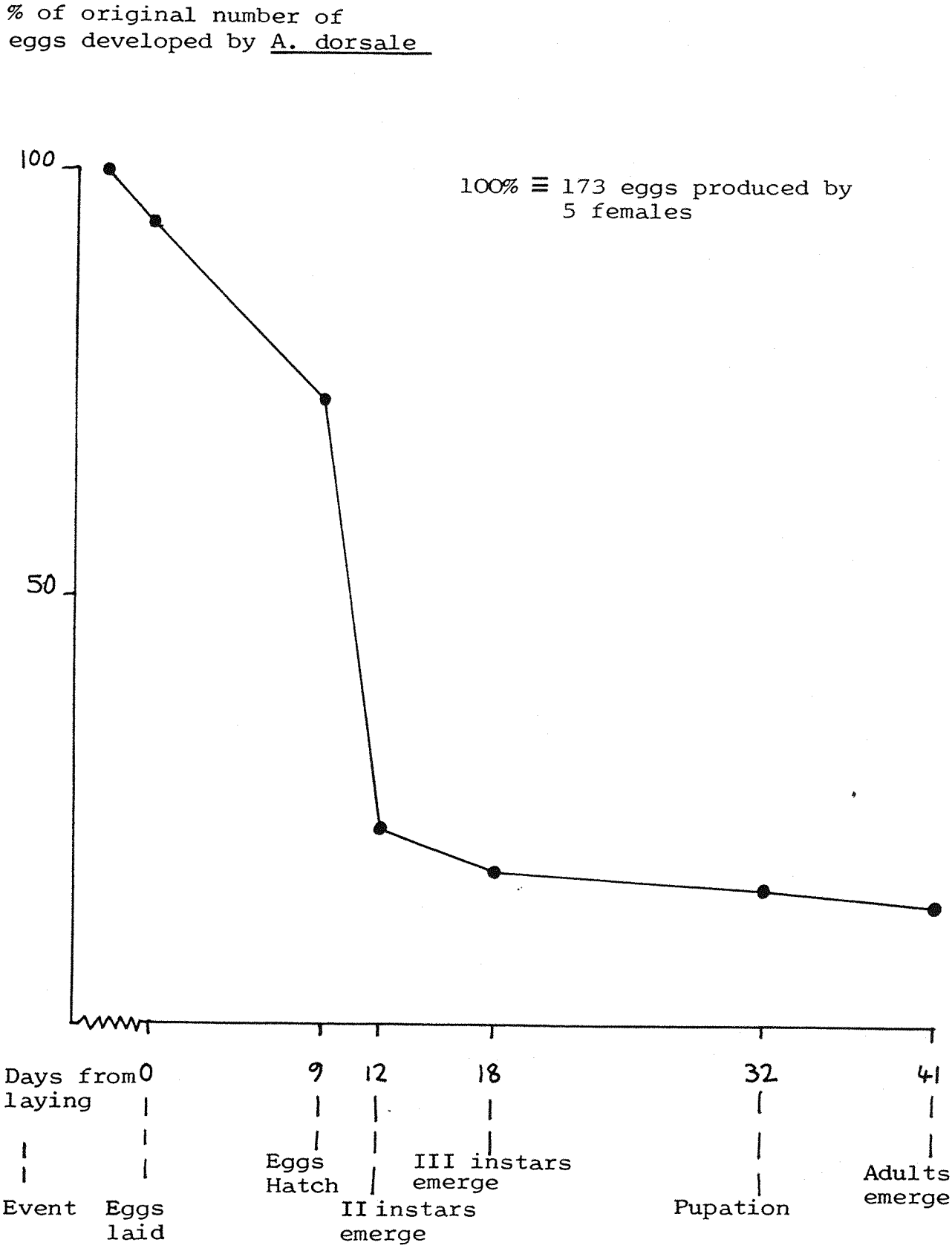
A survivorship curve (Fig. 4.2) was produced for A. dorsale from egg laying to adult emergence by monitoring the fate of offspring from eggs through to emergence of adults. The time-scale for the survival curve was calculated from the average development times of five larvae.

All the females still contained a few eggs at the end of egg laying as did many sampled from the field (Chapter 7.2). This retention of a few eggs may give the females sufficient energy reserves to survive to breed in a second year (Murdoch 1966). The eggs that were laid were wrapped in fine soil particles and glued to the wheat leaves. The soil covering may protect the eggs from desiccation and fungal attack (Thiele 1977) and their being layed singly on plant surfaces may be a common coleopteran adaption against over predation of eggs (Crowson 1981).

The highest mortality of offspring occurred in the "active" larval stage rather than the "passive" egg and pupal stages. Although this is a laboratory result it corresponds well with the survivorship curves obtained by Grum (1975) for natural populations of six carabid species. Grum found that the highest mortality rates occurred at the active stages (both adult and larval) of the life cycle. Larval mortality dominated the cycle and Grum speculated that this was due largely to predation. Predation was not the cause of mortality in this experiment but the larvae (particularly first instar) were very prone to desiccation despite spending most of their time buried in the damp sand of their containers.

This experiment has many shortcomings but as with Grum's results (on non-agricultural carabids) it gives a general figure of only about 15% of the potential population emerging successfully as adults. If this is the rate of success in laboratory conditions of high humidity, abundant food and no predation, the added pressure of mortality due to pesticides is likely to be severe. The decline in numbers of several carabid species from 1970 to 1979 on a study farm in Sussex (Vickerman in litt.) may reflect this.

Fig. 4.2 The survivorship curve of A. dorsale from egg laying to pupal emergence in the laboratory



4.4 Changes in path and speed of movement of A. dorsale as a result of encountering prey items.

Behavioural mechanisms leading a predator to concentrate its hunting effort in areas where prey have aggregated are common amongst arthropods (Hassell 1978). Models exploring aggregation have concentrated on its role in promoting stability in predator-prey interactions while a high search rate has been identified as being important in keeping the prey population small (Hassell 1978). In annual crops, where stability over several generations is unlikely, aggregation can still be important since the pests involved must not only be attacked soon after infestation begins but may also be aggregated in the field and on the crop plants.

A predator may show specific behavioural changes associated with when it enters or leaves a patch of prey due to a number of arrestant stimuli (Waage 1977). A common change is for the predator to show a much-increased rate of turning and reduction in speed of movement following an encounter with a prey item (Banks 1957; Hassell and May 1973; Murdie and Hassell 1973).

A. dorsale showed just such changes of behaviour when it encountered prey in the sandwich box arena (Chapter 2.5). Table 4.2 summarises the changes between arenas containing no prey and those containing cereal aphids. Turns were defined as changes in direction of greater than 45 degrees within a distance travelled of 2 cm so that this response to prey could be discriminated from more random movements. This subjective definition was thought adequate because of the clear distinction between the straight line "RUN" behaviour and the twisting "SEARCH" behaviour (Chapter 3.4). The number of turns increased very significantly when A. dorsale came into contact with prey and there was a corresponding decrease in the speed of movement (measured directly during the trial) and the total distance moved during the trial.

Within the very simple environment of a sandwich box A. dorsale showed a behavioural response to cereal aphid prey which may lead it

Table 4.2 The changes in turning and speed of movement by A. dorsale after encountering prey

Parameter measured	NO PREY (n = 20)	PREY (n = 10)	Significance of difference between trials
Number of turns	7.5 ± 1.36	51.3 ± 4.8	t-test $p < 0.001$
Speed of movement - instantaneous measure ($cm\ s^{-1}$)	10.9	1.7	Mann-Whitney U-test $p < 0.002$
Total distance travelled for the trial (cm)	439 ± 47	133 ± 22	t-test $p < 0.001$

Figures are $\bar{x}$ (± S.E. where appropriate)

to aggregate in areas of high aphid density in the field. Within a wheat crop this response would have to be combined with climbing behaviour for A. dorsale to encounter aphids and this is examined in Chapters 5 and 8.

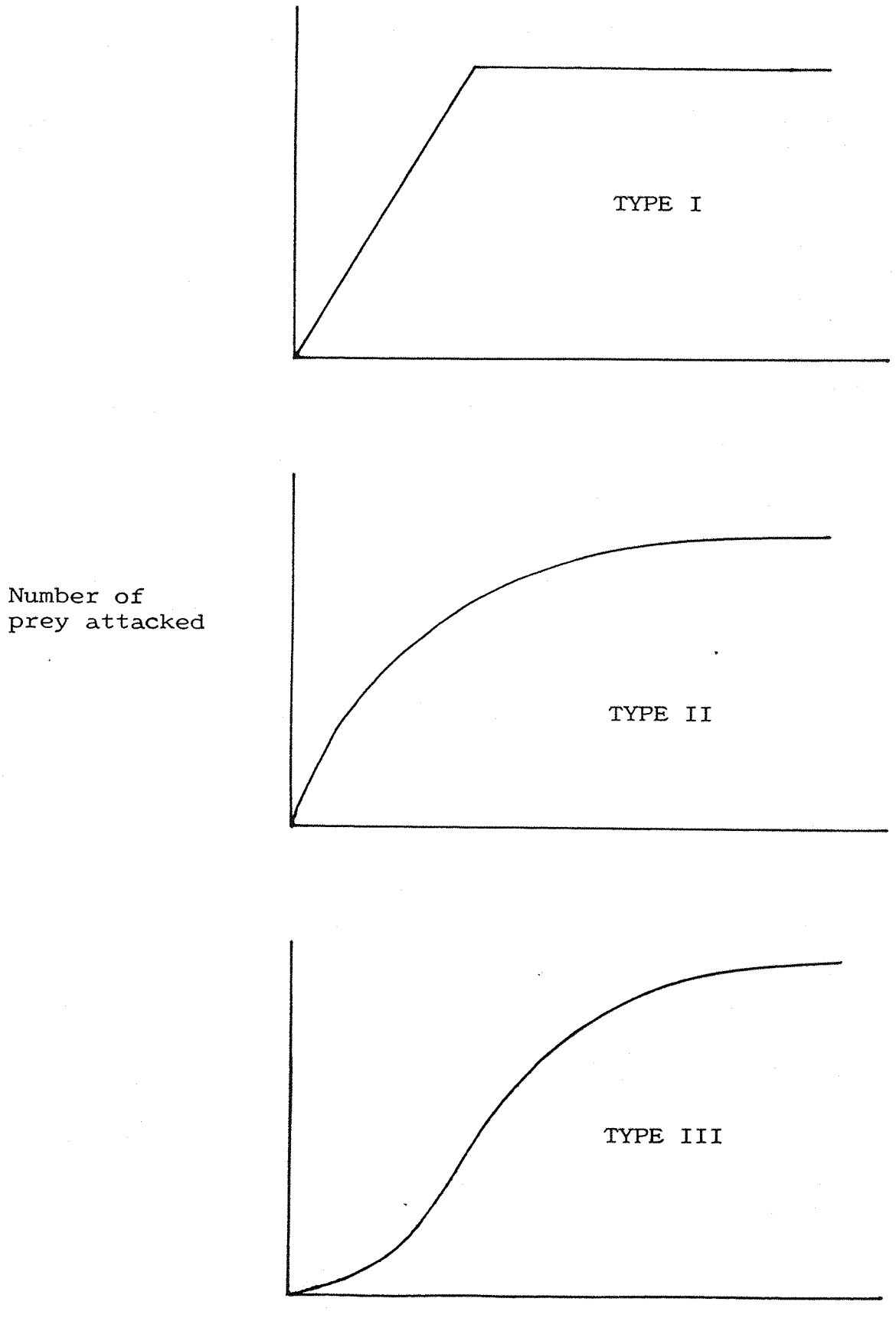
4.5 The functional response of A. dorsale to different sizes of cereal aphid prey

The term "functional response' refers to the relationship between the numbers of prey attacked per predator and the prey density (see Holling 1959; Hassell, Lawton & Beddington 1976). The functional response is a measure of searching and feeding capacity which when combined with the numerical response (Holling 1959) and the density of the predator gives an estimate of its effect on a prey population.

Functional responses can be divided into the familiar three categories proposed by Holling (1959); type I, II or III (Fig. 4.3). Incorporation of the responses into differential equation population models (Murdoch & Oaten 1975) and difference equation models (Hassell 1978) has shown that only the type III response can lead to stability and hence potential regulation of pest numbers. The many examples of type II responses for invertebrates (see Hassell, Lawton & Beddington 1976 and Hassell 1978 for reviews) suggested that they had little potential for control. More recent work (Hassell, Lawton & Beddington 1977; Cook & Cockrell 1978; Akre & Johnson 1979) has shown that with more subtle experimental arrangements (i.e. using smaller, less obvious prey in more heterogeneous arenas) many invertebrates show type III responses.

This section examines the functional response of A. dorsale in a very simple arena but with the subtlety of presenting one of several prey sizes. The prey were cereal aphids and were divided into four size categories; I (0.8 mm), II (0.8-1.1 mm), III (1.1-1.4 mm) and IV (1.4-1.7 mm). In addition to the functional responses, handling times and percentage successful encounters were also recorded for each prey size class.

Fig. 4.3 The three types of functional response proposed by Holling (1959)

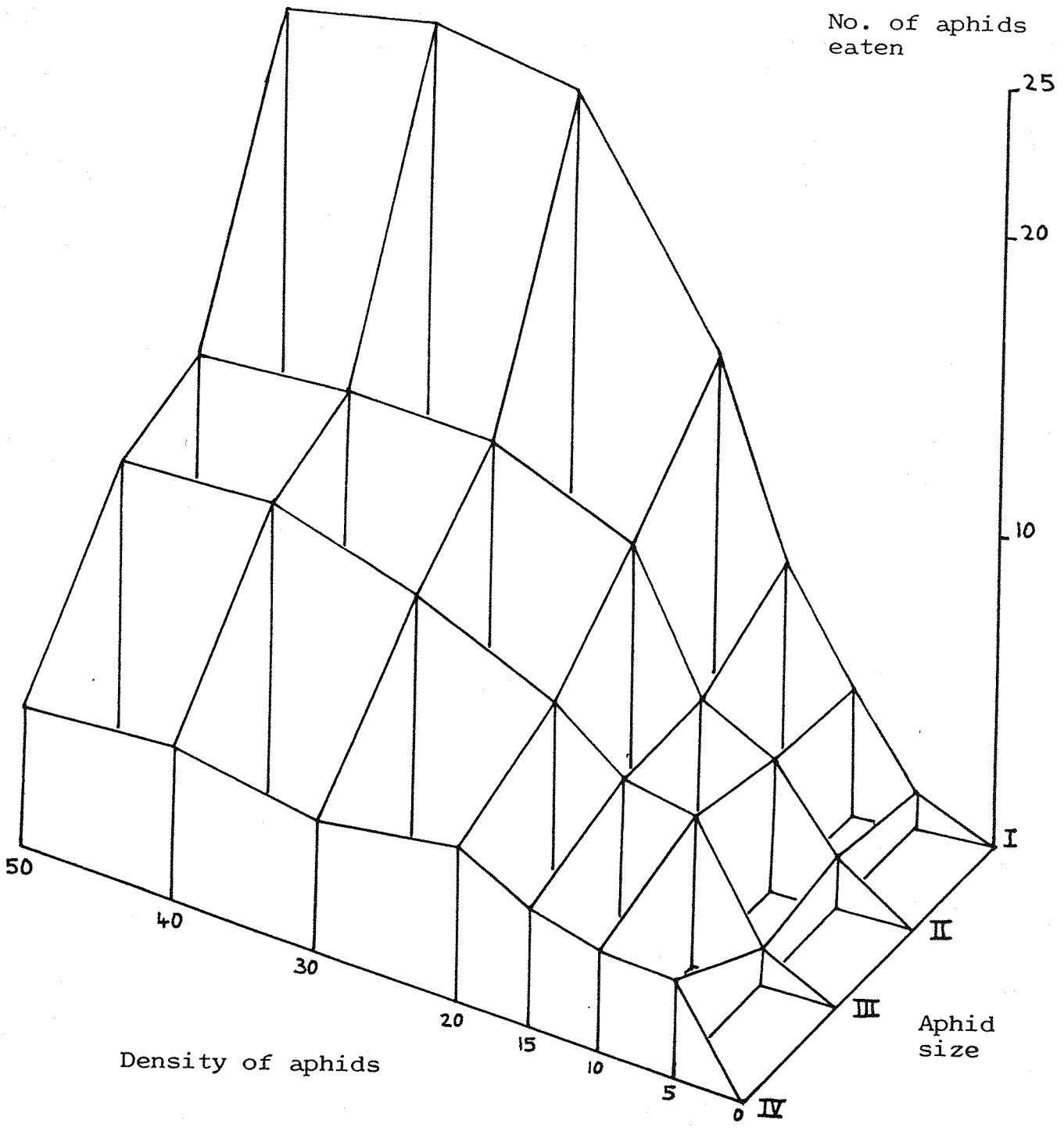


The type of functional response changed with the size of aphid prey (Fig. 4.4); on a cursory examination the response changes from a type III to type II with increasing size of aphid. The use of Cock's method (1977) of plotting graphs of ln (nos. of surviving prey) against numbers of prey eaten helps to discriminate between type II and III response curves. Using this plot the perfect type II response shows as a straight line with positive slope while a type III response shows as a "V" shape. Plots of the four responses obtained here (Fig. 4.5) suggest that A. dorsale showed a type III response to aphids of size I-III and a type II response to size IV aphids. The problem with this method is that if there is any scatter of data around the response curve these plots become difficult to interpret (see Fig. 4.5, the responses to prey of size III and IV).

Attempts to discriminate between type II and III responses statistically have not been entirely satisfactory. First attempts (Hassell, Lawton & Beddington 1977) were by testing the fit of data (by analysis of variance) to the straight line regression of Rogers (1972), used to abstract the parameters a' (attack rate) and T_h (handling time) of the random predator/parasite models. If the data fitted then the response was type II, if it did not it may be type III. This method is subject to at least two criticisms; Rogers' model is not suitable for conventional statistical analysis because the two variables in his regression are not independent of one another (see the review by Cock 1977), but more importantly proof that a response is not type II does not mean that the response is definitely a type III. The use of parabolic regression by Akre & Johnson (1979) eliminated the statistical problems but again the technique consisted of showing that a response did not fit a type II model but not that it did fit a type III. Similarly, later attempts to extract the attack rate and handling time parameters (McArdle & Lawton 1979) have been satisfactory statistically but could only be applied to type II responses.

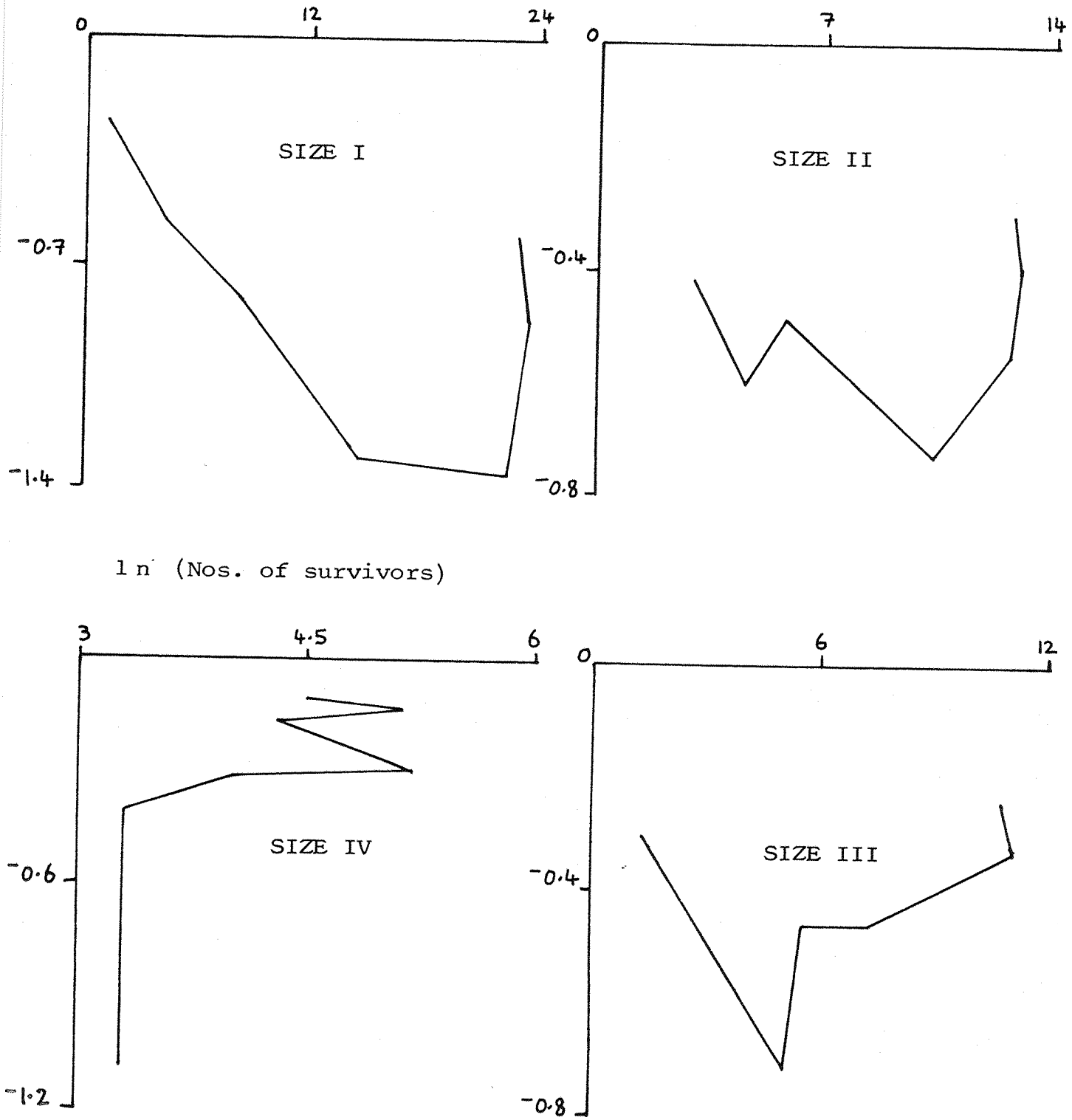
A different technique was used here which is both satisfactory statistically and gives positive identification of type II or type III responses. The technique makes use of the "Polynomial Regression" option for statistical analysis of curves in the "Statistical Package

Fig. 4.4 The functional responses of A. dorsale to four size classes of aphid prey



N.B. Points are mean values of 10 replicates

Fig. 4.5 Plots of ln (number of survivors) against number of prey eaten (after Cock 1977) for A. dorsale feeding on four sizes of aphid prey



for Social Sciences" (Nie et al. 1975) and some elementary calculus. The main principles of this form of analysis are as follows.

The general equation of any straight line can be written as

$$Y = A + B X$$

where
- Y = dependent variable
- X = independent variable
- B = slope of the line
- A = intercept of line with Y-axis

In polynomial regression, successive powers of the independent variable are inserted in this equation with the original variable to give an equation of the form

$$Y = A + B X + B^2 X^2 + ... + B^n X^n$$

With the inclusion of each successive power the fit of this line to the data always improves because the line is bent to more closely follow the distribution of data points. Whether this increase is significant can be statistically tested using the squares of the correlation coefficients (R^2) obtained with each additional power. The appropriate F-test (null hypothesis that the k^{th} order term contributes nothing to the goodness of fit) is given by:

$$F = \frac{(R^2 \text{ with } k^{th} \text{ order term}) - (R^2 \text{ without } k^{th} \text{ order term})}{(1 - R^2 \text{ with } k^{th} \text{ order term})/(N - k - 1)}$$

with 1 and $(N - k - 1)$ degrees of freedom. This test allows the objective choice of the simplest polynomial equation to fit the curve (Nie et al. 1975).

These polynomial regression equations are described by their degree, that is the highest power in the equation. So $Y = A + B X + B^2 X^2$ is a second degree equation.

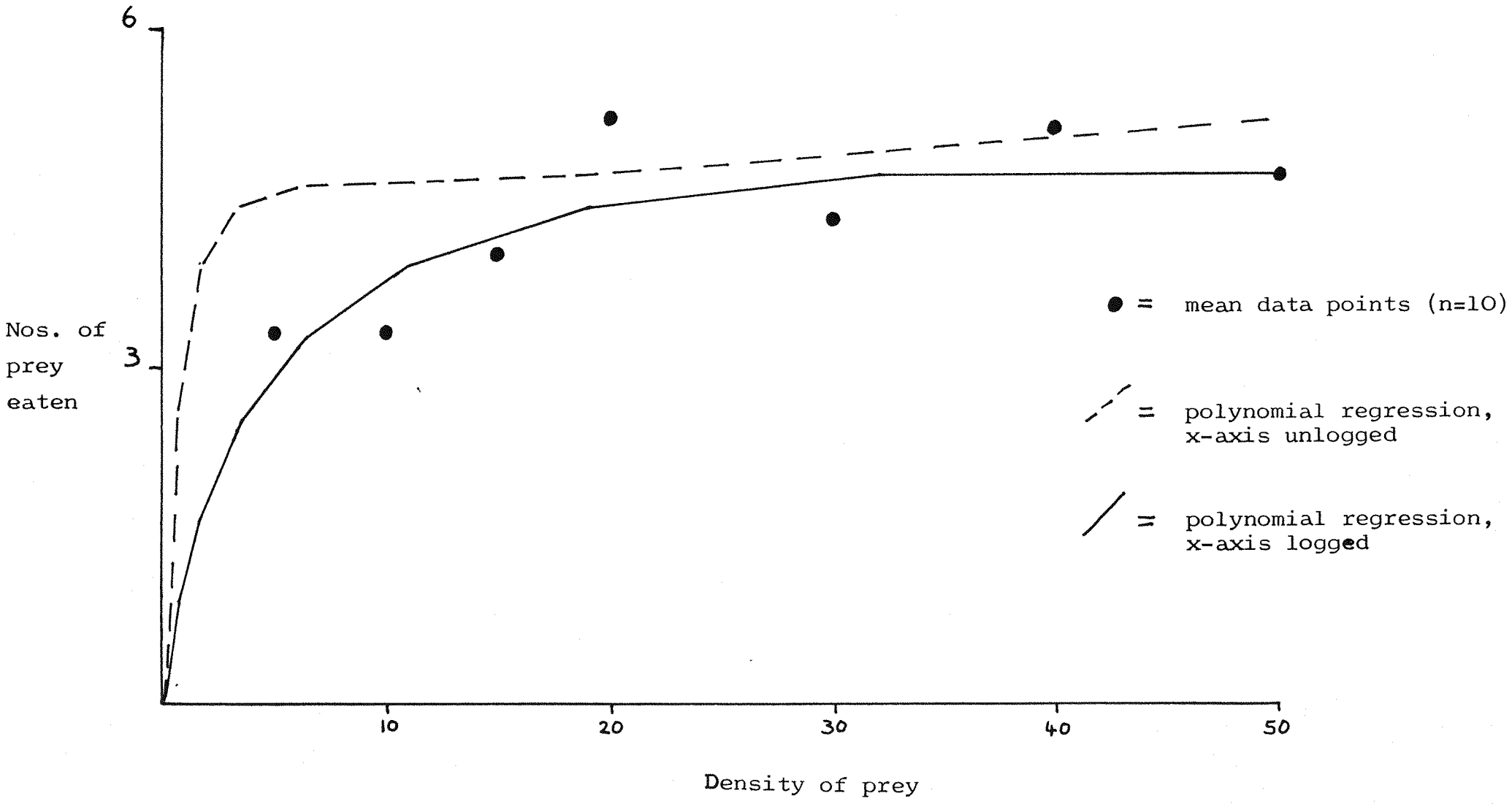
These equations describe curves which have (the degree of the equation - 1) bends in them; a second degree equation is a curve with one bend in it. However the fitting of an eighth degree equation, for instance, does not mean that the data are best fitted by a curve with seven bends. The analysis will fit the equation to the data until no more data points remain; at this stage any number of bends up to the maximum for a polynomial of that degree may have been fitted. This points to one of a number of problems with this type of analysis which will now be dealt with.

1. Logging of data

In most cases it will be desirable to log the x-axis for computational reasons. As the program raises the values of x to successively greater powers rounding errors in the regression calculations become unavoidable, these are considerably reduced by the use of logs. This will also be the case if it is wished to use the polynomial equation in further calculations (see 2. below).

There is another reason for logging the x-axis which is particularly relevant to functional responses. Often the responses obtained for invertebrates rise sharply (see Hassell et al. 1977) so that most of the data go to form a long assymptotic tail to the curve. The curves generated by polynomial regression are not of this form and if the experimental response does consist mainly of this assymptotic region then the fit will not be good. This can be overcome by logging the x-axis which has the effect of contracting the assymptotic "tail" allowing the close fitting of a polynomial curve to the data. This process is shown in Figure 4.6 for the example of a functional response to size IV aphids being fitting with curves based on logged and unlogged values of x. The fit of both curves is reasonable in the assymptotic region of the response but for unlogged data the fit in the all-important rising area of the response is bad. For the functional responses to prey of size I, II or III the shape of curve fitted actually changes when the x axis is logged.

Fig. 4.6 The fit of unlogged and logged polynomial regression lines to the functional response data for size IV aphid prey



2. The degree of polynomial required

As was shown earlier, whether or not raising the power of the polynomial increases the goodness of fit can be statistically tested. For the purposes of identifying type II or III response curves this may be too rigorous. It is only necessary to find a point of inflexion between zero and the response assymptote to indicate a type III rather than a type II response. To do this is mathematically easy for a third degree polynomial but rapidly becomes more complicated with higher order polynomials leading to the necessarily imprecise and time consuming use of iteration or curve sketching to find the inflexion.

The fitting of curves on a log scale to the four functional responses was tried using up to third, fifth and eighth degree polynomial regression equations. These curves were compared on the basis of the values they gave for the point of inflexion (if any) in the response curve. The points of inflexion were found in the following way:

For each functional response three polynomial equations were produced of the form

$$Y = A + B X + B^2X^2 + B^3X^3 + \ldots\ldots + B^nX^n \qquad (1)$$

The first differential coefficient of this equation is:

$$\frac{dY}{dX} = B + 2B^2 X + 3B^3 X^2 + \ldots\ldots + nB^n X^{n-1} \qquad (2)$$

(from which can be derived the maxima and minima of the function).

By differentiating (2) we obtain the second differential coefficient:

$$\frac{d^2Y}{dX^2} = 2B^2 + 2.3\ B^3 X + \ldots\ldots + n(n-1)\ B^n X^{n-2} \qquad (3)$$

The values of X which when substituted into (3) lead to $d^2Y/dX^2 = 0$ are the points of inflexion for the function. These

values can be found easily (by solving the roots of (3)) if the original equation (1) is a fourth or lower degree polynomial. For higher degree polynomials a process of iteration is required.

Statistical comments

The values of X (density of prey) and Y (number of prey eaten) for the points of inflexion for the four functional responses when analysed with polynomials of increasing degree are given in Table 4.3. The table also includes values of X and Y to show where these regressions intercept the X-axis. The F-ratios and corresponding significance levels for the regressions are given along with the R^2 values.

Intuitively these regressions should pass through the origin; a straight line regression can be constrained to do this and then analysed statistically (Snedecor & Cochran 1967). This is not applicable to polynomial regression, so the curves were biased towards zero by including zero points in the data set for each response. The same number (10) of points were included at zero as at other densities. All the fitted curves intercepted the X-axis very close to the origin implying that they describe the functional responses adequately. Changing the degree of polynomial used did not greatly alter the intercept (see Table 4.3).

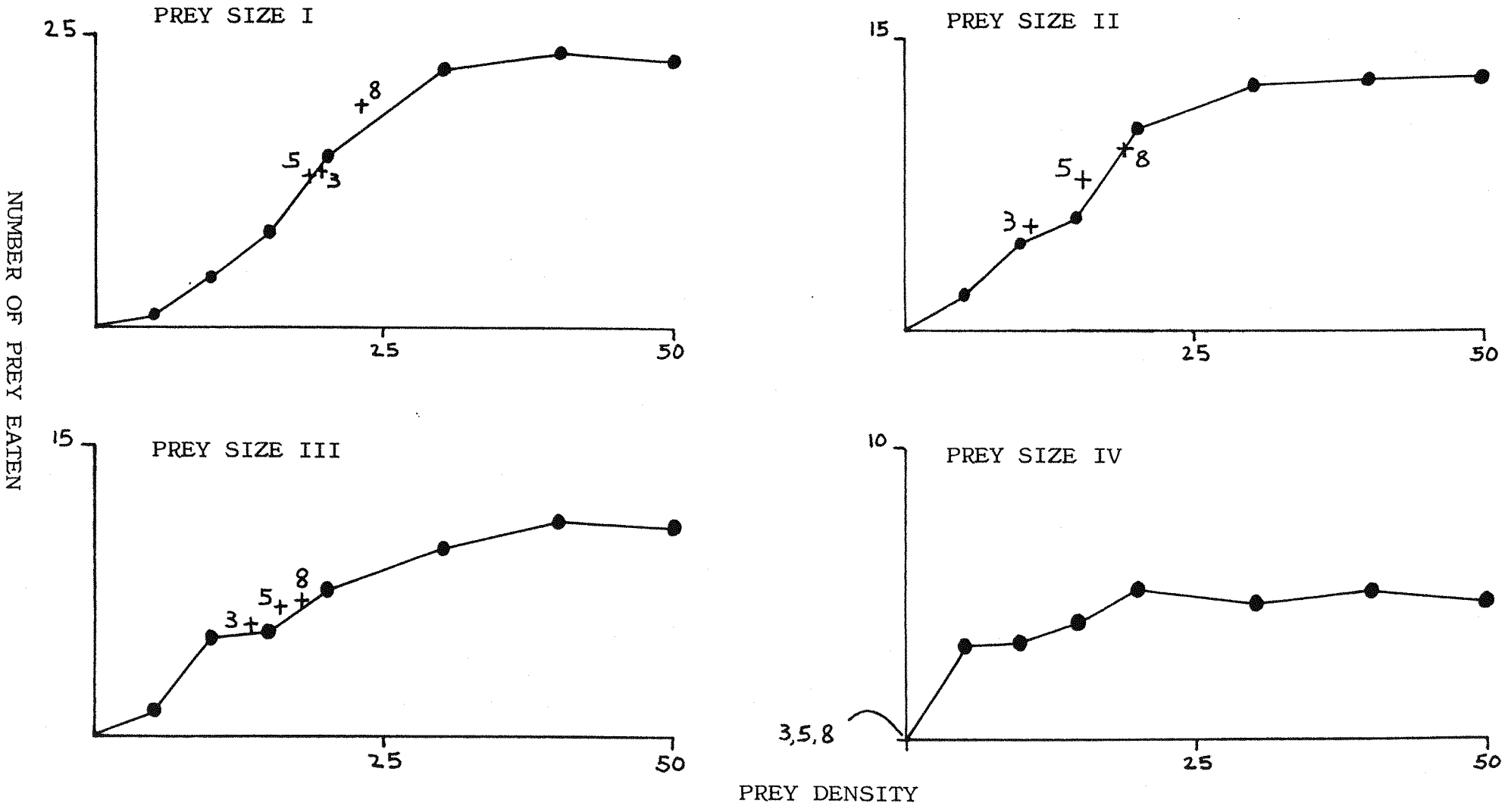
Curves describing type II or III responses differ because the latter contain a point of inflexion; these points were found for all the curves fitted to the data by the methods described earlier. The curves describing the functional responses for prey of size I to III all have points of inflexion within the range of the responses (i.e. they are type III). The curve describing the response to size IV prey has a point of inflexion at the origin but not over the range of the response (i.e. it is type II). These results were reproduced consistently with changing degree of polynomial (see Fig. 4.7); variations in the precise coordinates of the point of inflexion are probably due to slight differences between the curves fitted and to rounding errors where iterative calculation was needed to obtain the points of inflexion.

Comparison of R^2 values at each prey size with changing degree of polynomial used shows that the goodness of fit of the line increases

Table 4.3 Summary table of polynomial regressions of different degree of functional response data from A. dorsale feeding on four different sizes of cereal aphid prey

Degree of polynomial	Intercept near origin	Point of inflexion	d.f.	F-ratio	Significance level of F-ratio	R^2
			PREY SIZE I			
3	0, 0.159	19.5, 13.6	3, 86	93.0	$p < 0.001$	0.78441
5	0, 0.518	18.3, 13.0	3, 86	102.0	$p < 0.001$	0.78066
8	0, 0.031	27.8, 19.1	4, 85	81.5	$p < 0.001$	0.79326
			PREY SIZE II			
3	0, 0.007	10.7, 5.5	3, 87	61.6	$p < 0.001$	0.67989
5	0, 0.152	15.5, 7.7	3, 87	64.4	$p < 0.001$	0.68946
8	0, 0.062	19.3, 9.3	4, 86	48.3	$p < 0.001$	0.69215
			PREY SIZE III			
3	0,-0.0008	13.4, 5.6	3, 91	46.8	$p < 0.001$	0.60664
5	0,-0.006	16.3, 6.6	3, 91	46.8	$p < 0.001$	0.60686
8	0,-0.019	18.1, 7.0	3, 91	46.9	$p < 0.001$	0.60716
			PREY SIZE IV			
3	0, 0.016	0, 0.0	2, 77	15.4	$p < 0.001$	0.28654
5	0, 0.036	0, 0.04	2, 77	15.5	$p < 0.001$	0.28659
8	0, 0.036	0, 0.04	2, 77	15.5	$p < 0.001$	0.28659

Fig. 4.7 The points of inflexion for third, fourth and eighth degree polynomial regressions on the functional responses of A. dorsale to different sized aphid prey.



+ = point of inflexion

3,5,8 = degree of polynomial fitted

= mean points of raw data

as the degree of polynomial increases. R^2 is a measure of correlation and should not therefore be used for comparing regressions but using F-ratios was not always possible because the degrees of freedom changed as the number of terms in the polynomial changed. The F-ratio tests on the regressions (Snedecor & Cochran 1967) show that the fit of the polynomial curve is good ($p < 0.01$) whether a third or up to an eighth degree polynomial was used.

For the purposes of characterising functional responses (i.e. determining the point of inflexion) the calculations are more simple for third compared to higher degree polynomial equations. So because curves fitted are essentially the same for different degree polynomials it should only be necessary to fit a third degree polynomial to distinguish between type II or III functional responses.

The physical and behavioural basis of the observed functional responses.

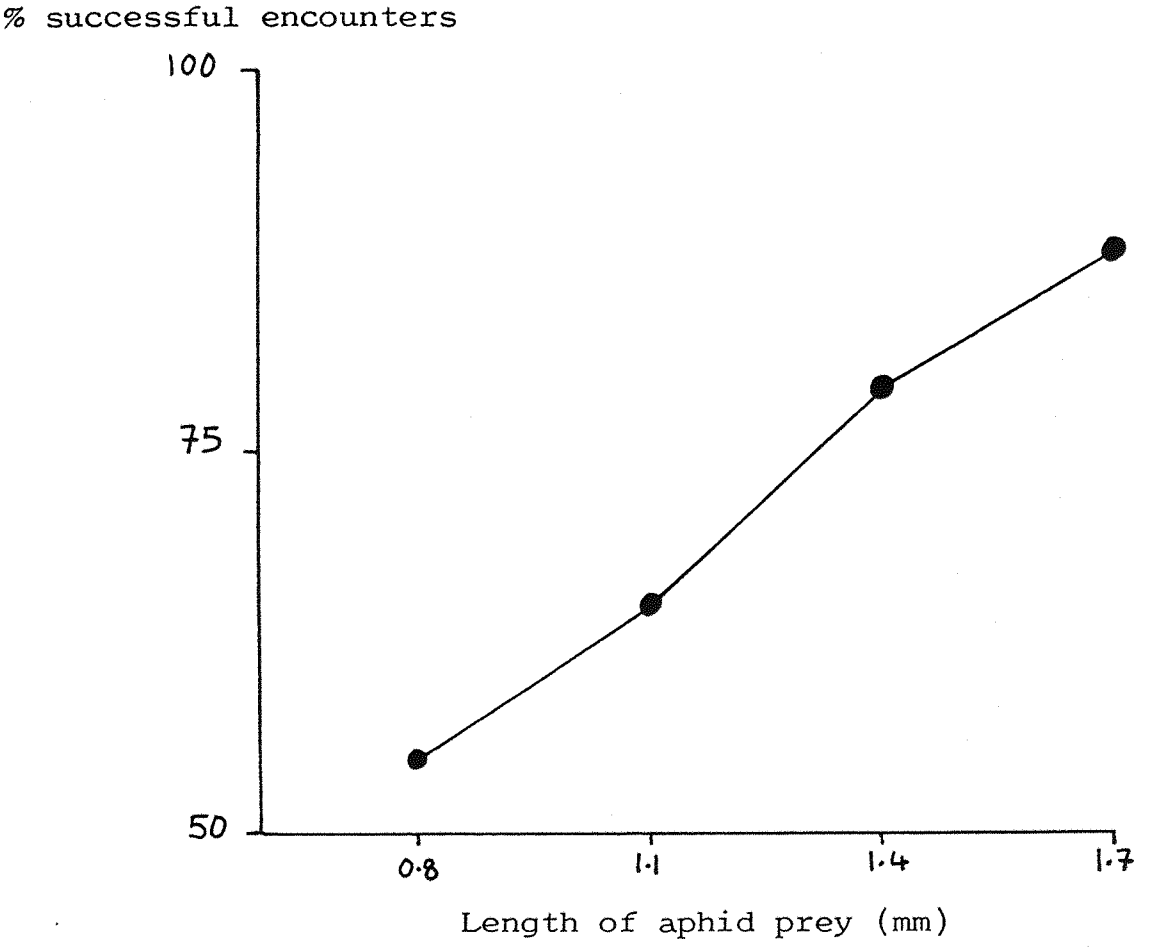
A functional response will be based on a number of factors such as size of prey, ability of prey to escape, appetite of the predator and so on. Two easily recorded statistics which reflected these factors were the percentage successful encounters and handling time. These were defined as:

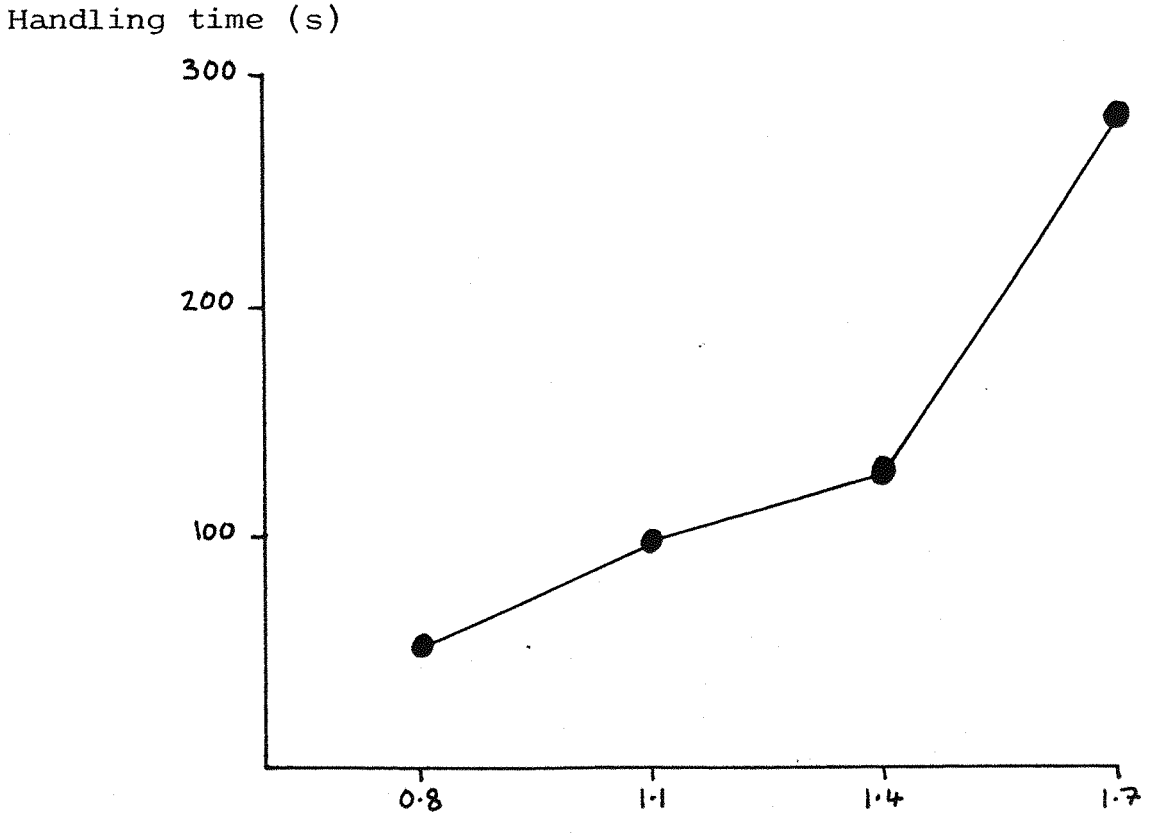
percentage successful encounters; the proportion of physical contacts where the predator detected the prey which ended in the prey being killed. Detection was taken as being when the predator attempted to search for or attack the prey after the initial contact.

handling time; the time from the initial physical contact with the prey to when the predator moves off in search of further prey items.

The way in which these two statistics vary with prey size (Fig. 4.8) may be largely explained by simple physical properties of the prey. Cereal aphids show incomplete metamorphosis meaning that nymphs have the same body form as adults making comparison of physical characteristics between different sized aphids possible. A. dorsale detects prey by touching them with its antennae (Chapter 3.8) so a simple measure of the prey profile i.e. length or area, as a measure of how "noticeable" the

Fig. 4.8 The relationship between % successful encounters or handling time and the length of the aphid prey





prey is may account for the changing successful encounter rate with prey size. Similarly, because cereal aphids are small compared with the beetle and have no obvious defence, a simple estimate of the aphid volume may account for the change in handling time with aphid size.

To assess these hypotheses, the upper limits of each aphid prey size class (0.8, 1.1, 1.4 and 1.7 mm) were simply squared or cubed to give estimates of area or volume respectively. Regressions of length, $(\text{length})^2$ and $(\text{length})^3$ against the corresponding mean percentage successful encounters or handling times were made (Table 4.4). These showed that, as predicted, percentage successful encounters was most strongly related to a simple measure of prey length, and handling time to a simple measure of prey volume. The regressions were significant although only the four mean values of the dependent variable were used per regression (hence the low d.f.).

The hypothesis that percentage successful encounters and handling times are based on simple physical properties of the prey is further supported by comparing values of each statistic obtained at low prey density (ten aphid prey per box) with those obtained at high prey density (50 aphid prey per box). Pairwise comparisons were made of percentage successful encounters for the different sized aphid prey at low and high density. A Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to compare the encounter rates as this test makes no assumptions about the underlying frequency distribution of these encounters. The test showed no significant difference between percentage successful encounters at high or low aphid densities (Table 4.5).

A similar comparison was made for handling time by calculating separate regression lines of prey length vs. handling time for the two prey densities (Table 4.6). These regression lines were then compared using F-ratio tests (Snedecor & Cochran 1967). The variances of the two data sets were compared and just exceeded the $p = 0.05$ F- value meaning that they were different. This decreases the sensitivity of the test on the regression slopes because if the slopes are found to be not significantly different this could be because they really are not different or because the difference between the variances masks any difference in slope.

Table 4.4 The regression relationship between handling time or percentage successful encounters and aphid length, $(length)^2$ and $(length)^3$

Parameters		Intercept	Slope	d.f.	F-ratio test values for the regressions	Significance level of F-ratio test
Percentage successful encounters (arcsin transform) vs. -	length	27.5	24.8	1 & 2	323	$p < 0.005$
	$(length)^2$	42.0	9.9	1 & 2	201	$p < 0.005$
	$(length)^3$	46.8	4.9	1 & 2	57	$p < 0.025$
Handling time vs. -	length	-159.7	293.3	1 & 2	13	NS
	$(length)^2$	-24.9	98.1	1 & 2	22	$p < 0.05$
	$(length)^3$	19.5	50.6	1 & 2	41	$p < 0.025$

Table 4.5 The comparison of percentage successful encounters or handling times at low and high aphid prey densities

Parameter	Low Prey Density (10 aphids/arena)	High Prey Density (50 aphids/arena)	Statistical Test used	n or d.f.	Probability level for the test
Percentage successful encounters	Average 73.4 (n = 13)	Average 69.9 (n = 13)	Wilcoxon matched-pairs signed-ranks	n = 13 (pairs)	NS
Handling Times (s)	Intercept $\pm$ S.E. -137 $\pm$ 38	Intercept $\pm$ S.E. -167 $\pm$ 50	F-ratio test on variances	63 & 63 d.f.	$p \simeq 0.05$
	Slope $\pm$ s.e. 218 $\pm$ 30	Slope $\pm$ s.e. 250 $\pm$ 39	F-ratio test on slopes	1 & 126 d.f.	NS
	(1 & 63 d.f.)	(1 & 63 d.f.)	F-ratio test on intercepts	1 & 127 d.f.	NS

Table 4.6 The change in the relationship between % successful encounters or handling time and sections of the functional response with increasing aphid size

Parameter	Density range used (Y)	Intercept	Slope	d.f.	F-ratio	Significance level
Percentage successful encounters (X) (X-axis is arcsin transformed)	5-20	13.2	-0.134	1 & 2	35	$p < 0.05$
	10-30	27.7	-0.338	1 & 2	27	$p < 0.05$
	15-40	40.4	-0.516	1 & 2	21	$p < 0.05$
	20-50	50.4	-0.659	1 & 2	20	$p < 0.05$
Handling Time, s (X) (X & Y axes logged)	5-20	3.29	-0.342	1 & 2	62	$p < 0.05$
	10-30	5.03	-0.638	1 & 2	3818	$p < 0.001$
	15-40	5.86	-0.766	1 & 2	2044	$p < 0.001$
	20-50	6.46	-0.866	1 & 2	9528	$p < 0.001$

N.B. X is the mean percentage successful encounters or mean handling time for each aphid prey size used.

Y is the mean number of aphids eaten of each aphid size for the density range shown.

As the difference in variances is only just significant and the probability associated with the slopes being the same is very high ($p > 0.20$) it is reasonable to assume that the slopes of the lines are the same. The F-ratio test for the difference between the intercepts of the two lines showed that they were not significantly different. Despite the loss of accuracy of the regression analysis due to the difference in variances it can be concluded that the handling time for a prey item does not differ with changing prey density.

The percentage successful encounters and handling times, although independent of prey density, will affect the shape of the functional response to each prey size. It might be expected that percentage successful encounter would have most effect at low prey densities where, because the predator is discovering few prey, it would be the pre-eminent factor controlling numbers eaten. Conversely handling times would be the main factor controlling numbers eaten at higher prey densities where the predator runs short of time in which to eat more prey.

To test this a series of regressions were performed which compared the average number of aphid prey eaten over a small section of the functional response with either the corresponding percentage successful encounters or the handling times, the four points of each repression line being provided by the four different sizes of aphid prey. According to the predictions of the previous paragraph the significance of the regression with percentage successful encounters should decrease as progressively higher prey density sections of the functional response are looked at. The converse should occur with handling times. This was the result obtained (Table 4.6) and while the trend is not as dramatic with percentage successful encounter as with handling time it is clear.

In retrospect it is easy to see that handling time will be closely linked to the functional response assymptotes because although it is independent of prey density the trials themselves are limited in time. But for percentage successful encounters the link will not be so close because the encounter rate is not related to the prey density or the

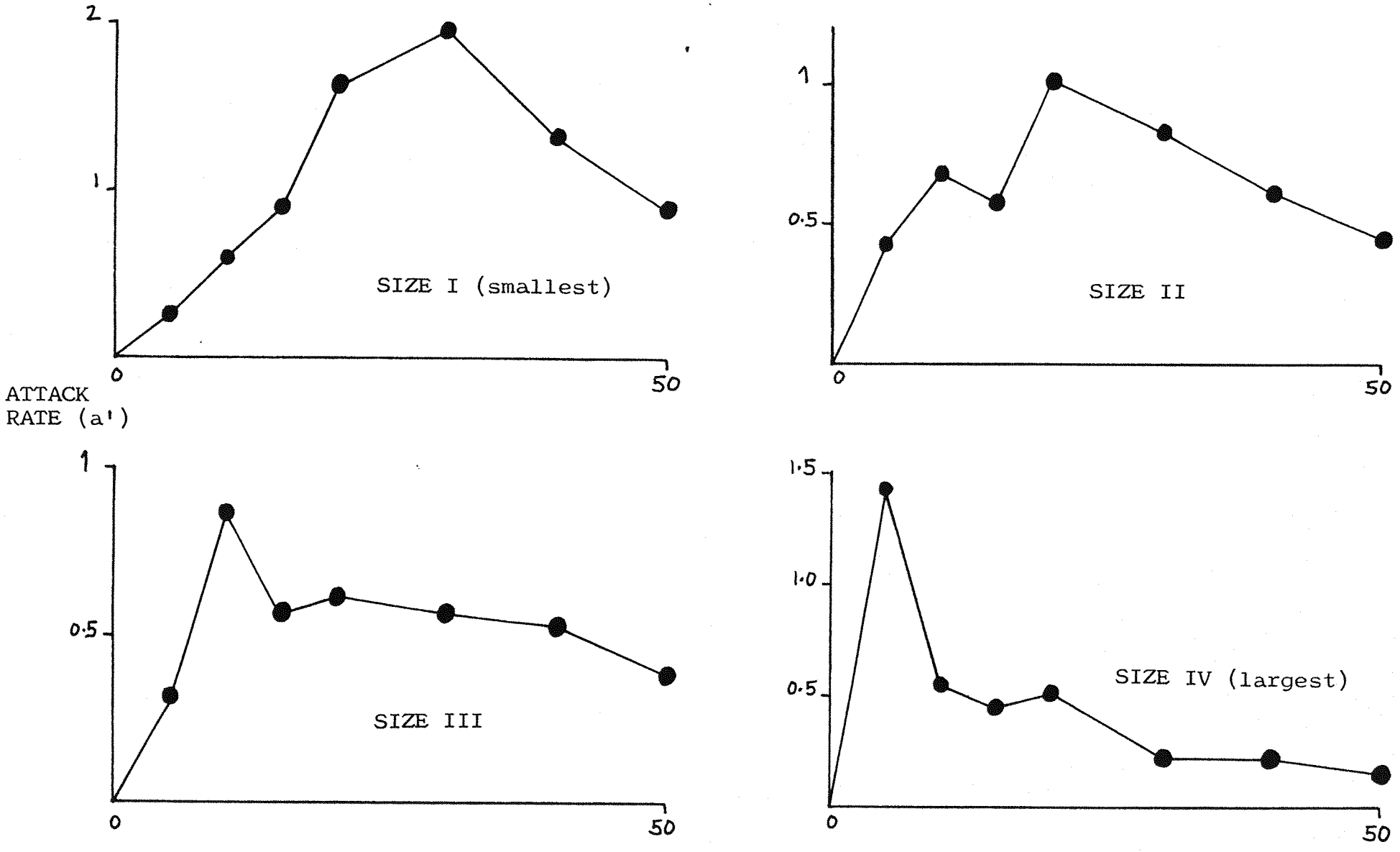
time period of the trial. The regressions suggest that percentage successful encounters are generally related to numbers of prey eaten over the whole response and that handling time is most closely related to or even controls the assymptote of the response.

A classical model of a type II functional response is the "Random predator" equation of Rogers (1972) which essentially frames the response in the two components of handling time (T_h) and attack rate (a'). These can be shown to be constants for a type II response but one or other (or both) must vary to produce a type III response. Hassell, Lawton & Beddington (1977) assumed that T_h was constant in their examples of type III responses and then used the random predator equation to calculate the changing value of a', which they then graphed. For A. dorsale, measurements of the handling time at high and low prey density showed that it remained constant meaning that it is the attack rate which changes with density. The observed values of T_h for the different aphid sizes were substituted into the random predator equation and graphs plotted of the change in a' with prey density (Fig. 4.9). As prey size increases, the attack rate reaches its peak at lower densities of prey and the actual peak value seems to decline. The latter observation is to be expected because the attack rate is partly calculated from the number of aphids eaten which decreases with increasing aphid size.

Large aphids are more easily caught than small ones and are also probably more easily detected than small ones. It is not surprising then that the attack rate is high from the start for large aphids and then declines with handling time effects. While for small aphids a proportion of the beetles will not detect the prey and this will lower the attack rate. As the density of small aphid prey increases, an increasing proportion of the beetles are "switched on" to their presence resulting in an increasing attack rate. As with large size prey this attack rate falls off again as total time spent handling limits the number of prey eaten.

If the above is true the variance in numbers eaten should be high when only a few beetles are finding prey but should decrease as

Fig. 4.9 The change in the attack rate (a') of A. dorsale with increasing prey density for four sizes of aphid prey.



more of the beetles find prey. The variances were plotted on a relative scale, the measure of variance being the standard error of the numbers of prey eaten divided by the mean of the numbers eaten for each aphid size at the different prey densities (Fig. 4.10). The decline in variance of numbers eaten becomes less marked with increasing prey size as expected, and the attack rate graphs show that the maximum rate occurs at progressively lower prey density with increasing prey size.

Summary

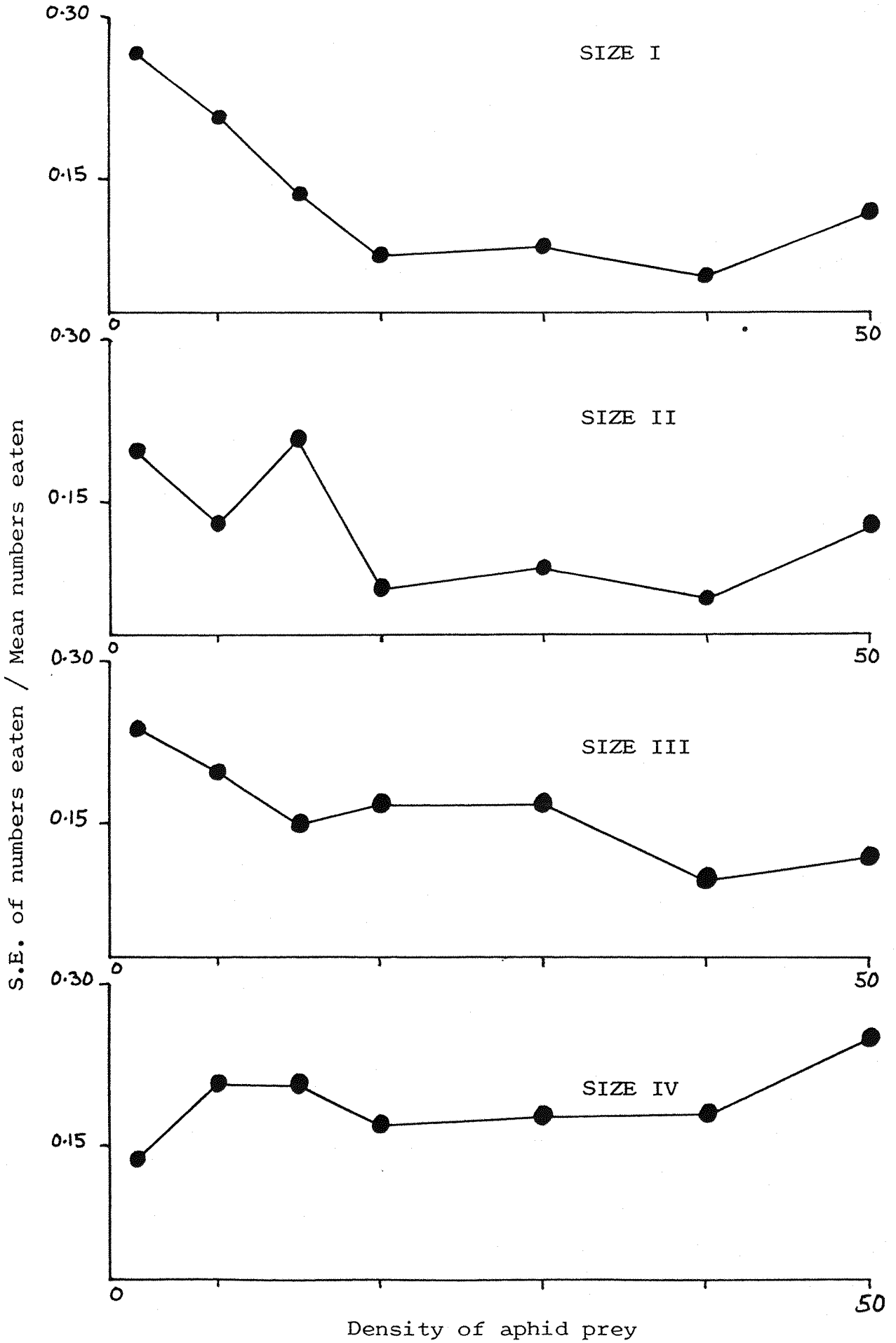
Visual inspection of a graph of the four functional responses suggested that there was a difference in shape between the response to size IV prey and the responses to the other three prey sizes. This was confirmed by plots of ln (survivors) vs. number of prey eaten and by the polynomial regressions; both techniques identified the responses to prey sizes I, II & III as type III and the response to prey size IV as a type II response. This type of result was predicted by Hassell *et al.* (1977) who suggested that sigmoid functional responses were most likely to be found when predators were confronted with *small* or non-preferred prey.

A. dorsale can show a type III response to prey, this is rapidly attenuated by prey size, and aphids may be among the smaller prey items captured in the field. The type III response may also be attenuated by prey which can escape more actively than aphids. The basis of the response appears to be that *A. dorsale* overlooks small prey at low densities. As prey density rises, initial encounters with the prey become more likely and the beetle is then stimulated to search for more prey. This stimulation to search causes the upturn in the functional response while handling time controls the levelling off of the response.

4.6 The length of time food is retained in the gut by *A. dorsale*

Over short periods the voracity of a predator can be measured by obtaining its functional response and deriving the handling time and attack rate parameters. Over longer periods satiation becomes

Fig. 4.10 The change in variation of number of prey eaten with changing prey density measured by the index: (S.E. of nos. eaten)/(Mean of nos. eaten).



increasingly important and voracity may be better measured by estimating the through-put of the predator's gut.

A. dorsale ingests parts of the prey's cuticle, making it possible to dissect the beetle and find identifiable prey remains in the gut. By dissecting individuals at increasing times after a period of controlled feeding it was possible to assess when solid particles of prey had left the gut. This was used as an initial measure of the through-put rate of food and hence as a crude estimation of the time between feeds.

At each sample interval after the initial feed five A. dorsale were dissected and aphid remains recorded on a presence/absence basis in three distinguishable sections of the gut (Fig. 4.11). As might be expected when recording on a presence/absence basis the decline in aphid remains when it occurred was rapid. As the data were non-parametric the Mann-Whitney U-test (Siegel 1956) was used to assess this decline objectively.

For each beetle the total number of aphid remains in the three gut sections were summed and the following between-sample comparisons made:

A) 3 h sample vs. 27 h sample
B) 27 h sample vs. hypothetical "no remains in gut" sample

For both comparisons the null hypothesis was "no difference" between the samples in the number of aphid remains recorded per beetle.

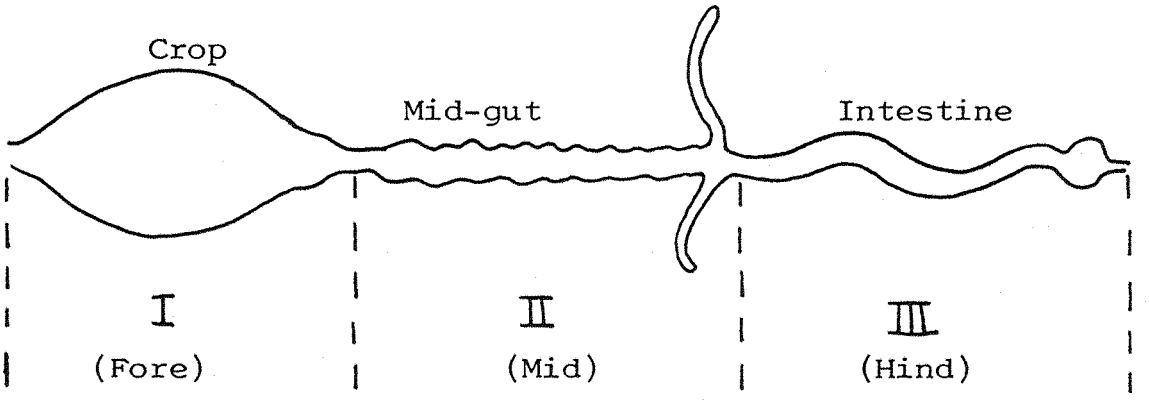
The probabilities associated with this null hypothesis for the Mann-Whitney U-test were:

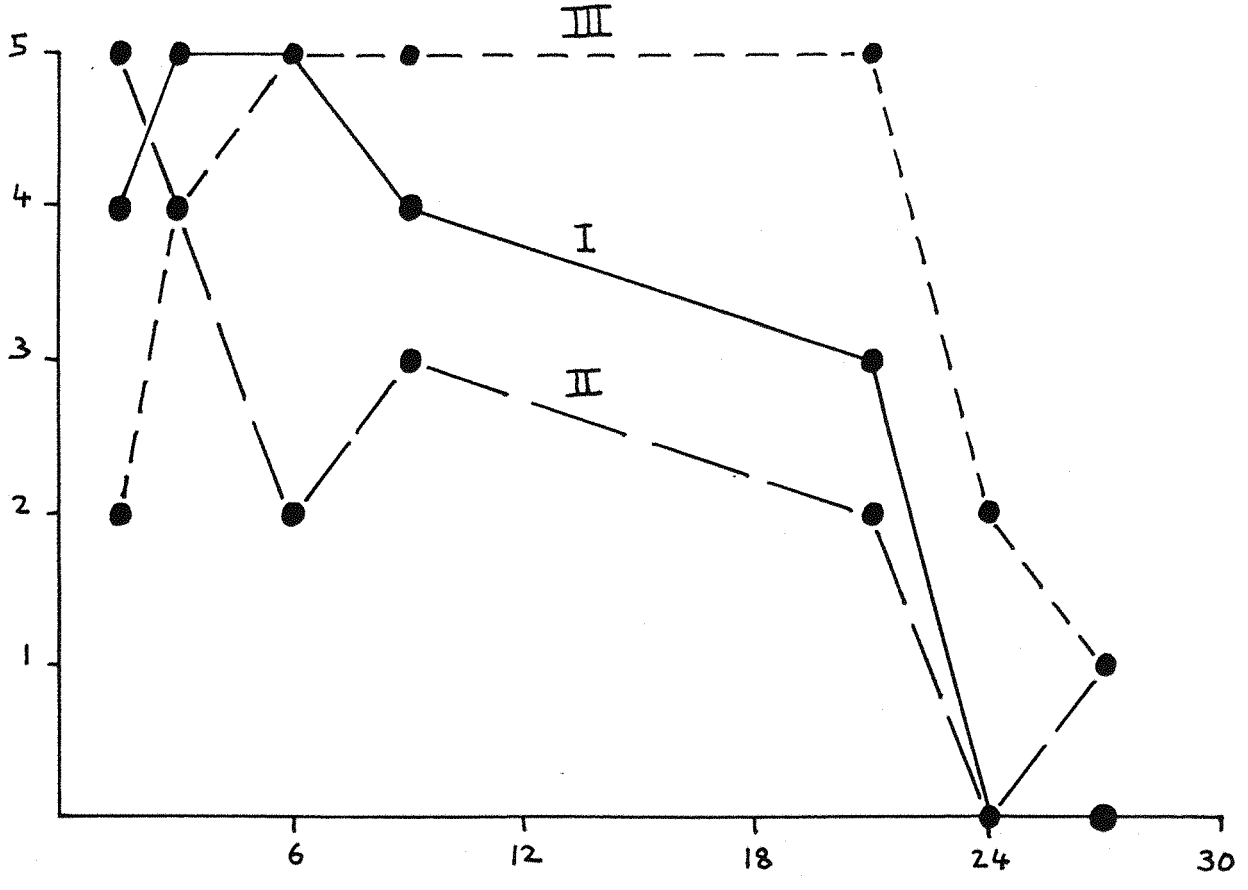
A) $p < 0.008$
B) $p > 0.133$

Using the $p = 0.05$ criterion of significance, significantly more aphid remains were recorded in the 3 h sample than the 27 h sample and

Fig. 4.11 The presence of aphid remains in three sections of the A. dorsale gut over a 27 h period after feeding

The 3 functional-based divisions of the gut in which aphid remains were recorded (see Section 2.6):





the 27 h sample did not differ significantly from a hypothetical sample containing no aphid remains.

The observed decline to no solid aphid remains in the A. dorsale gut after 27 h was statistically significant.

4.7 The effect of temperature on the voracity of A. dorsale

The results of the previous Section (4.6) showed that the solid remains of prey ingested by A. dorsale were excreted after about 24 h. If the absence of solid remains means that the beetle's appetite has returned this result implies that A. dorsale would eat its fill every day rather than feeding and then being satiated for some days afterwards. This assumption of an appetite renewed daily is also made in theoretical work which relates functional responses to predator-prey population processes (Murdoch & Oaten 1975; Hassell et al. 1976; Hassell 1978). In most cases the functional responses have been determined in the laboratory over a few hours (see Hassell 1978 for a summary). In both cases this assumption has obvious implications for the effectiveness of predators in controlling prey.

In this experiment the voracity of A. dorsale has been assessed daily over several weeks. Voracity was assessed in relation to temperature because temperature is generally the most important variable affecting the activity of poikilotherms (Gilbert et al. 1976; Barlow & Dixon 1980; Carter et al. 1980). The night time temperatures to which A. dorsale is exposed during its field active period range from $0^{o}C$ to at least $15^{o}C$. It would not be unusual for physiological processes to double or treble in rate over this range of temperature (Schimidt-Nielsen 1975) and voracity is physiologically based.

In this experiment a range of temperatures from $0^{o}C$ to $19^{o}C$ was used, consumption of prey being recorded for at least 10 days at each temperature (except $0^{o}C$, see later). Prey items were provided in large excess to the beetles' requirements to ensure that temperature and not prey depletion affected voracity.

The first trials (at 15.4°C and 19°C) were maintained for 3-4 wk so that changes in voracity with time could be examined. Analysis of the results of these trials showed that voracity did not change with temperature so further trials were carried out over much shorter periods (10 days). Regression analysis of number of prey eaten against time for each sex at each test temperature was used to show how voracity changed with time (Table 4.7). With one exception (females; 15.4°C) voracity did not change significantly with time (using the F-ratio regression test of Snedecor & Cochran 1967). There was no obvious reason for the highly significant increase in voracity of female A. dorsale at 15.4°C. As seven of the eight regressions were not significant it was assumed that assessments of voracity were not biased by trial lengths varying between about 1 and 4 wk.

Two further forms of analysis were carried out on the data; a nested (or hierarchical) analysis of variance to examine differences between the sexes and between individual beetles and a regression analysis to obtain an equation for the relationship between voracity and temperature.

The nested analysis of variance (Table 4.8) showed that for temperatures up to about 15°C there were no differences in numbers of aphid prey eaten either between sexes or between individuals (using the usual F-ratio test with a null hypothesis of no significant difference between the variances, Snedecor & Cochran 1967). At 19°C female A. dorsale (12.2 aphids/day) ate significantly more than males (9.8 aphids/day); variation between individuals was also higher but not significantly so at this temperature.

At 0°C none of the beetles tested were capable of movement and to avoid unnecessary mortality of test animals the trial was curtailed after two days. The results were not used in the regression analysis (see below) because they might bias the important temperature threshold below which the beetles could not feed (the intercept of the regression line with the X-axis).

Table 4.7 Regression analysis of A. dorsale voracity on time at different temperatures

Average test (°C) temperature	Sex	Equation of the line	Number of Observations	Significance of Regression (F-ratio test)
5.4	♂	Y = -0.17X + 2.61	50	NS
	♀	Y = -0.03X + 1.84	50	NS
8.9	♂	Y = -0.08X + 3.67	55	NS
	♀	Y = -0.07X + 4.10	55	NS
15.4	♂	Y = 0.01X + 5.20	135	NS
	♀	Y = 0.14X + 4.06	135	$p < 0.01$
19	♂	Y = -0.005X + 9.88	115	NS
	♀	Y = 0.15X + 11.80	115	NS

N.B. Y = number of aphids eaten

X = time from start of trial (days)

Table 4.8 A nested analysis of variance to test for differences in effect of temperature on voracity between individuals and between the sexes of A. dorsale

Average Test Temperature (^{o}C)	Numbers of Individuals used ♂	♀	Total number of test days	Total number of observations ♂	♀	Significance of the source of variation - Between sexes	Between individuals	
0	5	5	2	10	10	0	0	*
5.4	5	5	10	50	50	NS	NS	
8.9	5	5	11	55	55	NS	NS	
15.4	5	5	27	135	135	NS	NS	
19	5	5	23	115	115	$p < 0.05$	NS	

* Individuals were not capable of movement at this temperature, so voracity for both sexes was zero.

Three regressions of voracity on temperature were carried out, these being males, females and males + females combined. All three produced highly significant regression lines (Table 4.9). The nested analysis of variance showed that there was a difference in voracity between the sexes only at 19°C. The separate male and female regression lines were compared to show whether this reflected a basic sex difference for the relationship between temperature and voracity as a whole.

An analysis of variance was made of the regression lines (Snedecor & Cochran 1967) to produce three F-ratios which compared:

(1) The residual variances of the lines.
(2) The slopes of the lines.
(3) The intercepts of the lines.

There are two important statistical points to note here: if the residual variances are significantly different this makes the test comparing the slopes less sensitive, i.e. if subsequently the slopes prove to be different this is a "true" result, if they are not different this could be either because the slopes really are not different or because their different variances mask the difference in slopes.

Comparison of intercepts on the Y-axis is possible because the regression is formed as Y on X; in this case we wish to compare intercepts on the X-axis (i.e. the temperatures at which male and female A. dorsale stop eating) which is not possible statistically (Snedecor & Cochran 1967; Sokal & Rohlf 1969).

The analysis showed for male vs. female A. dorsale that:

1. Residual variances

The F-ratio values used to compare the variances were:

$$\frac{17.84}{14.11} = 1.26 \text{ with } 353 \text{ \& } 353 \text{ d.f.}$$

Table 4.9 Regression analysis of *A. dorsale* voracity on temperature

Group	Equation of the line	Number of Observations	Significance of regression (F-ratio test)
MALES	$Y = 0.555X - 1.783$	355	$p < 0.001$
FEMALES	$Y = 0.702X - 2.751$	355	$p < 0.001$
MALES AND FEMALES	$Y = 0.628X - 2.267$	710	$p < 0.001$

N.B. Y = number of aphids eaten/day
X = test temperature (^{o}C)

For 353 and 353 d.f. the $p = 0.05$ level of significance for an F-test is 1.18.

The variances are significantly different.

2. Comparisons of slopes

The F - ratio used to compare the slopes was:

$$\frac{\text{variance between slopes}}{\text{variance for pooled slopes}} = \frac{33.8}{15.98} = 2.12 \text{ with } 1 \text{ \& } 706 \text{ d.f.}$$

For 1 and 706 d.f. the $p = 0.05$ level of significance is 5.02.

The slopes are not significantly different.

Statistical comparison of the x- intercepts of the male and female regressions is not possible but the values for the intercepts are given by:

Male A. dorsale

$$Y = 0.555X - 1.783$$

If $Y = 0$ then $\quad X = \frac{1.783}{0.555} = 3.21$

Female A. dorsale

$$Y = 0.702X - 2.751$$

If $Y = 0$ then $\quad X = \frac{2.751}{0.702} = 3.92$

The difference in intercept is small ($0.7^{\circ}C$) and is even less important because the two regression lines actually cross at (6.59, 1.87) making differences between males and females across the whole range of test temperatures ($0 - 19^{\circ}C$) slight.

Between trials at the different temperatures the adults were starved to maintain their reproductive immaturity. At the end of the temperature trials the adults were dissected to assess their reproductive state and sex (for the regression analysis). All the adults were at

State I, the sexually immature stage. Of the 10 adults half were male and half female.

The reproductive state of the adult A. dorsale did not change through out the period of the test; also, regression analysis showed that voracity was constant from day to day at each test temperature. This means any change in voracity should be due only to a change in test temperature.

Further regression analysis showed significant relationships between number of aphid prey eaten per day and temperature for all the adults and for males and females separately. All three regressions showed that for every increase of $1^{o}C$ in temperature the adults ate an extra 0.6 aphids per day. Although not conclusive, comparison of the male and female regression lines suggested that there was no difference between male and female voracity.

A nested analysis of variance showed that there was no significant variation between individuals and that for three of the four test temperatures there was no difference between the sexes. Only at $19^{o}C$ was there any difference.

4.8 The effect of reproductive development on the voracity of A. dorsale

During the field active period both sexes of A. dorsale go through dramatic changes in internal physiology and morphology (Chapter 7.2). In summary, both sexes lose the fat bodies predominant in the body cavity at the start of the field season with a corresponding increase in the size of the reproductive organs. Trials showed that adults could be maintained in the laboratory in a pre-reproductive state by a cycle of alternate feeding and starving (Chapter 2.1). The fat bodies alone cannot provide the necessary materials and energy for the development of the reproductive organs as happens in some other beetle species (Crowson 1981).

There are no clear examples in the literature of the quantitative differences in voracity that reproductive state can cause (Thiele 1977; Erwin et al. 1979). Qualitative work (Sunderland 1975; P.C. Jepson pers. comm.) has shown some differences between sexes and between

non-gravid and gravid females. It may be possible, therefore, that the stage of reproductive development could affect the voracity of A. dorsale throughout its field active period.

Three groups of A. dorsale were used to look at this:

(1) Individuals maintained at a reproductively immature stage in the laboratory (LAB I).

(2) Reproductively immature individuals recently collected from the field (FIELD I).

(3) Reproductively mature individuals from laboratory cultures (LAB M).

N.B. it was not possible to compare reproductively mature individuals collected from the field because of the difficulty of catching sufficient numbers of live individuals to be useful experimentally at the appropriate time (see Chapter 7 for numbers of live beetles caught overnight).

Individuals in each group were presented with aphid prey in excess and numbers of prey eaten recorded daily for 3 wk. At the end of this period individuals were dissected to record their sex and reproductive state. The aphids were third instar-to-adults and the experiment was conducted at 9°C, a rough average temperature for nights during late May and early June.

After dissection the beetles fell into the following seven categories:

			Label used in text
Group 1)	LAB I		
	10 individuals:	5 males	LAB I [♂]
		5 females	LAB I [♀]

			Label used in text
Group 2)	FIELD I		
	10 individuals :	5 males	FIELD I [♂]
		5 females	FIELD I [♀]
Group 3)	LAB M		
	20 individuals:	8 males (mature)	LAB M [♂]
		6 females (stage 2)*	LAB M [♀2]
		6 females (stage 3-5)*	LAB M [♀3-5]

*Five categories of reproductive development were defined for female A. dorsale (Chapter 7.2); for this experiment females were: immature (1), developing sexually but with no eggs possessing a chorion (2) or developing with eggs with chorion visible/fully developed (3-5). The division was made between females (2) and females (3-5) because in the former the adults still contain large fat reserves in the body cavity whereas in the latter these have largely been used up. This morphological difference may be reflected in voracity.

As with the temperature vs. voracity experiment (Section 4.7), trials were continued over several weeks with numbers of prey eaten recorded daily. Graphs of the change in numbers eaten per day over these weeks showed that during the first few days voracity changed considerably but after this settled to a more constant level (Appendix I). For the LAB I results this left a maximum of 10 days when numbers eaten appeared constant. It was necessary for analysis (see below) to have sample sizes and days per sample equal so 10-day sections were picked visually from all the graphs (Appendix I) to be used in comparing the reproductive groups and sexes. Regression analysis was performed on these 10-day sections to show statistically whether voracity was constant by showing whether the gradient of the fitted line differed from zero (Table 4.10). The analysis showed that for both sexes

Table 4.10 Regression analysis of numbers of aphids eaten per day (Y) on time (days) of trial (X) for A. dorsale at different stages of reproductive development

Reproductive Type	Sex	Intercept	Slope	d.f.	F-ratio	Significance Level
Laboratory immatures	♂	3.7	-0.08	1 & 48	0.64	NS
	♀	4.1	-0.07	1 & 48	0.21	NS
Field immatures	♂	5.8	-0.05	1 & 48	0.08	NS
	♀	6.0	-0.05	1 & 48	0.12	NS
Laboratory matures	♂	3.4	0.14	1 & 48	1.01	NS
	♀ (2)	4.1	0.30	1 & 48	0.53	NS
	♀ (3-5)	4.4	0.11	1 & 48	0.36	NS

in all the reproductive groups voracity did not change significantly over the 10-day visually-picked sections. This meant that inter-group analysis involved the simple comparison of a constant number of prey eaten per day rather than a more complex comparison of changing rates of numbers eaten per day.

The nested analysis of variance (Snedecor & Cochran 1967) was used to look at the difference in variation between individual beetles and between groups (the different sexes or reproductive groups). The computer program used for the analysis required that numbers of individuals within groups were the same and also that the number of samples per individual was the same. To achieve this, where numbers of individuals were different, individuals were randomly discarded from the larger groups e.g. when comparing LAB I ♂♂ with LAB M ♂♂ . The number of days recorded per individual was 10 in all cases, 10 consecutive days being picked for each reproductive group during which voracity remained constant (see earlier). Extra data were discarded from the analysis. The mean number of aphids eaten per day (Table 4.11) for each group used in the analysis was calculated from these 10-day sections of data.

There was no significant variation between individual beetles in any of the comparisons made using the nested analysis of variance; any differences were due to group variation alone.

The first nested analysis of variance compared the sexes within groups (Table 4.12) because no differences would allow combining of data within these groups making the between-group comparisons straightforward. The analysis showed no difference between the sexes or between individuals in any of the reproductive groups (including the LAB M group, whether it contained ♀ 2 or ♀ 3-5). Where applicable in the following analyses, male and female results were lumped together within reproductive groups.

The next analysis compared the reproductive groups (Table 4.13) to show whether immature beetles differed from mature beetles (i.e. LAB I vs. LAB M[♀ 2] and LAB I vs. LAB M[♀ 3-5]) and whether

Table 4.11 The mean number of aphids eaten per day (± S.E.) for each reproductive grouping for the data used in the nested analysis of variance

Reproductive Group	MALES	FEMALES	MALES & FEMALES
FIELD I	5.5 ± 0.48	6.24 ± 0.43	5.88 ± 0.32
LAB I	3.2 ± 0.29	3.70 ± 0.42	3.47 ± 0.25
LAB M (♀ 2)		4.66 ± 0.44	4.43 ± 0.30
LAB M (♀ 3-5)	4.2 ± 0.41	5.02 ± 0.50	4.61 ± 0.33

Table 4.12 Four nested analyses of variance to show the difference between sexes and between individuals within reproductive groups of A. dorsale in numbers of aphids eaten per day

Groups to be Compared	Variance between Groups (sexes) d.f.	F-ratio	Significance level	Variance between individuals d.f.	F-ratio	Significance level
FIELD I ♂ vs ♀	1 & 8	4.07	NS	8 & 90	1.43	NS
LAB I ♂ vs ♀	1 & 8	0.59	NS	8 & 90	0.293	NS
LAB M ♂ vs ♀ (2)	1 & 8	1.06	NS	8 & 90	0.542	NS
LAB M ♂ vs ♀ (3-5)	1 & 8	2.85	NS	8 & 90	0.543	NS

Table 4.13 A nested analysis of the variance between reproductive groups and between individuals in numbers of aphid prey eaten per day

Groups to be Compared	Variance between Groups d.f.	F-ratio	Significance level	Variance between individuals d.f.	F-ratio	Significance level
FIELD I vs LAB I	1 & 18	45.35	$p < 0.01$	18 & 180	0.75	NS
FIELD I vs LAB M (♀ 3-5)	1 & 18	14.15	$p < 0.01$	18 & 180	0.52	NS
LAB I vs LAB M (♀ 2)	1 & 18	6.77	$p < 0.05$	18 & 180	0.87	NS
LAB I vs LAB M (♀ 3-5)	1 & 18	8.31	$p < 0.01$	18 & 180	0.91	NS
LAB M (♀ 2) vs LAB M (♀ 3-5)	1 & 18	0.23	NS	18 & 180	0.60	NS

laboratory-maintained beetles differed from field beetles (LAB I vs. FIELD I). Comparisons between the FIELD I and LAB M groups are not easy to interpret because any differences may be due to their differing reproductive stage or due to one group having been maintained in the laboratory. But a FIELD I vs. LAB M[♀ 3-5] comparison was made to show the scale of the difference between laboratory and field beetles.

The LAB I group ate significantly less aphids per day (3.47) than either the LAB M[♀ 2] (4.43 per day) or the LAB M[♀ 3-5] (4.61 per day) groups. There was no significant difference between the LAB M[♂ + ♀ 2] and the LAB M[♂ + ♀ 3-5] groups. The FIELD I [♂ + ♀] beetles ate significantly more (5.88 per day) than the LAB I [♂ + ♀] beetles (3.47 per day) and the LAB M [♂ + ♀ 3-5] (4.61 per day). As the LAB M[♂ + ♀ 3.5] ate more per day than the LAB M[♂ + ♀ 2] it can be assumed that the FIELD I beetles also ate significantly more aphids per day than the LAB M [♂ + ♀ 2] group.

The reproductive-stage groupings can be ranked, with the field individuals, in order of voracity:

	Group	Mean aphids eaten per day
	FIELD I [♂ + ♀]	5.88
not signifi-	LAB M [♂ + ♀ 3-5]	4.61
cantly different	LAB M [♂ + ♀ 2]	4.43
	LAB I [♂ + ♀]	3.47

The final nested analysis of variance (Table 4.14) compared between-group differences for the separate sexes. The FIELD I males ate significantly more (5.52) aphids per day than males from the LAB I (3.24 per day) or LAB M (4.20 per day) groups. There was no significant difference between LAB I males and LAB M males. The same pattern emerged for females with FIELD I females eating significantly more aphids per day (6.24) than either the LAB I (3.70 per day), LAB M [♀ 2] (4.66 per day) or LAB M [♀ 3-5] (5.02 per day). There were no significant differences between the laboratory-maintained

Table 4.14 A nested analysis of the variance within sexes between reproductive stages and between individuals in numbers of aphids eaten per day

Groups to be Compared	Variance between groups			Variance between individuals		
	d.f.	F-ratio	Significance level	d.f.	F-ratio	Significance level
MALE A. DORSALE						
FIELD I vs LAB I	1 & 8	20.2	$p < 0.01$	8 & 90	0.81	NS
FIELD I vs LAB M	1 & 8	16.49	$p < 0.01$	8 & 90	0.249	NS
LAB I vs LAB M	1 & 8	2.71	NS	8 & 90	1.13	NS
FEMALE A. DORSALE						
FIELD I vs LAB I	1 & 8	28.41	$p < 0.01$	8 & 90	0.62	NS
FIELD I vs LAB M (♀2)	1 & 8	11.17	$p < 0.05$	8 & 90	0.58	NS
FIELD I vs LAB M (♀ 3-5)	1 & 8	5.78	$p < 0.05$	8 & 90	0.58	NS
LAB I vs LAB M (♀ 2)	1 & 8	2.86	NS	8 & 90	0.88	NS
LAB I vs LAB M (♀ 3-5)	1 & 8	4.88	NS	8 & 90	0.83	NS
LAB M (♀ 2) vs LAB M (♀ 3-5)	1 & 8	0.42	NS	10 & 90	0.77	NS

females, immature or mature. The following ranking of the reproductive stage groups from most to least voracious shows similar trends for male and female beetles:

MALES		FEMALES	
Group	Mean aphids eaten per day	Group	Mean aphids eaten per day
FIELD I	5.52	FIELD I	6.24
[LAB M	4.20	LAB M[♀ 3-5]	4.61]
LAB I]	3.24	LAB M[♀ 2]	4.43
		LAB I]	3.47

N.B. brackets indicate no significant difference between groups in the ranking.

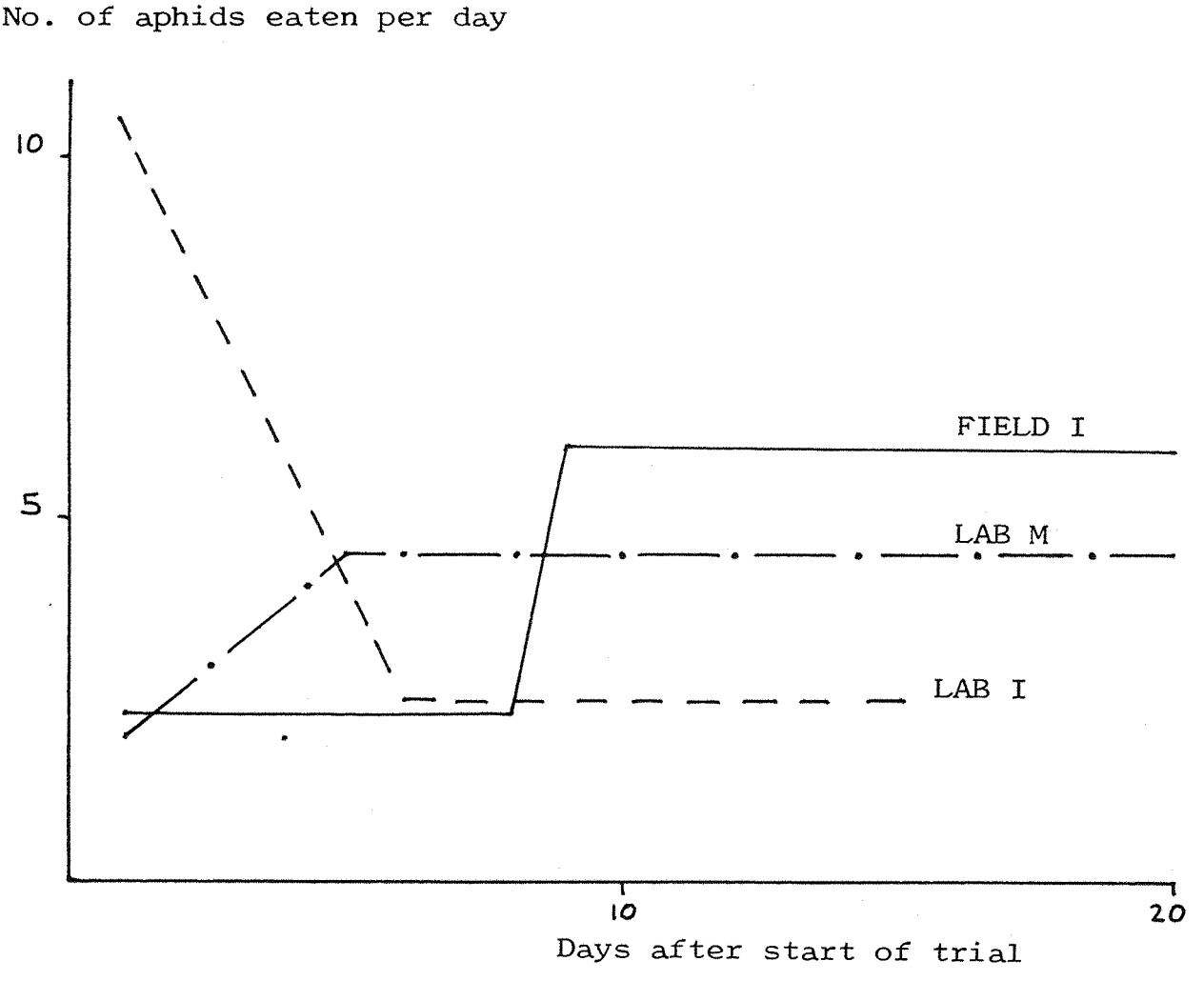
These results have implications for laboratory work which measures consumption capacity of predators, particularly if measured over short time periods. The graphs of the change in number of aphids eaten per day against time from the start of the experiment (Appendix I) show two important points:

All the three groups of beetles show a strong cyclical trend in the numbers of aphids eaten per day even though the graphs show the averages for each sex which should obscure the cycles. The cycle has a 2-day period (Appendix I) implying that measurement of voracity over one day even with replicates may give an elevated or depressed estimate. The amplitude of the cycles was commonly two to three aphids per day.

The groups of beetles were removed from their previous environment and placed directly into the sandwich boxes used for this experiment. In each case the group reached an equilibrium voracity level in a different way (Fig. 4.12), probably reflecting their differing histories and reproductive stages:

LAB I: these beetles were maintained on a 3-day starved/ 3-day fed cycle to prevent them developing reproductively. At the

Fig. 4.12 Crude visual assessment of the trends in the change of numbers of aphids eaten per day by the different A. dorsale reproductive groups. (for original graphs of data see Appendix I)



N.B. The horizontal sections of the lines are the means of the data over that period, the slopes are approximations to the rate of change in voracity for that period.

beginning of this experiment the beetles had been starved for 3 days and this is probably why their voracity was very high at first but then quickly descended to a more steady level.

LAB M: these beetles had been kept in the laboratory with enough aphids provided to allow reproductive development but the prey were not in as large an excess as in the experiment. The small rise in the beetles' voracity over the first few days probably represents their adjustment to the extra diet and the extra commitment to reproductive development that this would allow.

FIELD I: this group of beetles was taken from the field in spring before they had become active; no reproductive development had started (Chapter 7.2). The beetles show two different levels of voracity, the lower of which is very close to that of the LAB I group which had been prevented from developing reproductively for months in the laboratory. The FIELD I group then suddenly appeared to increase their voracity by 3.5 aphids per day. This may represent their having switched from a stage of no reproductive development (as in the LAB I group) to an active development stage in response to the increased day-length, temperature and food of the experiment. This switch may take longer or be impossible in individuals kept at an immature stage over long periods in the laboratory.

Clearly, voracity should be assessed over a period of weeks rather than days if the predators are kept in different conditions from those of the experiment prior to the assessment. Reproductive development can alter voracity markedly and predators taken directly from the field may be very different from those which have been kept in the laboratory for some time.

It was not possible to measure the voracity of reproductively-mature A. dorsale from the field because they were difficult to catch in numbers. The level of voracity of these individuals in comparison to the three groups tested can only be guessed at. If the FIELD M bear the same relation to the FIELD I as LAB M bear to LAB I then FIELD M may eat eight aphids per day.

The importance of variation in levels of voracity is assessed in the following discussion and in Chapter 9 (a simulation model).

4.9 Discussion

In the introduction (4.1) several parameters were referred to (Table 4.1) which can provide relative measures of a predator's ability to find prey. That the effect that the natural environment of these predators has on these parameters cannot be seen intuitively has proved a continual stumbling block to biological control programs (Huffaker & Messenger 1976). Laboratory-made measurements should not be considered to relate to the field situation but instead should be thought of as indicating the potential of a predator for biological or integrated control.

(i) The larval vs. adult potential for control.

Predators may search for prey at all stages of the life cycle; the late appearance (June onwards) of the larvae of A. dorsale and the general vulnerability to desiccation and predation of coleopteran larvae (Crowson 1981) made it seem unlikely that they would be major predators of cereal aphids. Their voracity was assessed in relation to adult voracity as an additional indication of their control potential (Section 4.2). Although voracity increased markedly with increasing larval instar even the largest (third) instars ate less than half the number of aphids consumed by reproductively immature A. dorsale adults. The first instars (also the most numerous) ate about one-twentieth the number of aphids consumed by the adults. This combined with the high larval mortality (see below) means they would have little impact on aphid populations even if the larvae did climb the wheat to reach the aphids. A. dorsale larvae were never caught in D-vac samples (Section 7.3) and laboratory studies (Dicker 1951) implied that the larvae spend most of their time close to the soil or in their burrows.

(ii) The fecundity of A. dorsale in relation to biological control

The fecundity of female A. dorsale was found to be average for this size of carabid i.e. about 30 eggs per female (Thiele 1977).

Larval mortality was, however, very high (80%); this was probably due to deficiencies in laboratory rearing conditions (Section 4.3). But work by Grum (1975) indicates that this is a very similar level of mortality to that which he found in natural carabid populations. Such high mortality means that the larvae will be only marginally numerically superior to the adults which markedly reduces any effect they might have on aphid populations. In addition, such high natural mortality implies that populations of A. dorsale will have little resilience to mortality caused by the use of non-specific pesticides, further reducing their potential for biological control.

(iii) A small scale aggregative response by A. dorsale to aphids

The adult stage of the A. dorsale life cycle is most likely to be effective in the control of cereal aphids both because it is present early on in the crop and because of its voracity. In addition, to be an effective predator of cereal aphids A. dorsale should show the ability to concentrate on those areas of the habitat with the highest densities of aphids. Aggregation by predators to their prey has been recognised increasingly as being crucial to a predator's performance in biological control (Beddington, Free & Lawton 1978). The aggregation may take place on several scales; in the case of cereal aphids this may involve firstly aggregation to a crop supporting a high density of aphids, secondly to a specific area of the crop and thirdly to the parts of the crop plant where the aphids may be found. The first cannot be investigated other than in the field, the second and third are more easily open to investigation in the laboratory. The simple sandwich box arenas used are crude but the results showed that A. dorsale responds to the presence of aphids with arrestant behaviour which would keep the beetle in the area of the prey (Section 4.4) The increased rate of turning and reduced speed may be even more effective on the confined surface of a wheat plant at constraining a beetle to an aphid-rich area than in the sandwich box (see also Chapter 5.6).

(iv) The functional response of A. dorsale to cereal aphids

Once a single predator has found its prey the way in which it responds to the density of the prey becomes important: the

functional response. In reality, aggregation and the function response may be inextricably related; aggregation may control the time spent searching in an area by the predator which in turn may decide the nature of the functional response (Hassell 1978). Interpretation of functional response data for A. dorsale was in two stages; deciding which type of functional response was being shown and determining what contribution prey size and predator behaviour (in the sandwich box arena) made to the functional response.

Statistical analysis showed that A. dorsale had a type III functional response to aphids up to about 1.5 mm long but that this was rapidly attenuated to a type II for larger aphids. This is promising for A. dorsale preying on aphids in the field as a large proportion (60-90%) will be smaller than 1.5 mm (Carter et al. 1978). If. A. dorsale takes a mixture of prey species some of these will be larger than 1.5 mm, the effect of consuming these concurrently with aphids may be to change all the functional responses to cereal aphids (regardless of size) to a type II.

The behavioural basis of the type III functional responses.

Two simple behavioural statistics were recorded during the functional response trials: percentage successful encounters and handling times for the different-sized prey. Regression analysis implied that these were primarily controlled by prey length and prey volume respectively; a simple physical relationship. Further regression analysis implied that the shapes and assymptotes of the functional responses were in part decided by these two quantities. Comparisons between high and low aphid densities showed, however, that both percentage successful encounters and handling time remained constant. So the random predator equation of Rogers (1972) was used to show how the attack rate (a') changed with prey density. This, combined with an analysis of the way numbers of prey eaten varied with prey density, suggested that the underlying cause of the type III responses was that A. dorsale did not perceive the smaller aphid sizes at low density.

If aphid predation is reduced at low aphid density because A. dorsale does not perceive the aphids this could make the beetle a better or worse biological control agent depending on its ability to

aggregate and its degree of polyphagy. If A. dorsale feeds mainly on aphids and indiscriminately aggregates to patches of aphids in the field then a type III functional response should lead it to remain only in those patches of higher aphid density. In the early part of the season this could make the difference between a non-outbreak or outbreak year.

Alternatively if A. dorsale is a more general predator and finds patches of aphids by chance its failure to perceive aphids at low densities may lead it to concentrate on other prey types without searching for the patches of higher aphid density. So although the type III responses show that A. dorsale has the potential to control aphid populations, at least in the early stage of their development, if the beetle shows aggregation or polyphagy this potential could be enhanced or removed.

(v) Voracity over longer time periods

Functional responses of predators to prey are often an expression of feeding over a few hours only; to be effective in the field the predator must achieve a sustained level of voracity over days or even weeks. Two approaches were used to see if A. dorsale could sustain this level of voracity. The first was to record the time taken for A. dorsale to void its gut of solid aphid remains after a period of intensive feeding (Section 4.6). In the 20°C temperature of the laboratory this took about 27 h; in the field, where the average temperature is nearer to 10 or 15°C, this time may be increased by some hours. Given that the beetle is ready to feed again as soon as the gut is empty of solid remains, and that it can only feed at night, (Chapter 3.2) the time taken to void the gut (after feeding to satiation) should introduce a 2-day periodicity into the feeding cycle of A. dorsale. This need not mean that the beetle only feeds every 2 days but rather that on one day it will have a high prey consumption and on the next it will be lower and so on.

The second approach was to look at the voracity of A. dorsale over several weeks and show how it was affected by ambient temperature and the sex and stage of reproductive development of the beetle.

Plots of the change of numbers of aphids eaten per day over the weeks of the trials showed that the level of voracity did clearly change in a cyclical nature with a periodicity of about 2 days as predicted (see above). The temperature trials showed that voracity changed substantially (from 0 to 12 aphids per day) with temperature in a linear fashion over the range tested ($2^{o}C$ to $19^{o}C$) (for reproductively-immature A. dorsale). There was no difference between the sexes over this temperature range or between the sexes at the different reproductive stages tested. Voracity increased with increasing reproductive development reflecting the extra energy requirements of the beetles to produce ovaries, eggs, testes and so on. The voracity of beetles taken straight from the field was higher than comparable laboratory-maintained individuals. This may be because the laboratory maintained A. dorsale were no longer capable of developing reproductively, even with sufficient prey available.

Temperature and state of reproductive development both have a significant effect on voracity, implying that extrapalation from a simple laboratory experiment to a field situation is not possible. Both have implications for the potential of A. dorsale in biological control. A. dorsale is nocturnal and in mid to late May when it arrives in the field and would be expected to be most important in controlling early aphid invasions (Southwood & Comins 1976) the night temperatures are at their lowest. Measurements at the field sites used in this study (Chapter 7.3) indicated that an average nightly temperature could be $5^{o}C$ making the number of aphids eaten per beetle per night about one!

In the period mid to late May A. dorsale is beginning to develop reproductively (Chapter 7.2) and during this period there may be a sudden increase in voracity as the FIELD I group (Fig. 4.12 in Section 4.8). But the highest level of voracity will not be reached during this period as the beetles do not reach full maturity until June onwards.

In summary: adult A. dorsale have a much greater potential than the larvae for controlling aphid numbers. They show a searching behaviour which will tend to keep them in the area of an initial contact with a prey item and hence seem adaptive to the capture of aggregated prey (e.g. cereal aphids). The adults can show the important type III functional response to all but the larger instar and adult cereal aphids. The beetles' voracity is limited, however, in the early part of its field season (when it could be most effective as a biological control agent) both by field temperatures and by its state of reproductive development.

CHAPTER 5

CHAPTER 5

DOES A. DORSALE SHOW A PREY-SEARCHING ADAPTATION SPECIFIC TO CEREAL APHIDS?

(See Chapter 2.5 for material and methods)

5.1 Introduction

Early work on those Carabidae living in cereal crops showed that they did not take prey in the proportions presented to them (Smit 1957; Skuhravy 1959; Penney 1966); some form of selection was occurring. One very relevant example was the relationship between the density of cereal aphids in the cereal crop and the appearance of those aphids in the diet of A. dorsale. Not only could aphid remains be found in the gut of A. dorsale even though the aphids were at a very low density in the field but they could also form a substantial proportion of the diet when other Carabidae contained comparatively few aphids (Sunderland 1975). More recent work has shown that strong inverse correlations can be found between the numbers of cereal aphids and those of A. dorsale (Edwards et al. 1978) and a recent ranking of polyphagous predators of cereal aphids placed A.dorsale near the top (Sunderland & Vickerman 1980).

These results suggest strongly that A. dorsale has a preference for cereal aphids over the other types of prey available; flies, springtails, mites etc. Field sampling during this project (Section 7.3) confirmed the results of the earlier work; A. dorsale caught cereal aphids even though they were at low density in the field and its diet was often mainly cereal aphids. This chapter deals with the various possibilities for the mechanism by which A. dorsale may come to concentrate its searching on cereal aphids.

The sub-order Adephaga represents probably the oldest carnivorous line in the Coleoptera with the majority of its species belonging to the family Carabidae. Although over their long history the carabids have evolved morphologically to suit a number of predaceous roles they have never reached the degree of specialization shown by some

members of the Polyphaga. There are examples of species from the Polyphaga evolving to be able to detect the habitat of their specific prey by visual cues and even detect the pheromones used by their prey (Crowson 1981). By contrast, adaptions amongst the carabids seem to involve the close-range detection and handling of prey, e.g. the specialised Collembola-feeder Notiophilus with its large sensitive eyes and ability to pounce rapidly, or the individuals of the genus Cychrus with their narrowed heads and extra large palps to enable them to attack snails in their shells. In addition, the carabids as a family have a reputation for being general omnivorous (Thiele 1977) suggesting that extreme adaption to any one prey species would be unlikely.

Crowson (1981) in his review of the predatory behaviour of beetles subdivided prey capture into "search" or "ambush" techniques. With a few exceptions, e.g. cicindelid larvae, the Coleoptera "search" for their prey. Searching was subdivided into three sub-groups of increasing specialisation of the predator.

Sub-group	Coleopteran families commonly associated with subgroup
(1) Simple searching i.e. beetle searches in an undirected manner until coming into contact (visual or physical) with prey.	Cicindelidae Carabidae Staphylinidae
(2) Habitat selection i.e. beetle only searches areas of the habitat where the prey would normally be found.	Coccinellidae Cleridae
(3) Chemical detection i.e. beetle detects chemicals released by prey and follows them to their source.	Cleridae Cantharidae

Sub-group (1) would not require the predator to evolve a mechanism for long range detection of prey as would sub-groups (2) and (3).

Both vision and chemical detection have been implicated in this long range detection, vision being linked to the sighting of prey habitats rather than the prey themselves (Huffaker & Messenger 1976). Chemical, or kairomone (Brown, Eisener & Whittaker 1970), detection varies from the predator being stimulated by chemicals released by the host plant as a result of damage by the prey, to detection of aggregation pheromones used by the prey. Although not coleopteran, the chrysopids provide a pertinent example in that some of them (Huffaker & Messenger 1976) detect chemicals excreted in the honeydew of their aphid prey and then fly upwind (positive anemotaxis) until they find the aphids.

To sum up: phylogenetically the carabids are not known to have the ability to detect prey at long range by vision or kairomones. Other branches of the Coleoptera do show a varied range of adaptions to perform this task; some of these adaptions may yet be found in the Carabidae and would be of obvious advantage to a predator such as A. dorsale when searching for the spatially-aggregated aphids in cereal crops.

It is possible to make some predictions about the type of adaptations that A. dorsale should show to account for its apparent preference for cereal aphids. These predictions are based on some simple physical characteristics of A. dorsale, cereal aphids and the wheat field habitat. These are:

A. dorsale	:	Nocturnally active
		Cannot fly
		Can climb wheat
		Can disperse rapidly on the ground
Cereal aphids	:	Aggregated distribution on the plant
		Aggregated distribution in the field
		May release pheromones (e.g. alarm)
		Produce honeydew
Wheat crop	:	Dense monocrop
		Wind speed decreases rapidly towards the ground

A. dorsale is nocturnal, making visual detection of cereal aphid prey extremely unlikely. Even in good light the insect eye is best adapted to see movement and not immobile prey such as aphids. Nor would vision be adaptive to finding likely prey habitats as patches of aphids are distributed in a crop of very even appearance. (At the time when A. dorsale would be most useful for control the aphid population would be too small to damage the plants sufficiently to make their presence in the crop conspicuous through changed plant condition).

This leaves tactile or olfactory detection of odour cues; in either case A. dorsale needs to detect the cue from the ground to avoid climbing every wheat stem in the field to find aphid prey.

The two most likely tactile cues are honeydew deposits on the ground below aphid colonies and aphids which have fallen or walked on to the ground. Contact with either may stimulate A. dorsale to climb surrounding wheat stems in search of aphids. Both have the disadvantage that for A. dorsale to be successful when the aphids are at low density requires the beetle to cover huge areas of the wheat field to discover aphids either individually or in patches.

The most advantageous adaptation would be detection by A. dorsale of an air-born kairomone produced directly by the aphids or originating from their honeydew. The kairomone whether originating from the aphids or the honeydew, could be dispersed from the ground or the plant. There are two distinct ways in which air-born kairomones may attract a predator to its prey (Bossert & Wilson 1963; Wilson, Bosserts & Regnier 1969; Weaver 1978; Bradshaw 1981). A kairomone may be transmitted and received over long distance (several hundred metres) at very low concentrations; in this case the concentration gradient of the kairomone is so small that random variations, due to local air turbulence etc., prevent the use of the gradient for orientation to the prey. Instead the kairomone acts as a trigger to switch on some other method of orientation by the predator e.g. positive anemotaxis. Alternatively the transmission/reception of the kairomone may take place over short distances (0 to 20 cm) and involve a sufficiently steep concentration gradient to guide the predator to the prey (to date

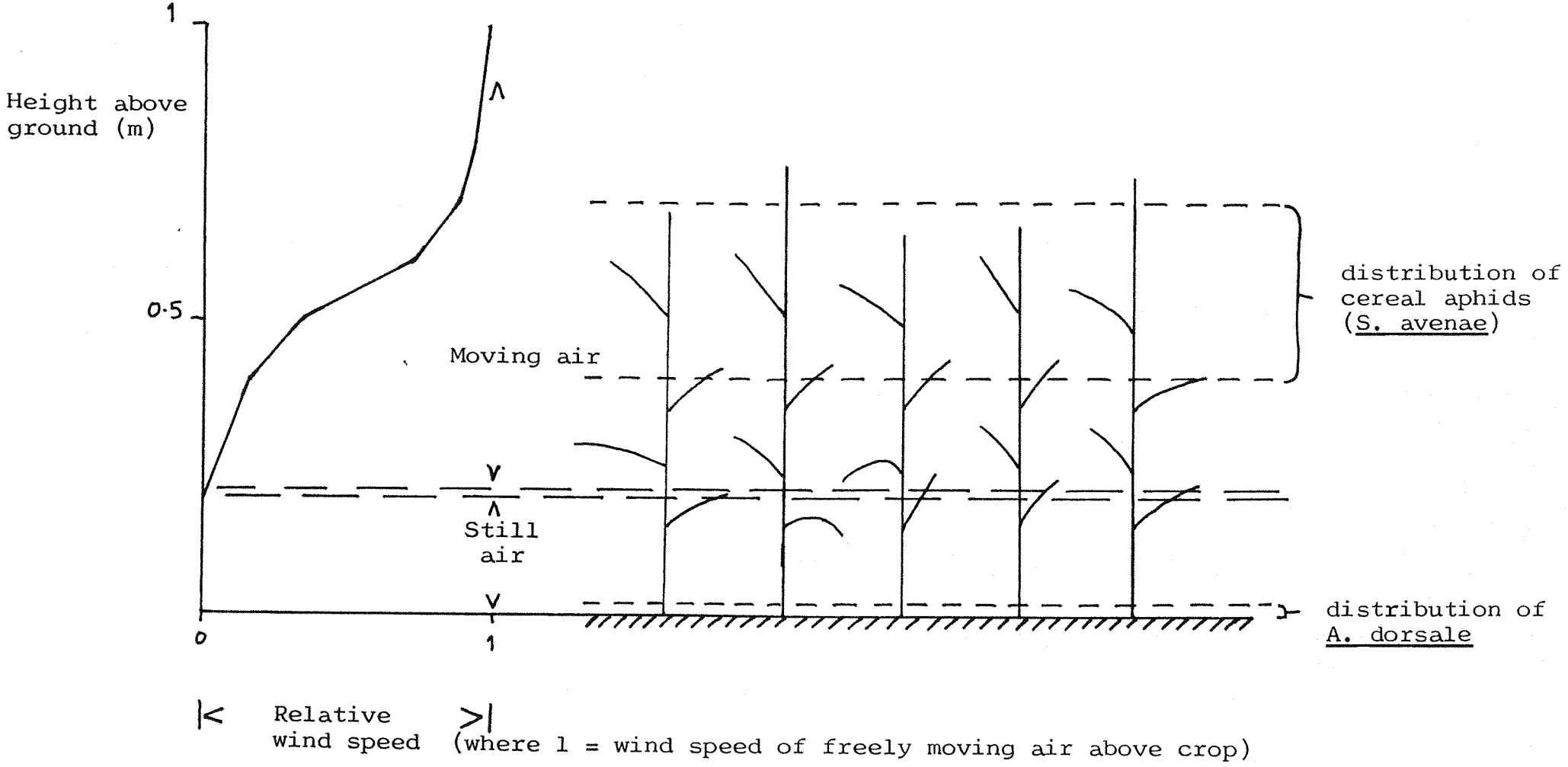
the work quoted suggests that this theoretical range of distances may be much smaller in practice, e.g. 0 to 10 cm). In some cases these two orientation systems may work in sequence, the first guiding the predator from long range and the second taking over at close range (as is known to happen for some moths responding to sex pheromones, Alcock 1975).

The distribution of prey and predator and the microclimate, specifically wind, in a wheat field clearly make some of the options discussed unlikely or impossible.

Wind is the biggest physical factor affecting the distribution and spread of air-born kairomones. The interaction between wind and crop (wheat) height is summarised in Figure 5.1 (after Rosenberg 1974; Cox, Healey & Moore 1976). Also shown are the approximate distributions of A. dorsale and cereal aphids (Vickerman & Wratten 1979) within the crop; clearly the former lives in a habitat with virtually no wind while the latter is regularly exposed to it. A kairomone originating from aphids or honeydew on the wheat plants would be spread by wind as a plume (Bossert & Wilson 1963) over a large area of the crop, reaching the ground over this area by molecular diffusion through the layer of still air. The kairomone concentration gradient in this area would be too low to be used for orientation by A. dorsale nor could the kairomone "switch on" a positive anemotactic orientation (movement up wind) as A. dorsale is some distance below any air currents. It could stimulate the beetle to climb but this would only be adaptive if aphids were very evenly distributed at reasonably high densities through the crop.

A kairomone originating from aphids or honeydew on the ground would spread by molecular diffusion allowing the build up of a concentration gradient around the source. The gradient could either lead A. dorsale to the honeydew or aphid(s) and these would stimulate the beetle to climb, or at a threshold concentration on the gradient the kairomone itself would cause the climbing response. For this mechanism to work A. dorsale would have to come within about 20 cm of the kairomone source. This is only a marginal improvement over tactile detection, A. dorsale would still have to search over huge areas

Fig. 5.1 The distribution of cereal aphids, A. dorsale and wind speeds within a cereal crop with reference to the detection by A. dorsale of aphid-produced kairomones.



of ground just to find the kairomone concentration gradients. This would apply particularly in the early season when aphids are at low density and aggregated within the crop (Dean 1973).

Both because of the phylogenetic characteristics of the Carabidae and because of known kairomone detection mechanisms it is unlikely that A. dorsale can detect aphids at long range. Visual cues can be discounted on several counts, leaving use of short range kairomone cues or tactile cues. For either of the two latter cues to be useful, A. dorsale must be able to search huge areas of wheat fields if it is to find aphids which are often both aggregated and at low density. Nevertheless field data (Chapter 7.3) show that A. dorsale does find aphids at very low field densities and this chapter investigates whether it makes use of the aforementioned olfactory or tactile cues. The chapter is organised so that it progresses from investigation of the highly sophisticated adaptation of kairomone detection to the much less efficient adaptation of tactile contact with aphids leading to the finding of aphid colonies on the plants.

5.2 The role of kairomones in the detection of cereal aphid prey by A. dorsale

(i) Introduction

The study of the transmission of messages by air-born odours presents a number of difficulties; the chemical secretions involved are produced in minute quantities, the secretions are difficult to analyse even with sophisticated equipment (gas chromatography, mass spectrometry etc.), precise response thresholds can be impossible to measure. In addition each odour may have several modes of action, each generated by the different chemical constituents of the odour and whether the odour is spread by diffusion or wind born turbulence.

Fortunately the study of these "odours" can be split into two parts; the intricate unravelling of the precise mode of action of the odour involving all of the above difficulties and a more simple initial stage where the potential odour source is presented to the receiver and a change of behaviour looked for. The apparatus needed

for the latter can be relatively simple (O.T. Jones pers. comm.) if its only task is to show whether communication by air-born chemicals is occurring.

An example will clarify this point:

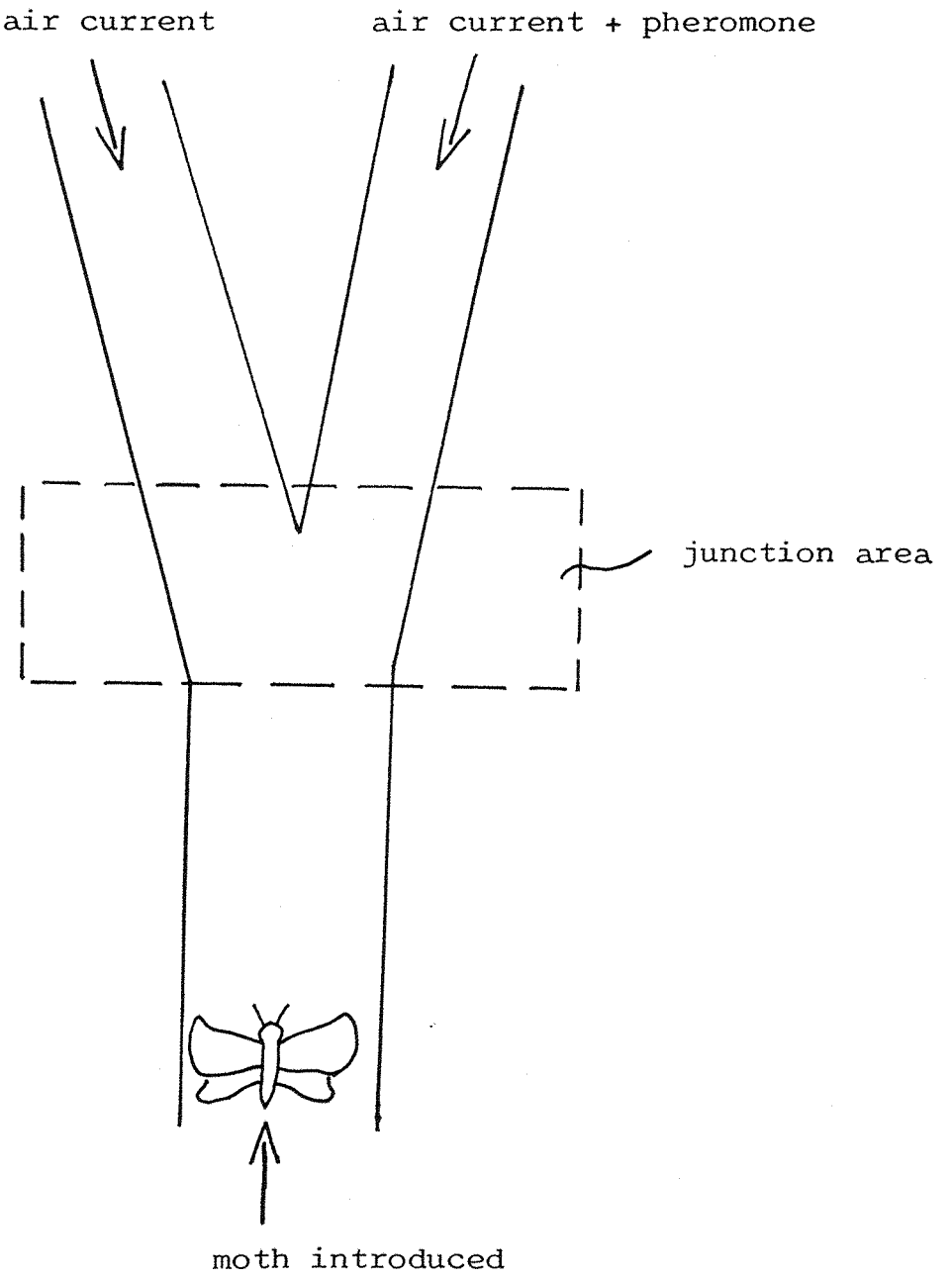
A traditional method for testing the attractant effect of air-born chemicals (as potential pheromones) on moths is the Y-maze (Fig. 5.2). In this apparatus the moth is presented with a choice between the arm with the air-born chemical and the arm without. While the apparatus is effective for deciding whether or not the chemical has an effect on the moth's behaviour, it cannot be used to show the precise way in which the chemical acts. At the junction area of the Y-maze the moth is presented with several cues in addition to the presence/absence of the chemical; there is a change in concentration of the pheromone and there are shearing and turbulence cues in the air flow at the junction. It is not possible to say whether the chemical is responsible for any attraction or whether it acts in conjunction with one of the other cues.

This experiment was designed to show only whether or not detection of aphid kairomones by A. dorsale occurred. A simple choice chamber apparatus (designed with help from O.T. Jones) was used to show whether aphids or their honeydew (presented as an established colony on wheat) affected the behaviour of starved A. dorsale.

As a kairomone could either directly attract A. dorsale to the half of the arena with aphids or switch on a behaviour which in the field could result in A. dorsale finding the aphids, several different aspects of behaviour were recorded. These aspects and the purpose of recording them were:

	Behaviour recorded	Purpose of recording
(1)	Which side of the arena was most often occupied by A. dorsale?	Is A. dorsale directly attracted to the aphids by a concentration gradient of kairomone?

Fig. 5.2 The Y-maze used for testing the attractant effect of potential pheromones on moths



(2)	Frequency of searching	Does the presence of a kairomone increase the frequency with which A. dorsale shows searching behaviour?
(3)	Speed of movement	Does the presence of a kairomone decrease the speed of movement of A. dorsale so that it stays in the area near the aphids?
(4)	Overall time budget	Does the presence of a kairomone change the amount of time spent in each behaviour?

(N.B. (4) is essentially a more detailed look at (2)).

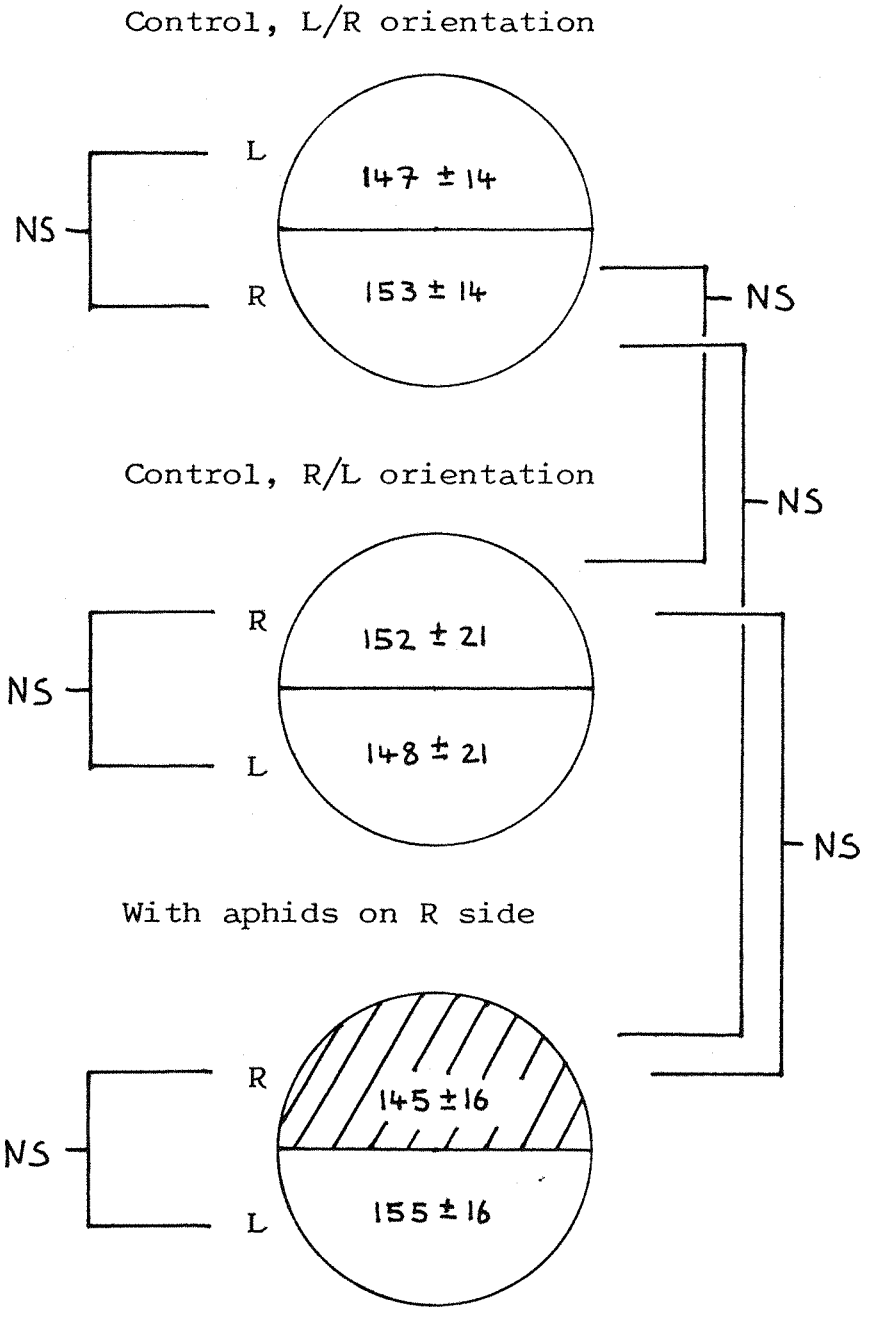
If long-range detection of kairomones was occurring then A. dorsale would show (2) or (3) but not the close range response of (1), (see Introduction). If close range detection was occurring then (1) along with (2) and (3) could be shown.

In addition care was taken to eliminate any bias A. dorsale may have shown to either side of the experimental room or the arena. This was achieved by setting up the choice chamber as a control with wheat in both sides but no aphids. The halves of the chamber were labelled so that after the first control series had been run the chamber could be exactly reversed and a second identical control series run. This would show up any inherent bias in the room or choice chamber which could then be allowed for when assessing the effect of the presence of aphids.

(ii) Results

Separate comparisons were made of total time spent in each side of the arena for each of the three arena arrangements (see left side of Fig. 5.3). Although data were very variable between individuals the use of 20 beetles per trial made it possible to use the t-test (Bailey 1964) for the comparisons. There was no difference between

Fig. 5.3 The difference in time spent in each half of the arena for the control and "with aphid" trials.



R = right side of arena
L = left side of arena
NS = no significant difference at p = 0.05 level; t-test.

Figures are mean ± S.E. of time(s) spent in each arena half, where n = 20

the total times spent in the L or R sides of the arena either for the two control or the with-aphids trials.

Comparisons were then made between arena arrangements for the total time spent on the R side of the arena (see right side of Fig. 5.3). There were no significant differences between arena arrangements.

(N.B. for the latter comparisons only the R sides need be compared; as trials were run for a constant length of time and individuals had to be in the R or the L side of the arena, the total times in the L side differed between arena arrangements by the same amount as those for the R side).

During recording of total time spent in each half of the arena the frequency with which individuals showed searching behaviour was recorded. Comparisons of these frequencies were made between the control and with-aphids trials (Table 5.1). As the same beetles were used for all tests the related-samples sign test (Siegel 1956) could be used to compare the frequency of searching (too low for a parametric test) between the different trials. There were no significant differences.

Frequency of searching may not be affected, instead total searching time may change. To test this the time occupied by each of the three basic behaviours (search, run, still; see Chapter 3.4) was recorded for control and with-aphids trials. In addition, speed of movement was also recorded. As the previous trials showed no difference between the two control trial arrangements only the R/L configuration (Fig. 5.3) was used when these recordings were made.

The total times spent in each behaviour were compared between the control and with-aphids trials using the t-test (Table 5.2). There were no significant differences between trials for searching, running or still behaviour.

Speed of movement was recorded several times for each of 10 beetles for each set of trials (less recordings were made for the control trials because the variation in speed was very low generally). The t-test was used to compare speed in the control and with-aphid trials, but there was no significant difference (Table 5.2).

Table 5.1 Comparison of the frequency with which searching behaviour was shown between the control and "with aphids" trial

Arena Arrangement	n	Mean frequency of searches	Sign Test
Control, L/R orientation	20	0.75	NS
Control, R/L orientation	20	0.60	NS
With aphids on the R side	20	0.65	NS

Table 5.2 Comparison of time spent searching, running or still and speed of movement between the control and the "with aphids" trials

Variable	Arena arrangement	n	mean	(S.E.)	t-test
Time spent searching (s)	Control:	20	16	(6.1)	NS
	With aphids:	20	15	(5.2)	
Time spent running (s)	Control:	20	146	(23)	NS
	With aphids:	20	152	(25)	
Time spent still (s)	Control:	20	138	(23)	NS
	With aphids:	20	133	(24)	
Speed of movement (cm/s)	Control:	38	2.2	(0.14)	NS
	With aphids:	71	2.1	(0.11)	

A major problem with experimentation involving air-born chemicals is the usually rapid saturation of the arena. If a concentration gradient response is being tested and the trial is allowed to run for too long, then the concentration of the chemical will be too high throughout the arena for a detectable gradient to exist. Accordingly these tests were run for 5 min only because the types of chemicals previously discovered to make up concentration gradients would take about this time to fill one side of the choice chamber (Bossert & Wilson 1963; Bradshaw 1981). Also, overexposure to a chemical may lead to individuals accommodating to the kairomone, i.e. ceasing to respond to it, and trials were limited to 5 min for this reason as well.

In summary, A. dorsale did not respond to the presence of aphids by its position in the arena (close-range response) or by its behaviour (long- or close-range response). There was no evidence of any increase in searching activity as might be expected if, as the introduction suggested, A. dorsale is most likely to respond to a kairomone concentration gradient to find aphid prey.

5.3 The role of honeydew and exuviae in the detection of cereal aphid prey by A. dorsale

A colony of aphids may give away its presence by less direct cues than kairomones released directly from the body of the aphid into the air. Aphids usually feed on the phloem sap of plants which, while rich in sugars, is poor in amino acids which are essential for growth. Aphids overcome this deficiency by ingesting large amounts of sap to acquire sufficient nitrogen and correspondingly excrete large volumes of sugars as honeydew (Blackman 1974). This honeydew is deposited on the plant surfaces and ground around the aphid colony, giving a clear marker of the aphids' presence. As well as digested sugars honeydew contains amino acids, minerals and so on, ingested from the host plant (Mittler 1953; Auclair 1958); any of these constituents may form the basis of the kairomone attractant. For instance, some chrysopids are attracted by the amino acid tryptophan in the honeydew of their aphid prey (Huffaker & Messenger 1976).

There is a further cue to the presence of an aphid colony. Like all insects aphids undergo ecdysis; this, combined with their sedentary life style, leads to an accumulation of discarded cuticles (or exuviae) around the colony. This may be one of the cues that hoverflies search for to lead them to an aphid colony where they oviposit (Dixon 1973).

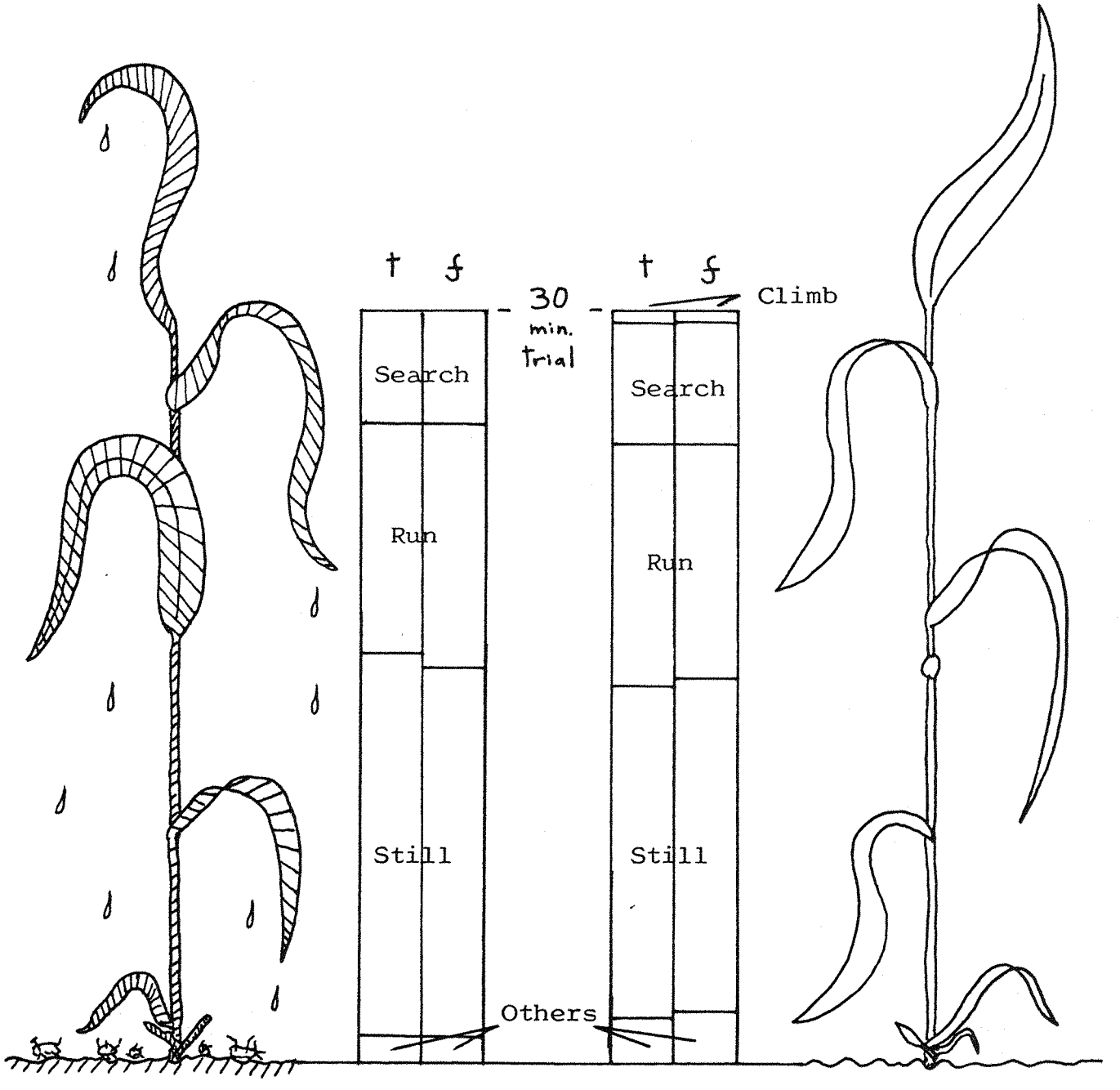
To show whether either of these cues is used by A. dorsale to find aphid colonies the beetles were introduced into two types of arena and their behaviour recorded. One arena, the control, contained wheat at growth stage (GS) 8-10 (Large 1954) grown in the absence of aphids. The other contained wheat (at GS 8-10) covered in the honeydew and exuviae produced by a large colony of aphids. All aphids were carefully removed from the latter arena so that only the honeydew and exuviae could act as cues to the beetles (the soil surface in this arena was also allowed to accumulate honeydew and exuviae).

The beetles' behaviour was divided into the three main categories of searching, running and still (see Chapter 3.4). In addition there was an "others" category to cover occasional behaviours such as grooming, and a "climbs" category in which height, duration and behaviour during the climbing of the wheat was recorded. The proportions of total trial time occupied by each behaviour and the frequency with which each behaviour was shown are summarised in Figure 5.4. The analyses of the time spent in, and frequencies of, each behaviour are given in Tables 5.3 and 5.4 respectively.

The t-test (Bailey 1964) was used to assess the difference in total time occupied by each behaviour during the 30 min trial in the control and honeydew + exuviae arenas (Table 5.3). The t-test was also used to look at the difference in the frequency with which each behaviour was shown in the control and honeydew + exuviae arenas (Table 5.4). There were no significant difference either in total time spent in each behaviour or in the frequency with which each behaviour was shown.

Individuals spent about half their time still with most of the rest being spent either running or searching (Fig. 5.4). The "others" category of behaviour involved grooming or occasional attempts to eat

Fig. 5.4 The effect of honeydew and exuviae on the frequency of and time allocated to the behaviours shown by A. dorsale during foraging.



HONEYDEW + EXUVIAE

Behaviours shown

CONTROL

N.B. t= time (as a proportion of total trial time)allocated to each behaviour.
f= frequency each behaviour was shown during the trial as a proportion of all frequencies shown.

Table 5.3 Comparison of the total time (s) spent in each behaviour in the control and the honeydew (H) and exuviae (E) trials

Behaviour	Arena	n	Mean	(S.E.)	t-test
Search	Control	10	285	(± 54)	NS
	H & E	10	263	(± 46)	
Run	Control	10	574	(± 99)	NS
	H & E	10	530	(± 109)	
Still	Control	10	804	(± 120)	NS
	H & E	10	875	(± 138)	
Others	Control	10	138	(± 63)	NS
	H & E	10	61	(± 34)	

Table 5.4 Comparisons of the frequency with which each behaviour was shown in the control and honeydew (H) and exuviae (E) trials

Behaviour	Arena	n	Mean	(S.E.)	t-test
Searching	Control	10	11	(± 2.0)	NS
	H & E	10	9	(± 1.5)	
Run	Control	10	8	(± 1.2)	NS
	H & E	10	11	(± 2.1)	
Still	Control	10	11	(± 1.6)	NS
	H & E	10	10	(± 1.9)	

N.B. The "Others" category was not analysed because of the very low frequency of recordings.

exuviae by A. dorsale. Climbing up the wheat only occurred in the control trials and only one climb was observed which lasted about 6 min and reached a height of 10 cm only. The beetle spent about 5 of the 6 min sitting motionless about 10 cm up the wheat stem.

Honeydew and exuviae deposits did not act as cues to alter either the frequency or the time occupied by any of the behaviours shown by individuals on the ground. There was no increase in the frequency of climbing on the wheat and no increase in overall time spent climbing. Honeydew deposits and aphid exuviae were not used as chemical or tactile cues by A. dorsale individuals to locate aphid colonies on wheat.

5.4 The effect of wheat stem structure, close to the ground, on the climbing frequency of A. dorsale in the absence of prey

(i) Introduction

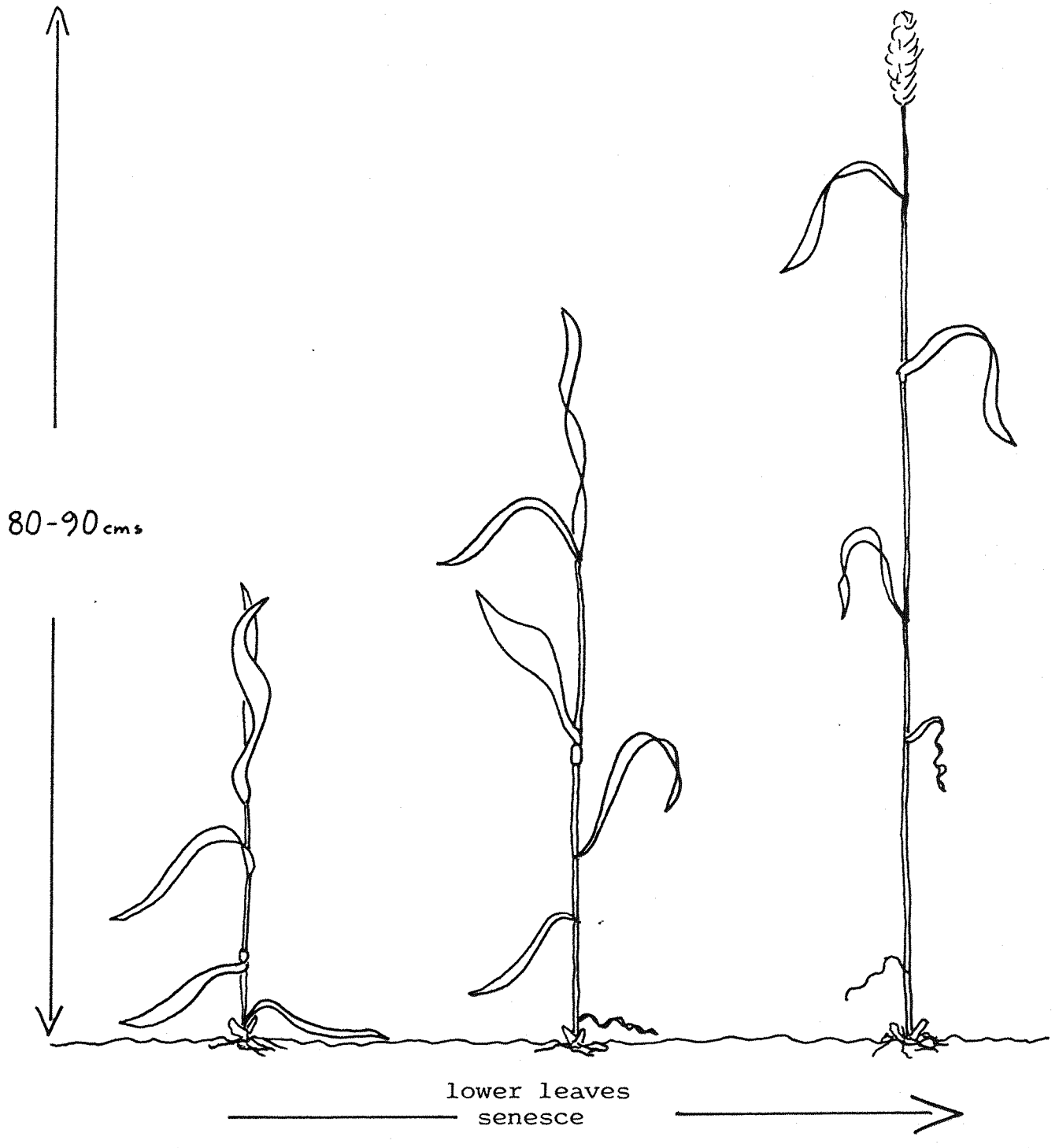
A. dorsale enters cereal crops in about mid May and is active there until about the end of June (Section 7.2); during this period substantial changes take place in the structure of the wheat (Fig. 5.5). As the crop matures the lower leaves senesce and wither, leaving only the stem for A. dorsale to climb. This could affect the amount of climbing (and hence aphid predation) that the beetle does in two ways:

The senescence of lower leaves means that A. dorsale will have to climb further to encounter aphids and if the climb is too long it may give up before the encounter.

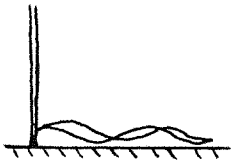
Studies of coleopteran tarsal setae (Stork 1980) imply that the genus Agonum does not have setae especially adapted to climbing. This was particularly apparent when the scanning electron micrographs of Agonum setae were compared with those of Demetrias, a small and actively-climbing carabid. With no special climbing adaptations the lack of structurally-sound leaves to climb close to the ground may deter A. dorsale from climbing.

To distinguish between the effects of plant structure and the effects of prey distribution on the frequency of climbing by A. dorsale

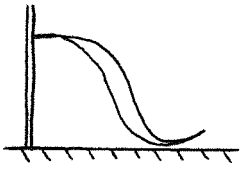
Fig. 5.5 The change in the number and condition of leaves and plant height, during the period that A. dorsale is active in the field. (plant drawings adapted from Large, 1954)



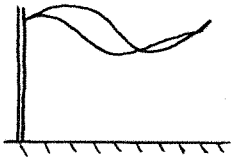
no prey were used in this series of experiments. Three different plant arrangements were used:



Stem/leaf: Main stem planted so that the lowest green leaf lay along the soil.



Stem/tip: Main stem planted so that the lowest green leaf had the tip only in contact with the soil.



Stem: Main stem planted so that no leaves were in contact with the soil.

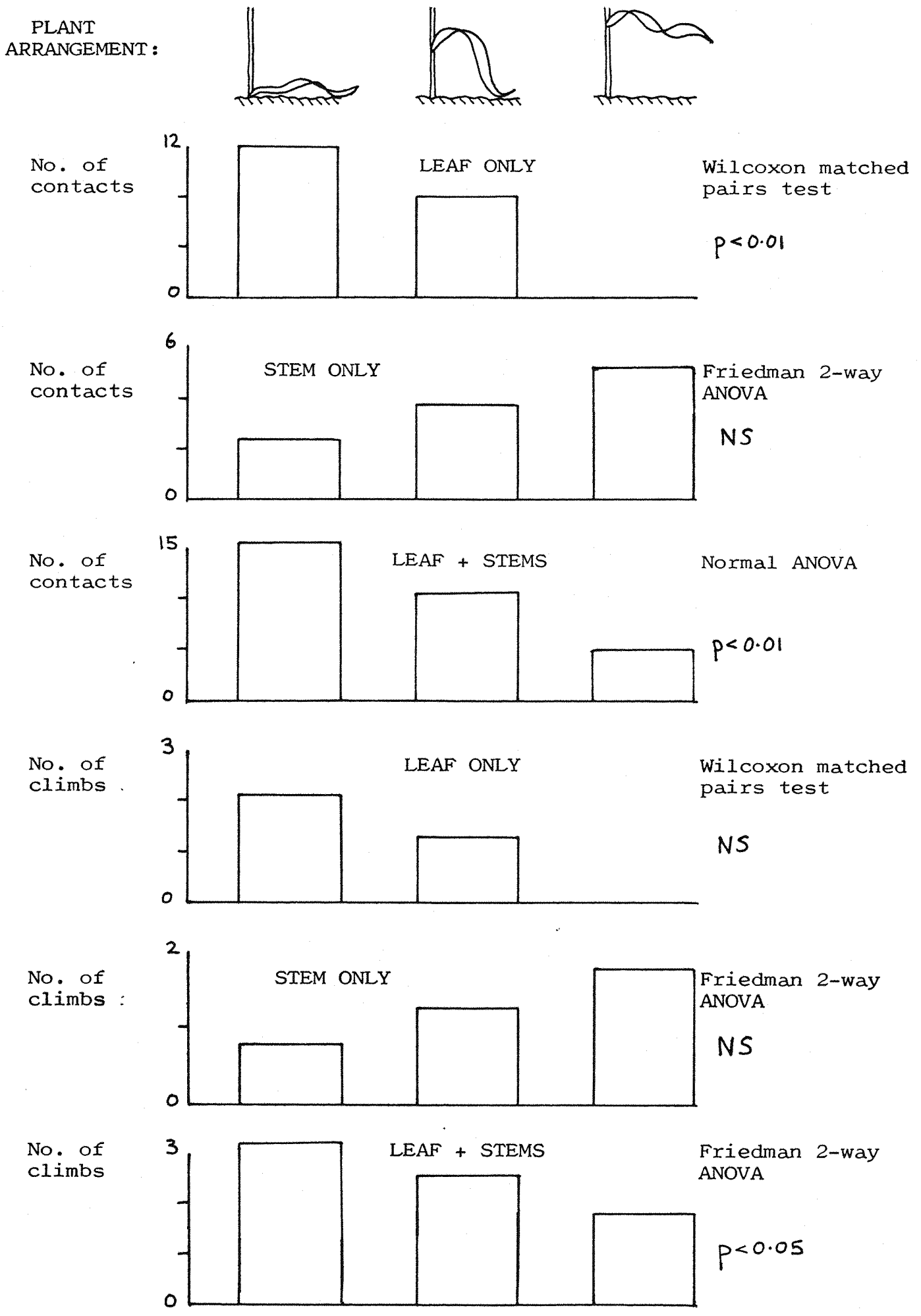
The plants presented a transition from "leaves and stems" to "stems only" in contact with the ground as would occur with time in the field (Fig. 5.5). The number of times that beetles came into contact with leaves or stems was recorded along with the number of resulting climbs, how high they were and for how long they lasted. Differences between the plant arrangements were analysed using mostly non-parametric tests because behaviours occurred infrequently and/or data were very variable.

(ii) Results

The data and results of the analyses on the number of contacts with leaves and stems and the number of resulting climbs are summarised in Figure 5.6.

As expected the number of contacts with leaves decreased as the area of leaf touching the ground decreased. Contacts with stems increased (though not significantly) as the area of leaf touching the ground decreased. The overall effect (leaf and stems) was that the number of contacts decreased as the leaf area touching the ground decreased.

Fig. 5.6 The change in the mean number of contacts with and climbs on wheat plants with different arrangements of the lower leaves.



The number of climbs resulting from contacts with leaves decreased (though not significantly) as contacts with leaves decreased. Similarly the number of climbs resulting from contacts with stems increased (though not significantly) as contacts with stems increased. The total number of climbs (leaf and stem) decreased significantly as the leaf area touching the ground decreased.

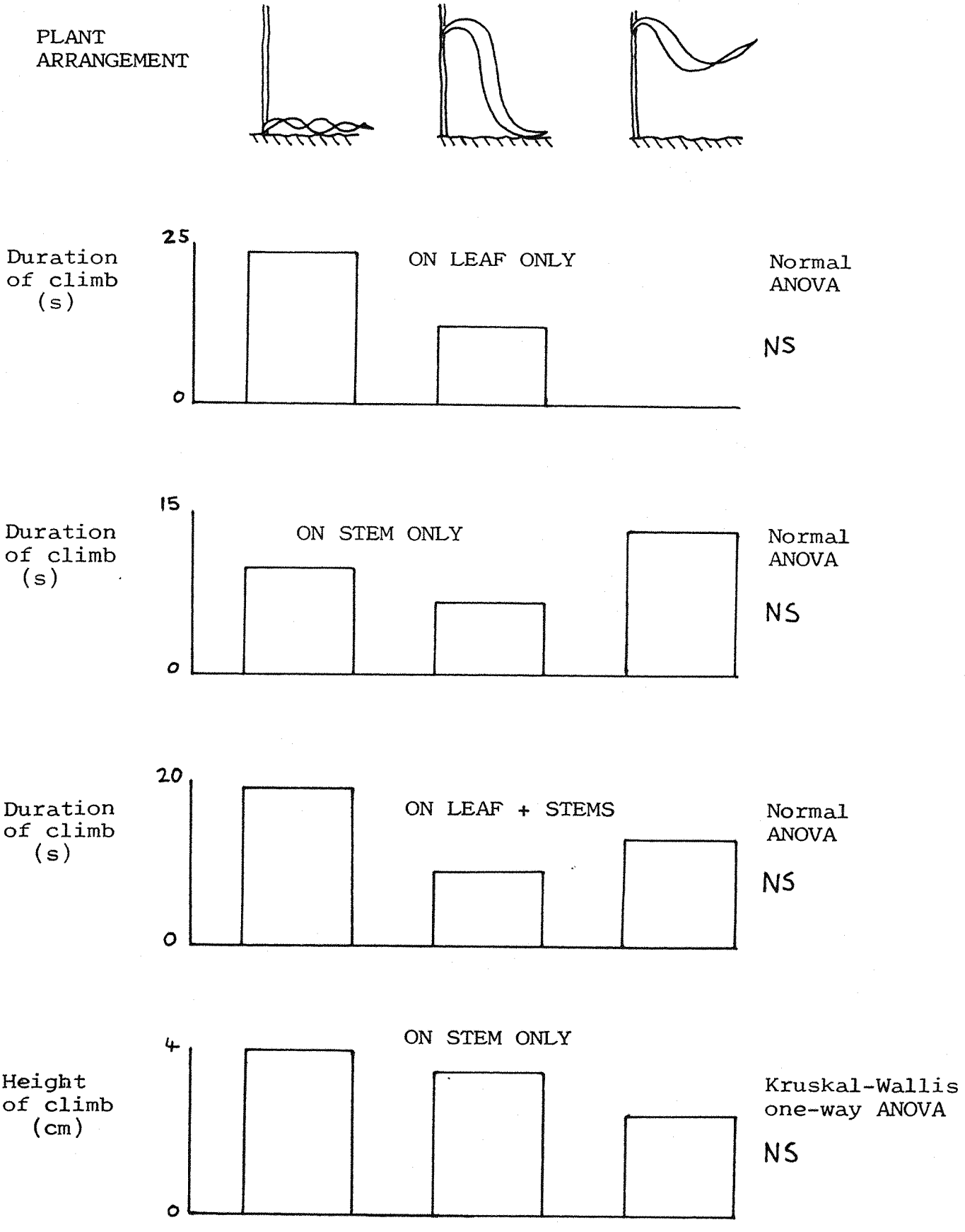
The proportions of contacts leading to climbs was different for stems and leaves. About 16% of contacts with leaves fully touching the ground led to climbs on to them, this increased to 20% for leaves only touching the ground at their tips. About 35% of contacts with stems led to climbs up them.

Data and analyses of duration and height of climbs are summarised in Figure 5.7, the height of climbs on leaves was not measured because the leaves were always too close to being horizontal to make judgement of height feasible. Duration of climbs did not change significantly on either leaves, stems or overall (leaves and stems) as the leaf area touching the ground decreased. The height of climbs on stems did not change significantly as leaf area touching the ground decreased.

(iii) Discussion

The larger the area of wheat leaves touching the ground the more often A. dorsale individuals came into contact with the leaves, and this led to a higher overall frequency of climbs onto the wheat. Contacts with stems, which led to climbs more often than contacts with leaves, decreased as leaf area touching the ground increased. In addition, climbs onto leaves did not result in individuals transferring onto the stem and climbing further up the wheat plants. Climbs up stems were usually not high enough to reach leaves that were not already touching the ground (see Fig. 5.7). In consequence, the largest number of climbs occur when the lower leaves are wholely touching the ground but a high proportion of these climbs are on the lowest leaf only. When there is only stem for the beetles to climb a higher proportion of contacts lead to climbs, but the climbs do not reach the leaves. The lower structure of the wheat plants while affecting climbing frequency will not affect aphid predation unless

Fig. 5.7 The change in mean duration and height of climbs with different arrangements of the lower leaves of wheat stems.



the aphids are on the lower parts of the plants. (The cereal aphid species considered in this study, S. avenae, is distributed mostly on the upper parts of the plant.)

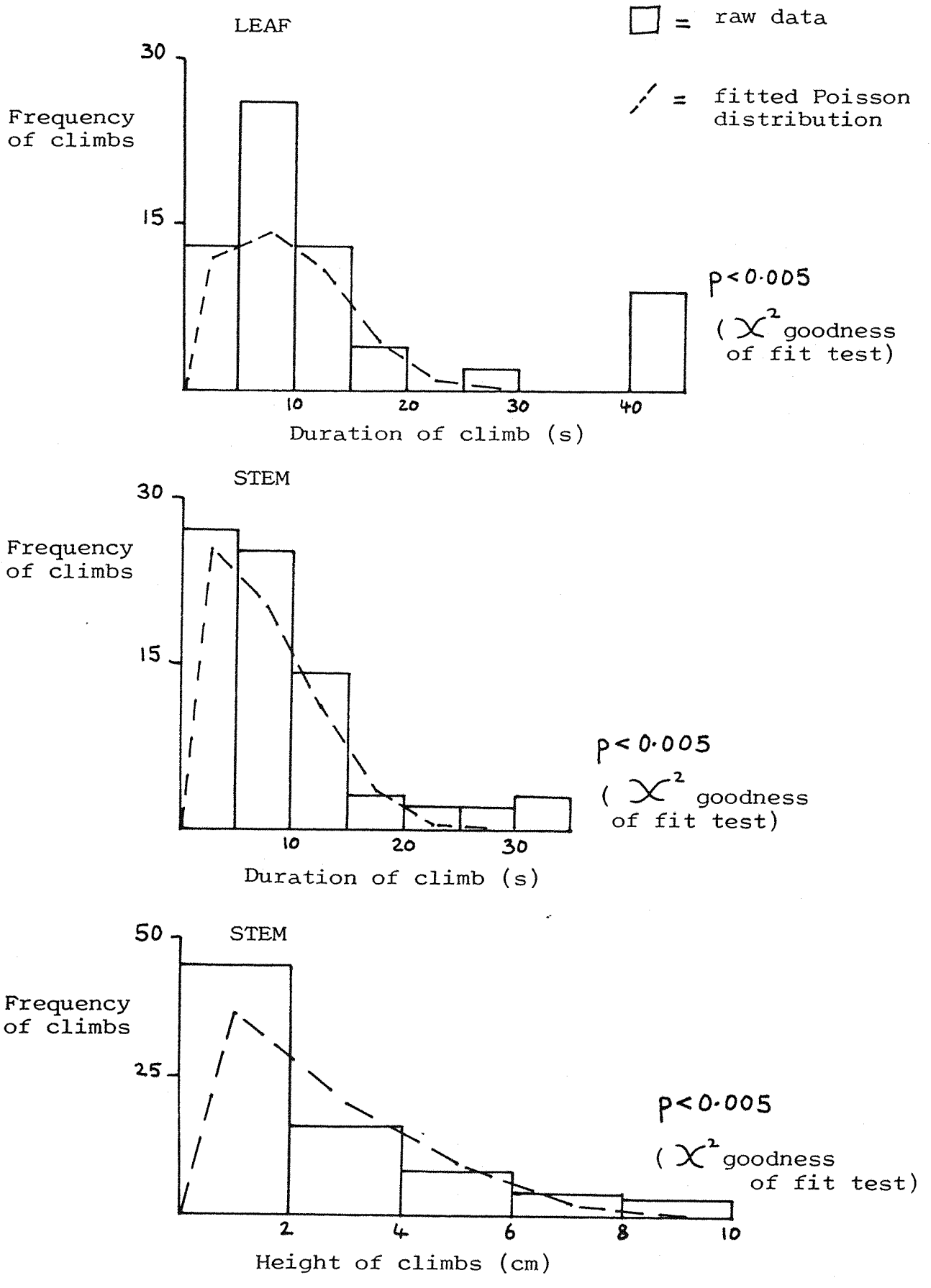
Although individuals mostly made short, low climbs they occasionally made higher and longer climbs. These latter climbs may represent an infrequent sampling strategy for higher parts of the plant by the beetle. If this were so it would be expected that there would be a higher frequency of these longer climbs than if the climbs were of random height and duration but centred on the lower parts of the plant. This can be tested by making a frequency distribution of height and duration of climbs for leaves and stems separately and comparing these with the Poisson distribution (assuming that higher, longer climbs are rare events). These frequency distributions and their corresponding Poisson distributions are shown in Figure 5.8, the distributions were compared using a X^2 goodness-of-fit test (Snedecor & Cochran 1967). All three data distributions differed significantly from the Poisson distribution in having a higher frequency of longer climbs than expected. This suggests that A. dorsale may be occasionally sampling higher parts of the plant, the following sections incorporate both wheat plants and aphid prey to show whether the beetle can sample aphid populations on the plant.

Finally, the paradox that the genus Agonum does not have tarsi evolved for plant climbing (Stork 1980) but in this experiment tended to climb vertical stems more often than horizontal leaves may have a simple explanation. When climbing a stem A. dorsale can grip by straddling the stem with its legs. The wheat leaf is too wide to be gripped like this so the beetle must rely solely on the adhesion provided by its tarsi, and hence is less able to climb.

5.5 The effect of aphid distribution between the ground and wheat seedlings on the climbing frequency and searching behaviour of A. dorsale

Highly specific adaptations to finding prey e.g. kairomone detection, can be very efficient in leading the predator directly to the prey. Such adaptations involve some energetic cost to the predator,

Fig. 5.8 The frequency distributions of length and height of climbs on leaves and stems of wheat.



e.g. the actual organs necessary for detection of the prey cost energy to produce and maintain (see Wilson 1975 for a review of the cost of sensory organs). If the prey is sporadic in its abundance the cost may not be "worthwhile"; instead the predator may evolve a less efficient but less costly mechanism. For A. dorsale this may be the finding of aphids on the ground which then stimulates the beetle to climb. The mechanism is less costly to evolve as it requires only the development of recognition of aphids after physical contact (a small part of the mechanism required in kairomone detection) followed by a behavioural response to climb after the encounter. It is less efficient because the presence of an aphid on the ground does not automatically mean that aphids will be present on surrounding wheat stems.

In this and the following Section (5.5) this more simple type of prey detection is investigated by looking at the effect of varying the aphid distribution between ground and plant. This Section makes use of the structurally very simple wheat seedling (maximum height 12 cm) and the simple sandwich box arena. By using this very simple system the basic mechanism by which A. dorsale finds aphids on plants may be easier to identify.

Aphid densities were equivalent per unit area on the ground or wheat seedlings at about one aphid per 10 cm^2. Beetle behaviour was compared in the four possible prey distributions:

No aphids in the arena
Aphids on the ground only
Aphids on the wheat only
Aphids on the ground and the wheat

(i) Results

The frequency of climbing on the seedlings and the time spent searching on the ground or the plant were compared using a sequence of non-parametric statistical tests. (Non-parametric tests were chosen because data were too variable and sample sizes too small to test for under-lying parametric distributions.) For each variable the results

for the four aphid distributions were compared using the Friedman 2-way analysis of variance (Siegel 1956). If this test showed no significant difference then the analysis was taken no further. If there was a significant difference then specific comparisons were made between pairs of distribution results using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956). These further tests showed which of the prey distribution results differed significantly. To do this the significance level of the Wilcoxon test must be changed so that the overall acceptable significance level for all the comparisons remains at $p = 0.05$. The acceptable probability level of $p = 0.05$ must be divided by the a priori number of possible comparisons (m). This is calculated using the formula

$$m = \frac{n(n-1)}{r!}$$

where n = number of treatments

r = the number of treatments in each comparison.

In this case $m = \frac{4(3)}{2(1)} = 6$

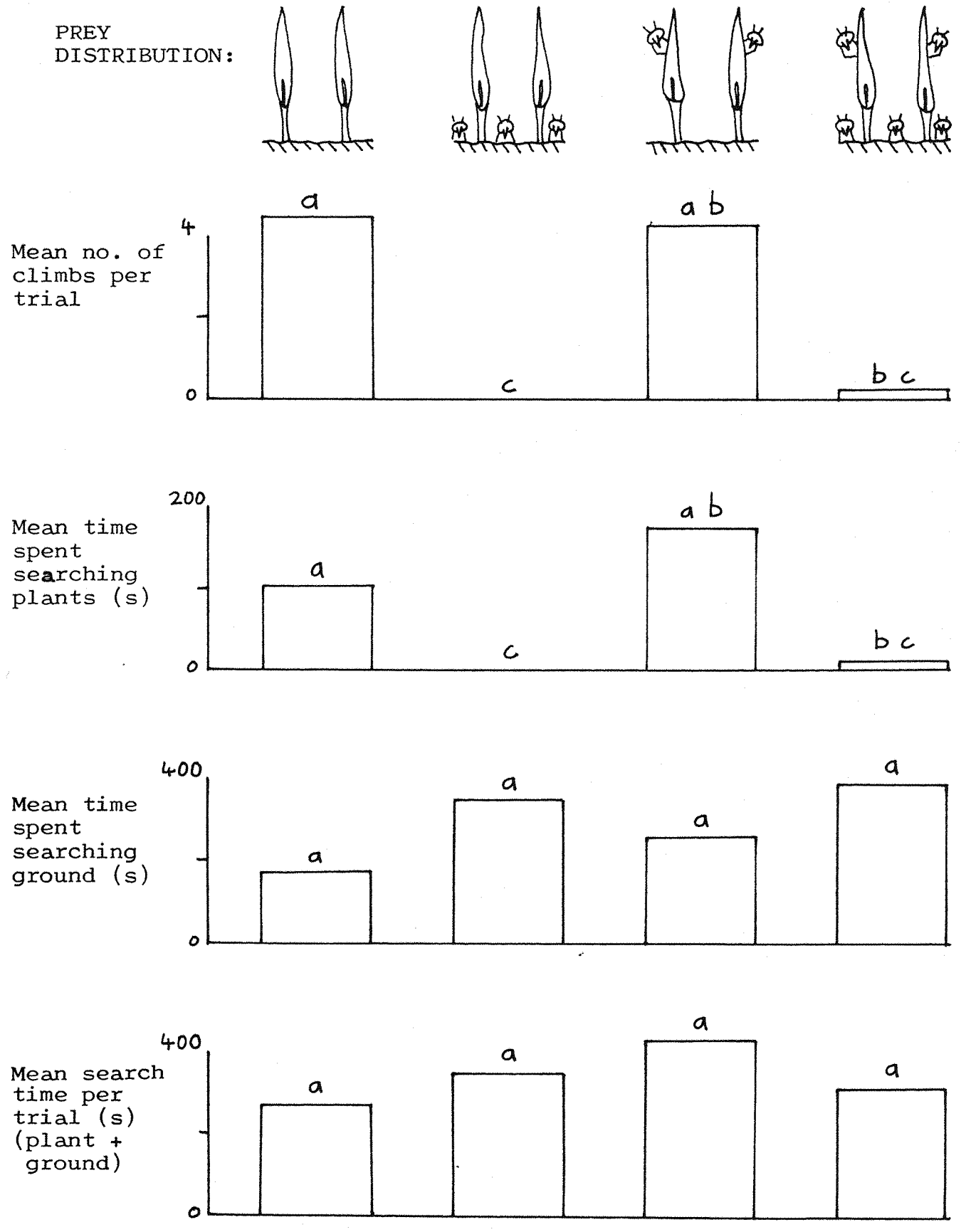
so dividing p by m we have

$$\frac{0.05}{6} = 0.0083 \triangleq 0.01$$

The acceptable probability for each comparison was taken to be $p \triangleq 0.01$ for convenience of reference in statistical tables.

The results and analysis of data are summarised in Figure 5.9. If there were aphids on the ground then A. dorsale did not climb whether there were aphids on the plants or not. If there were no aphids on the ground then the presence of aphids on the plants did not increase the frequency of climbing. A. dorsale may respond to the changing aphid distribution by changing the amount of time spent searching plant or ground rather than the actual number of climbs. A significant amount of time was spent searching the plants only if there were no aphids on the ground. When there were no aphids on the ground, the presence of aphids on the plants did not increase the time spent searching on the plant. The time spent searching on the ground did not change between prey distributions. As time spent searching on

Fig. 5.9 The change in the number of climbs, time spent searching and spatial allocation of search time with different prey distributions.



the ground was much greater than time spent searching on the plant, the total time spent searching did not change significantly between prey distributions.

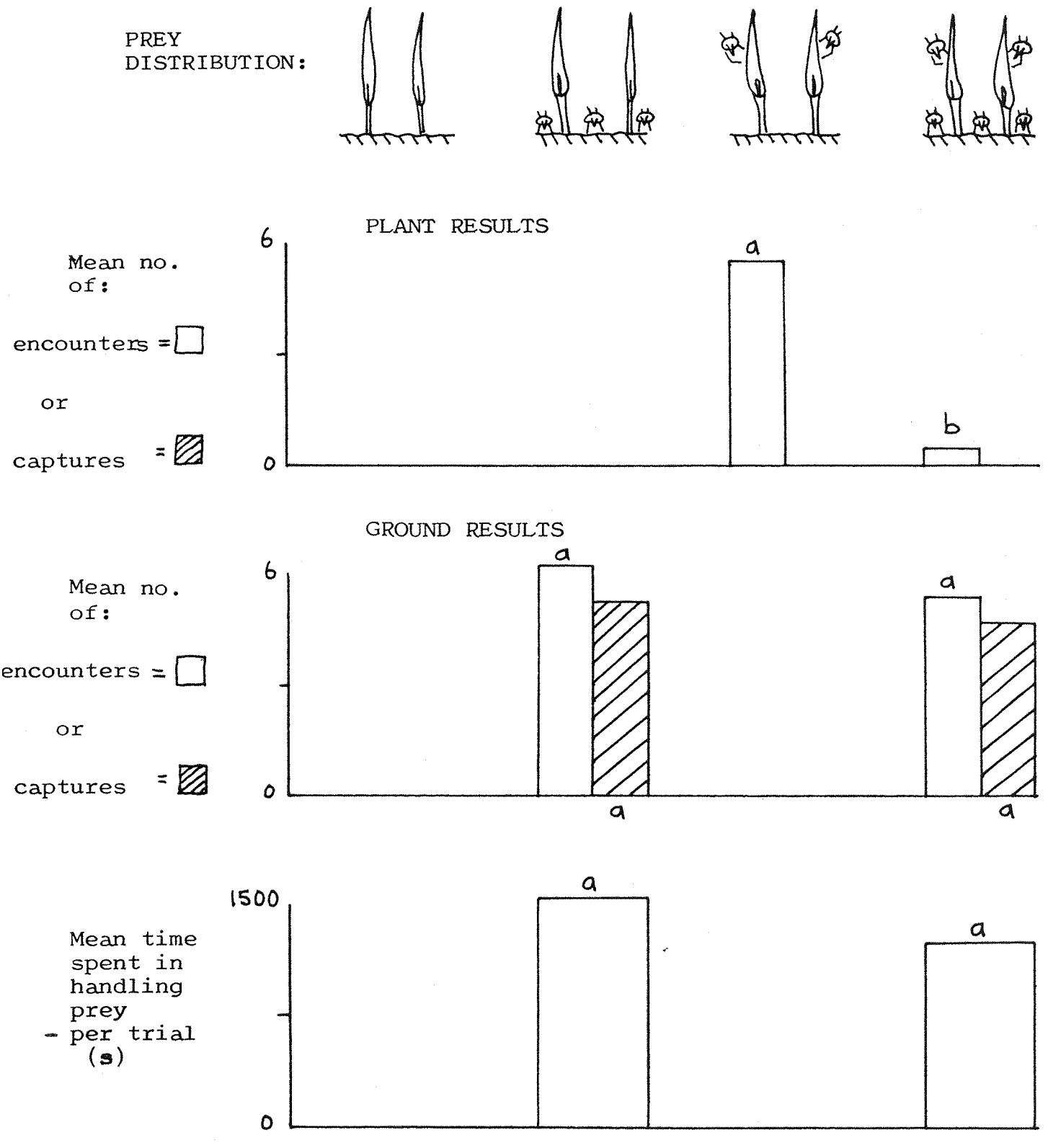
(ii) Discussion

Results show that A. dorsale spends most of its time searching on the ground, only if there were no aphids on the ground did A. dorsale search the plants. The presence of aphids on the plants did not lead to increased climbing or time spent searching on the plants.

These conclusions cannot be extrapolated to cover a field situation for the following reason: although A. dorsale walked over aphids on both plant and ground, only on the ground were aphids caught as a result of these encounters. The data on encounters, captures and prey handling times are summarised in Figure 5.10. Encounters on plants decreased when there were aphids on the ground, this was because both time and frequency of climbs had decreased. Observation during trials showed that in over 90% of "encounters" with aphids on the wheat seedlings A. dorsale walked over the top of the aphid without apparently noticing it. This was because the abaxial surface of the seedling leaf was concave in transverse section and aphids could escape detection by settling in this depression while A. dorsale had to straddle the depression to climb the wheat seedlings. Had A. dorsale captured aphids on the seedlings it may have climbed more or spent more time searching them; The next Section uses fully-grown wheat to look at this.

On the ground there were no significant differences between prey distributions in the number of encounters, captures or mean total times spent handling prey on the ground (Fig. 5.10). The Mann-Whitney U-test (Siegel 1956) showed that there was no significant difference for the percentage of encounters that led to capture of aphids, between these results (84%) and those recorded in Chapter 4.5 (86%). The same test showed that there was also no significant difference in handling time between these results (294 s per aphid) and those of Chapter 4.5 (283 s per aphid). This supports the conclusions of Chapter 4 that capture rate and handling time are based on simple physical properties of the prey (length and volume respectively).

Fig. 5.10 The change in the number of encounters with aphid prey andtime spent handling prey with different prey distributions.



Columns with the same letter are not significantly different at the p=0.05 level.

In summary, although results are inconclusive because A. dorsale could not forage effectively on the plants because they were seedlings, the experiment did show that the beetle was not stimulated to climb by encountering aphids on the ground. Instead A. dorsale behaved opportunistically and concentrated its foraging on areas where it had captured prey. The presence of aphids on the ground did not act as a cue to A. dorsale to search the wheat surfaces above for aphids.

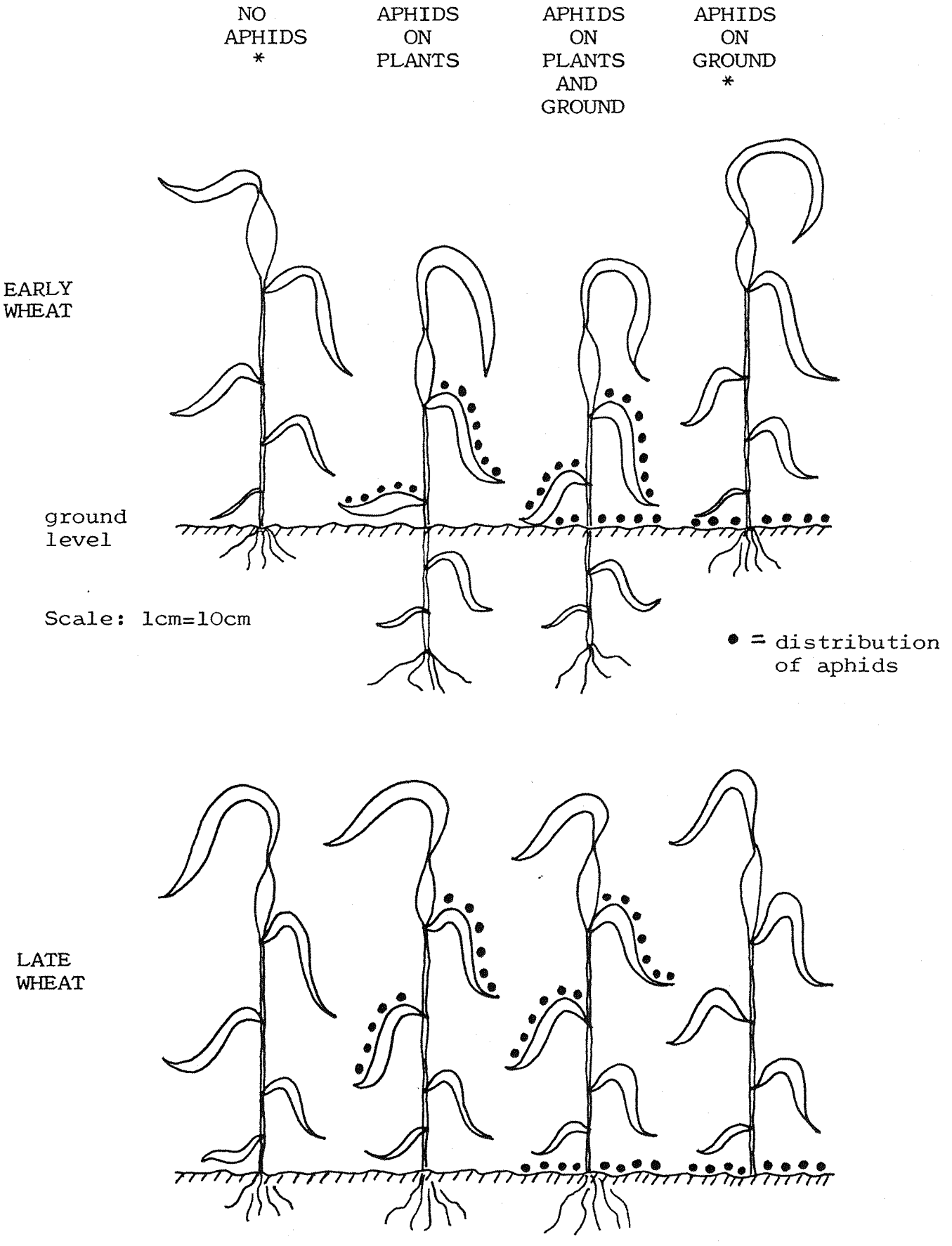
5.6 The effect of aphid distribution between ground and plant on the searching behaviour of A. dorsale using mature, field-grown wheat

The previous Section varied the prey distribution but used a highly simplified arena with wheat at a growth stage that A. dorsale would not encounter in the field (young seedlings). This was probably the reason for A. dorsale showing little tendency to climb and not being able to catch aphids on the plants.

This Section makes use of mature wheat plants removed from the field sites at Damerham farm (Chapter 7). These plants were at about G.S. 8-10 and were normally tillered. They were planted in large arenas at the same density as they would be found in the field. Six arrangements of prey and plants were used to produce two sets of trials representing early or late season conditions (Fig. 5.11). For the early season trials wheat was buried up to the fourth leaf so that aphid infestations were close to the ground. Late season was simulated by planting the wheat normally so that aphids were well above the ground. Aphid densities on the ground were equivalent per unit area to those on the wheat at about one aphid per 10 cm^2 (Equivalent to about 30 aphids per stem) for all prey arrangements.

The same (late season) set of wheat plants and results were used for the "no aphids" and "aphids on the ground" distributions in both early and late season trials. This was because initial observations showed that A. dorsale was not distinguishing between green and senesced leaves and was not climbing high enough for the differences in lower leaf condition and overall plant height caused by burying the

Fig. 5.11 The arrangement of wheat and aphids to simulate early or late season conditions in the wheat field.



(* These plants used in both sets of trials)

wheat for early season trials to be important (see also general discussion for this Section).

(i) Analysis of results

The 30 min recordings of the behaviour of individual beetles were divided into the familiar categories of Search, Eat[1] and Others (Run and Still) (Chapter 3.4). Also recorded were the number, height and duration of climbs. These results were used to find the total time occupied with each behaviour and obtain mean values of each climbing statistic for each individual.

For each variable the results for the four aphid distributions within each trial were compared using an analysis of variance. The Friedman 2-way ANOVA (Siegel 1956) was used because data were too variable and sample sizes too small for the rigorous application of parametric tests. (Related-sample tests (Siegel 1956) could be used throughout because the same beetles were used in all trials.) If this test showed no significant differences then the analysis was taken no further for that variable. If there was a significant difference then comparisons were made between pairs of distribution results using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) to show where the significant differences lay. The significance level of the Wilcoxon test must, however, be changed so that the overall acceptable significance level for all the comparisons remains at $p = 0.05$. To do this the 0.05 probability level is divided by the a priori number of comparisons to be made (m). This correction factor is given by the formula for the number of comparisons possible if n objects are compared r at a time:

$$m = \frac{n(n-1).....(n-r+1)}{r!}$$

Here $n = 4$, the number of prey distributions being compared, and we are comparing $r = 2$ at a time.

[1] Fortunately aphids were eaten where they were caught, making interpretation of results easier.

Hence

$$m = \frac{4\ (3)}{2\ (1)} = 6$$

So dividing p by m we have

$$\frac{0.05}{6} = 0.0083$$

the reduced probability acceptance level for the Wilcoxon test comparisons.

(ii) Presentation of results

The Friedman 2-way ANOVA identified those variables for which there was a significant difference between prey arrangements (Table 5.5). Differences in overall times (plant and ground) occupied by each behaviour were analysed first and these times were then broken down into separate plant and ground times for further analysis. Many of the variables did not differ significantly but means for all these variables are presented to show trends in the raw data. (N.B. although some data are presented in the Figures as "proportion of total trial time" all data were analysed in the form of actual time occupied by each behaviour). In addition the further analyses by Wilcoxon tests of those variables that did differ significantly are presented separately. So for both the early and late season trials three Figures are presented:

The mean number, duration or height of climbs on plants (Figs. 5.12 and 5.15).

The average proportion of time occupied by each behaviour on ground or plant (Figs. 5.13 and 5.16).

The Wilcoxon test analyses on those variables in Figures 5.12/13 and 5.15/16 that differed significantly between prey distributions (Figs. 5.14 and 5.17).

(iii) Early season trials

Climbs seemed greater in number, duration and height when there were no aphids on the ground (Fig. 5.12), but analysis of variance (Table 5.5) showed that only the duration of climbs differed significantly

Table 5.5 Use of the Friedman 2-way ANOVA to show for which variables there were significant differences between the four aphid prey arrangements in the early or late season trials.

PLANT ARRANGEMENT:	EARLY	LATE
Variable Recorded	Significance level of difference between prey distributions	
No. climbs	NS	NS
Duration climbs (s)	$p < 0.05$	NS
Height climbs (cm)	NS	NS
PLANT & GROUND RESULTS		
Search Time (s)	NS	NS
Others Time (s)	NS	NS
Eat Time (s)	$p < 0.001$	$p < 0.001$
PLANT RESULTS ONLY		
Search Time (s)	$p < 0.05$	NS
Others Time (s)	NS	NS
Eat Time (s)	NS	NS
GROUND RESULTS ONLY		
Search Time (s)	NS	$p < 0.01$
Others Time (s)	NS	NS
Eat Time (s)	$p < 0.001$	$p < 0.001$

between prey distributions. Further analysis of the duration of climbs by a series of pairwise comparisons between the four prey distributions (Fig. 5.14) showed that no one differed significantly from any of the others. As there were no consistent significant differences between the prey distributions, the climbs data from all four distributions were pooled and analysed to show the difference in number, duration and height of climbs between trials where individuals captured or did not capture aphids while on the wheat. The Mann-Whitney U-test (Siegel 1956) for paired comparisons with unmatched samples was used:

	Mean values for trials where: Aphids captured	No aphids captured	n	Significance of difference
No. of climbs made	4	3.3	24	NS
Duration of climbs	408	46	62	$p < 0.02$
Height of climbs	8.9	6.5	62	NS

Only the duration of climbs was significantly different.

Changes in foraging pattern by A. dorsale in response to the different aphid distributions could also be shown by differences in the allocation of time to behaviours shown on plant or ground. The upper bar charts in Figure 5.13 show that the proportion of time spent on the plants was always small and decreased when there were aphids available on the ground. This corresponded with increased time spent searching or eating on the ground. Time spent on the plants was high only when all aphids in the arena were on the plants. The lower bar charts in Figure 5.13 show how time was spent on the plants; the data are difficult to interpret because for some trials the number of climbs observed was very small.

Analysis of variance (Table 5.5) showed that for the overall (plant and ground) time spent in each behaviour only time spent eating changed significantly between prey distributions. For time spent in behaviours on the plants only search time changed significantly, on the ground only time spent eating changed significantly. Further

Fig. 5.12 The mean number, duration and height of climbs per beetle for the four prey distributions used in the early season trials.

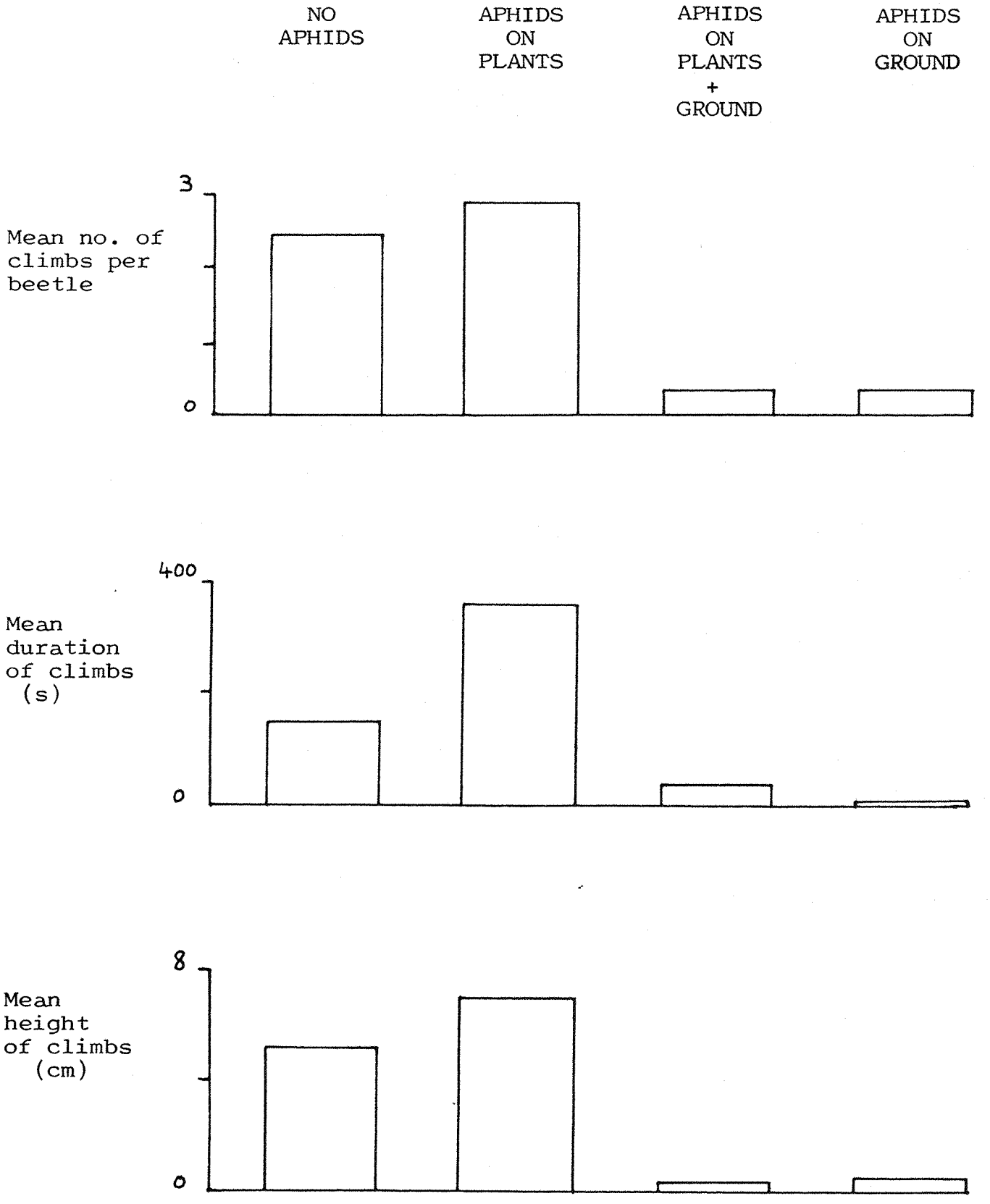


Fig. 5.13 Proportion of time allocated to each behaviour on the ground and on the plant in the early season trials.

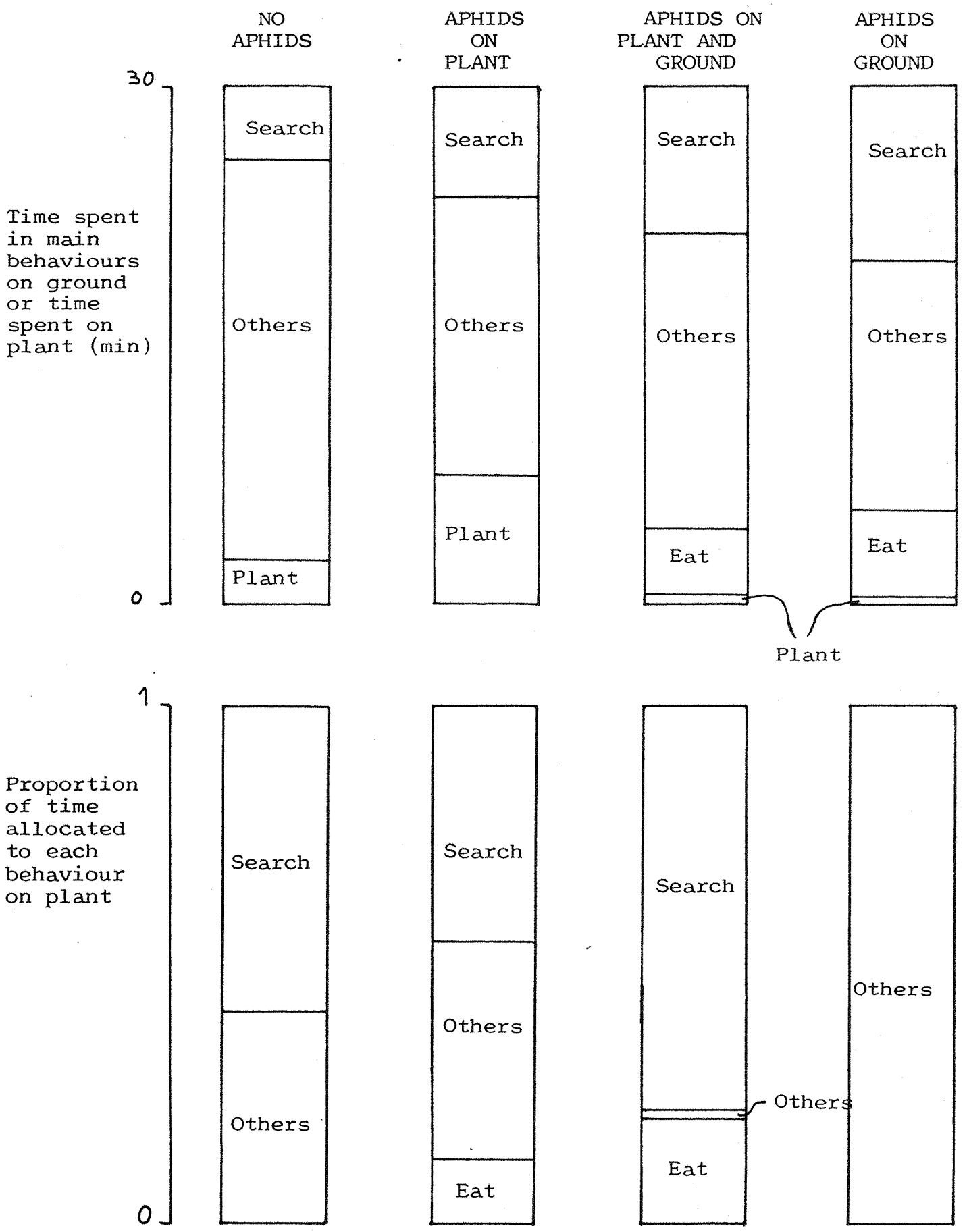
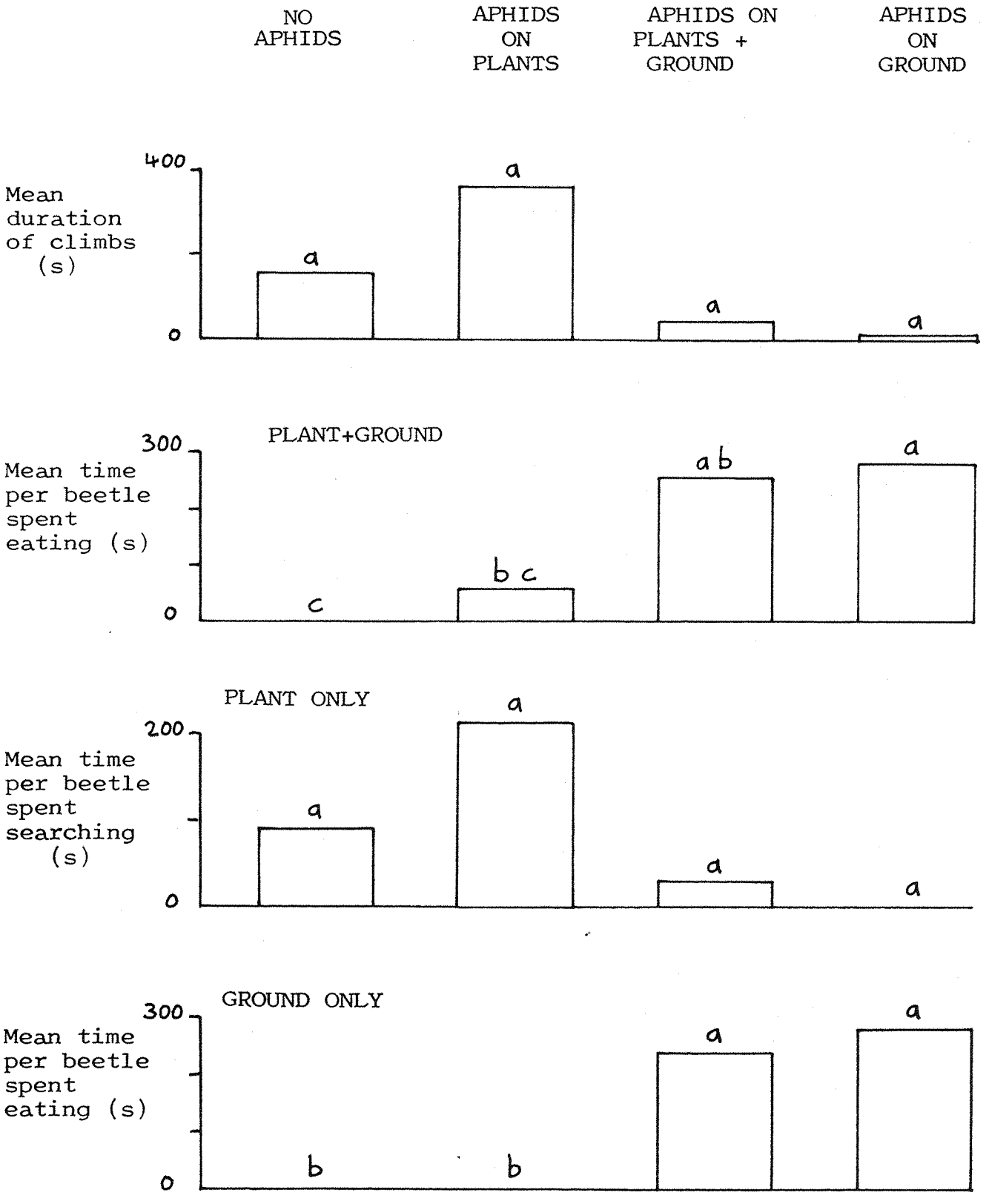


Fig. 5.14 The change in the duration of climbs and time spent searching or eating on the plants or on the ground with different prey distributions in the early season trials.



Bars with the same letter are not significantly different at the p=0.05 level.

analysis by paired comparisons between prey distributions (Fig. 5.14) showed that for time spent searching on the plant there was no difference between prey distributions (even though no time was spent searching for the "aphids on the ground" distribution) which indicates the variation between individuals in time spent on plants. Time spent eating, whether overall or just on the ground, was only significantly different from zero when there were aphids available on the ground. This is because most aphid captures occurred on the ground.

(iv) Late season trials

Again climbs seemed greater in number, duration and height when there were no aphids on the ground (Fig. 5.15), but analysis of variance (Table 5.5) showed that none of these three variables differed significantly between prey distributions. Further analysis of pooled data to show differences between "climbs where aphids were captured" and "climbs where no captures occurred" was not possible because no aphids were captured on plants in any of the trials (see Fig. 5.16).

There were some changes in the allocation of time to behaviours by A. dorsale in response to changing prey distribution. The upper bar charts in Figure 5.16 show that the proportion of time spent on plants was again always small and that it decreased when there were aphids available on the ground. This corresponded with an increase in the proportion of time spent searching and eating on the ground. The lower bar charts (Fig. 5.16) show how time was spent on the plants, again the data are difficult to interpret because of the low frequency and short duration of climbs (Fig. 5.15).

The analyses of variance (Table 5.5) showed that, for overall time, only time spent eating differed significantly between prey distributions. For time spent on the plant there were no significant differences in behaviours between distributions. On the ground time spent both searching and eating changed significantly between prey distributions. Further analyses by paired comparisons between prey distributions (Fig. 5.17) showed that most time was spent searching on the ground if there were aphids available there, although searching was not

Fig. 5.15 The mean number, duration and height of climbs per beetle over the four prey distributions used in the late season trials.

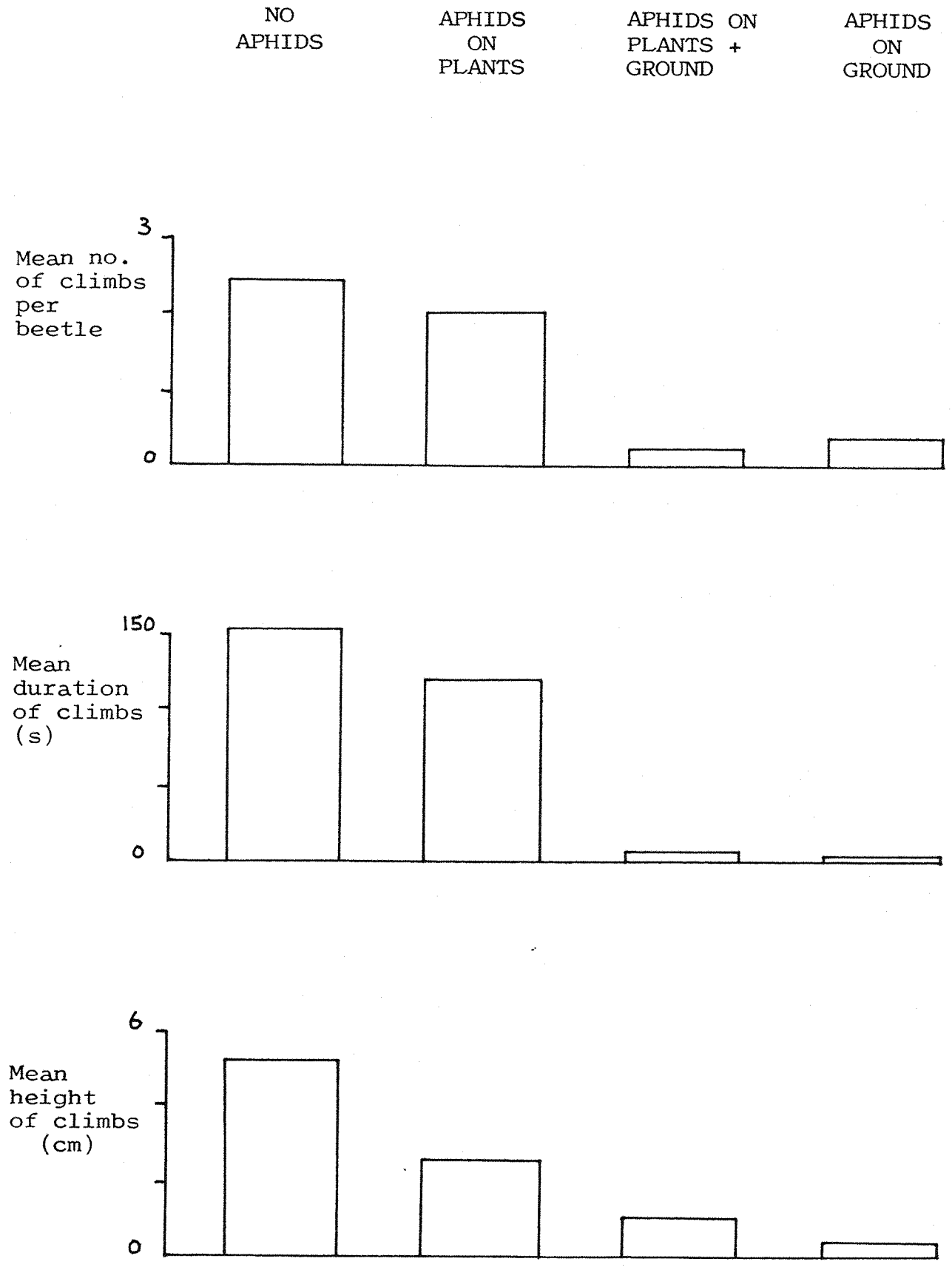


Fig. 5.16 Proportion of time allocated to each behaviour on the ground and on the plant in the late season trials.

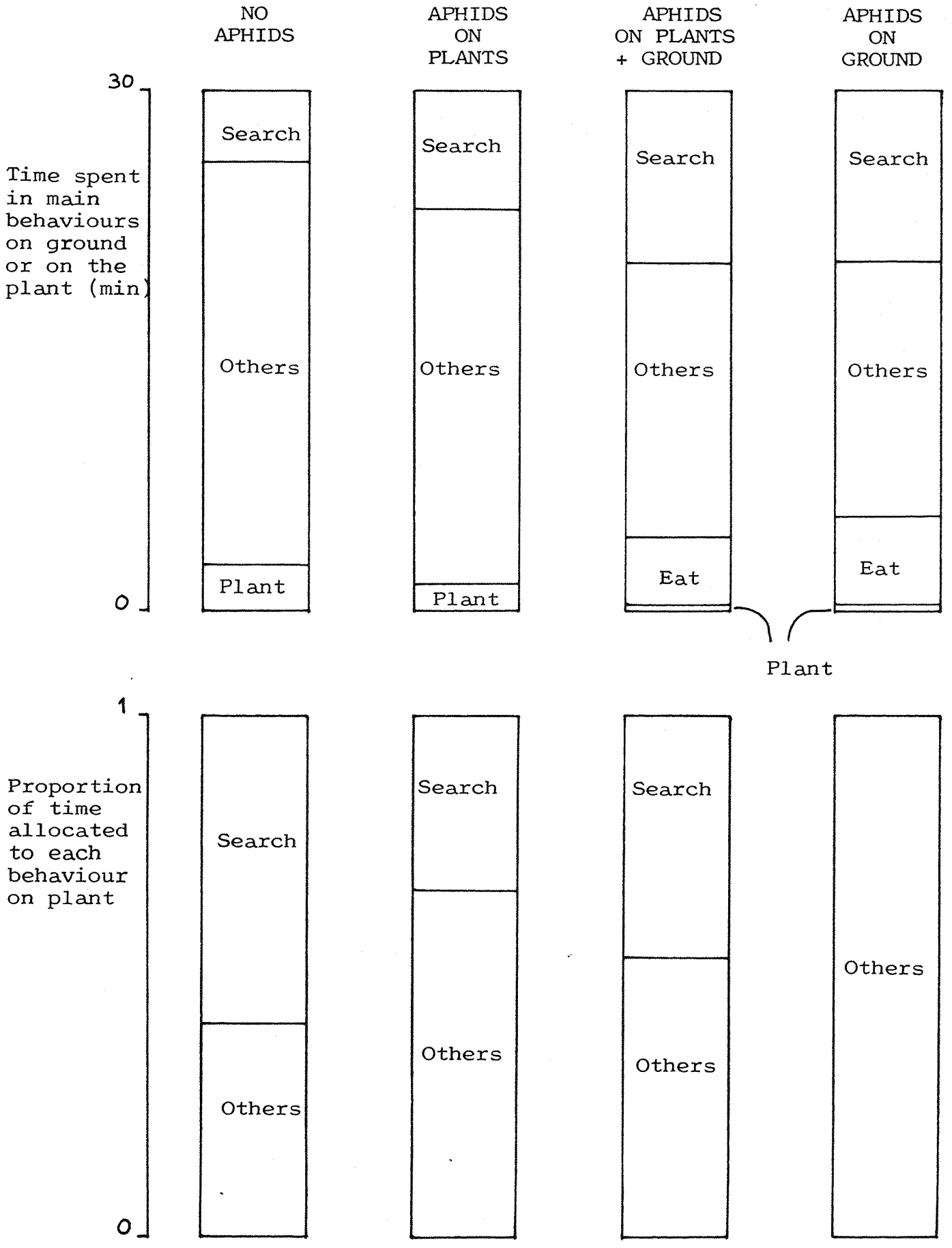
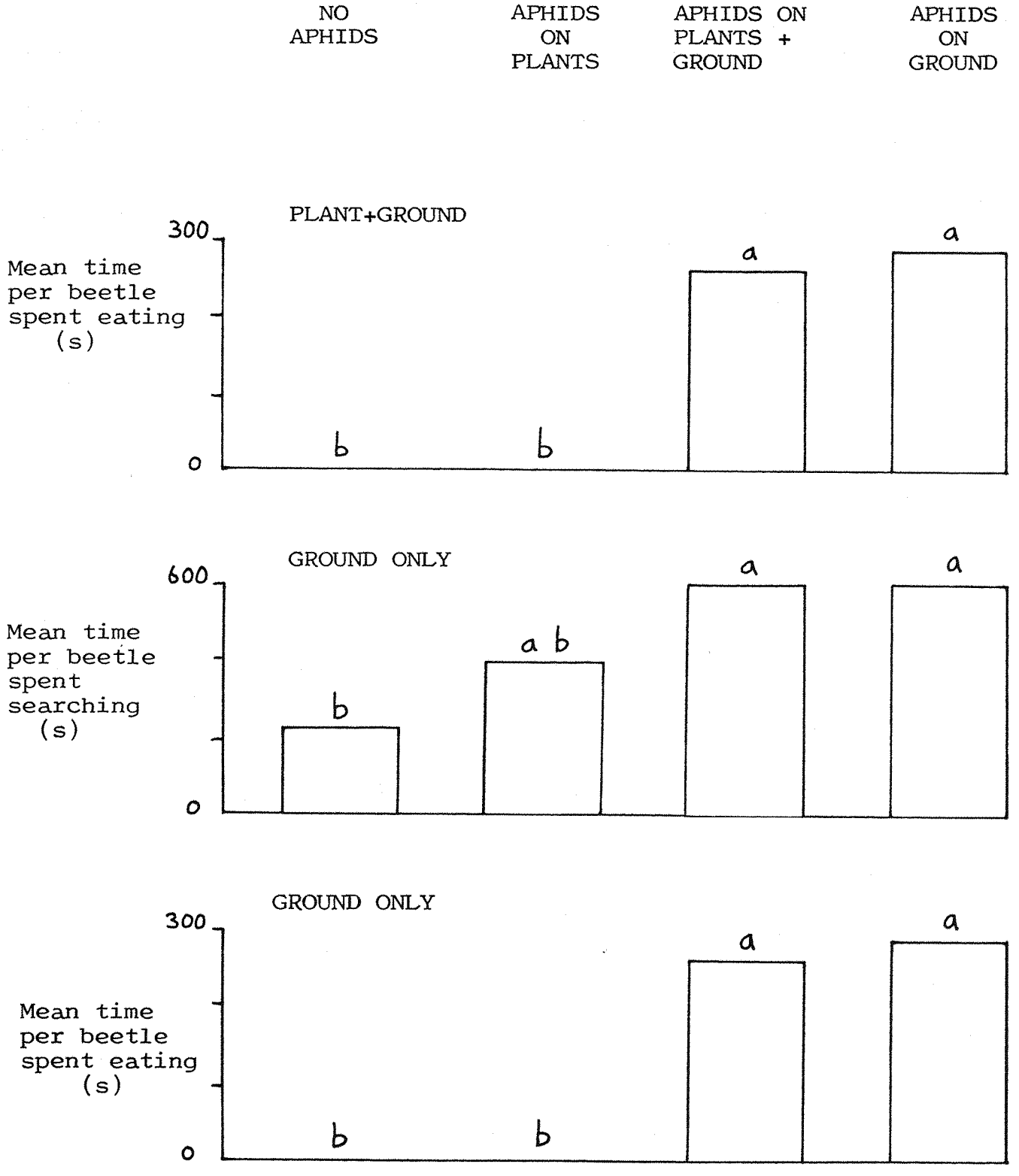


Fig. 5.17 The change in time spent searching or eating with different prey distributions in the late season trials.



Bars with the same letter are not significantly different at the p=0.05 level.

consistently reduced if there were no aphids available. Time spent eating, whether overall or ground only, was only significantly different from zero if there were aphids available on the ground. This is not surprising as captures of aphids occurred on the ground only in these trials.

(v) General discussion of results

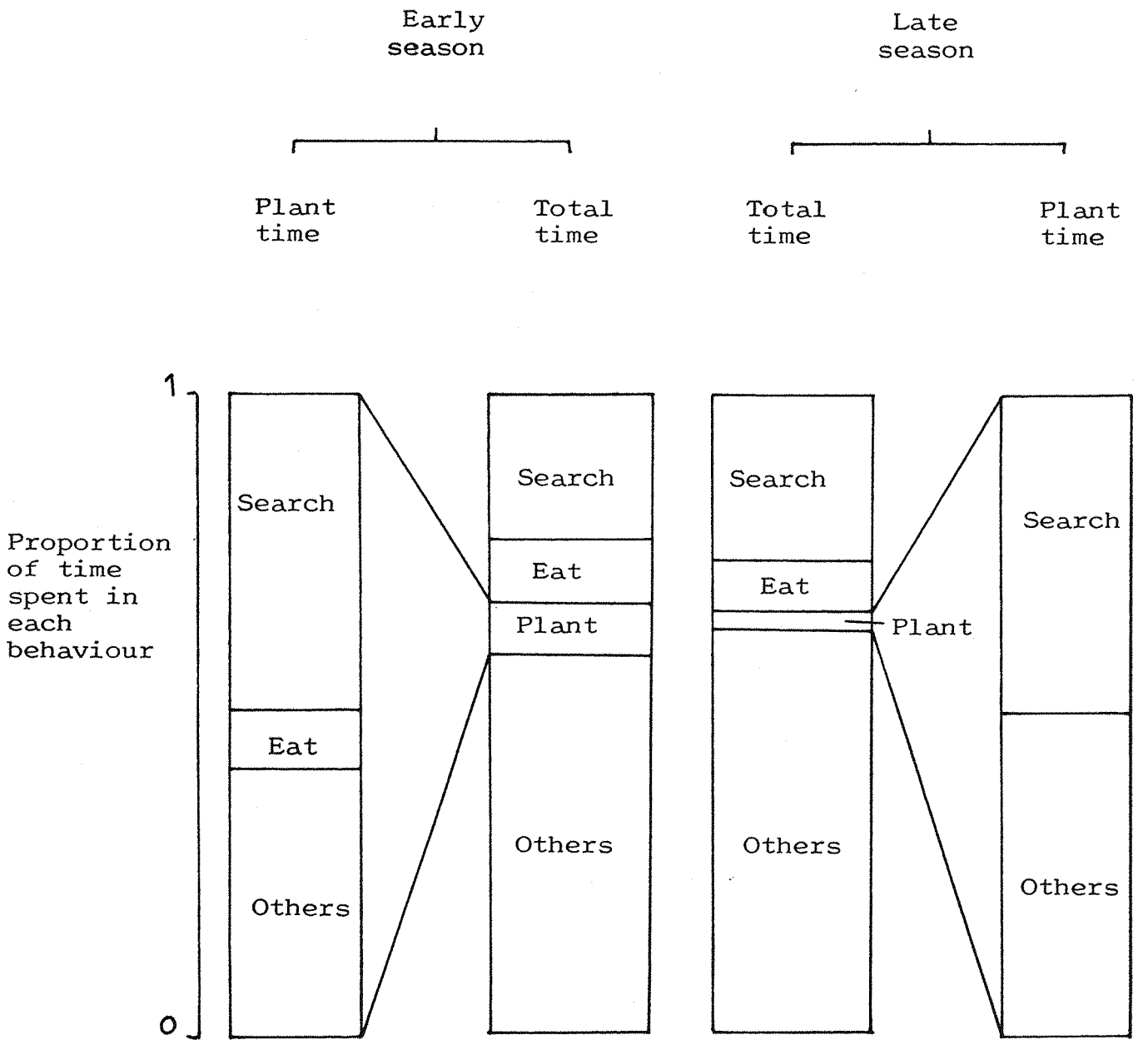
The object of this experiment was to see if A. dorsale could respond to changes in the distribution of cereal aphids between ground and plant in a way that suggested that it had specific adaptations for finding aphids in the field. Examples of this would be if the capture of aphids on the ground stimulated A. dorsale to climb and search the plants for more aphids, or if the capture of aphids on the lower leaves of the wheat led A. dorsale to search the higher leaves and ears (where there are usually higher densities of aphids in field populations).

In both the early and late season trials the capture of aphids on the ground by A. dorsale led to increases in searching and eating there, but not to increases in climbing. The capture of aphids on plants by A. dorsale increased the duration of the respective climb but did not increase the frequency of subsequent climbing behaviour. Furthermore, only a small proportion of the total time available was spent on the plants, suggesting that A. dorsale was not responding adaptively to the change in aphid distributions between trials.

The lack of response to the aphids on the plants (even when aphids were on the lower leaves as in the early-season trials) was also reflected in the general behavioural time-budget of A. dorsale during trials. A comparison of the average proportions of time allocated to each behaviour between the early and late season trials (Fig. 5.18) shows them to be very similar. On plant or ground most time was spent either in the Search or Others (Run and Still) categories of behaviour, but only a small proportion of time was spent on the plants.

Further evidence that A. dorsale was not stimulated to climb by catching aphids on the ground was provided by the sequencing of behaviours i.e. which category of behaviour most often follows another. The categories are now given as a reminder:

Fig. 5.18 The average proportion of time occupied by the three major behaviours on Early or Late season wheat, on the plant and on the ground.



CLIMB	-	all behaviour on the wheat
EAT	-	catching and eating of prey on the ground
RUN	-	fast locomotion (no searching) on the ground
SEARCH	-	slow, prey-searching locomotion on the ground
STILL	-	motionless on the ground

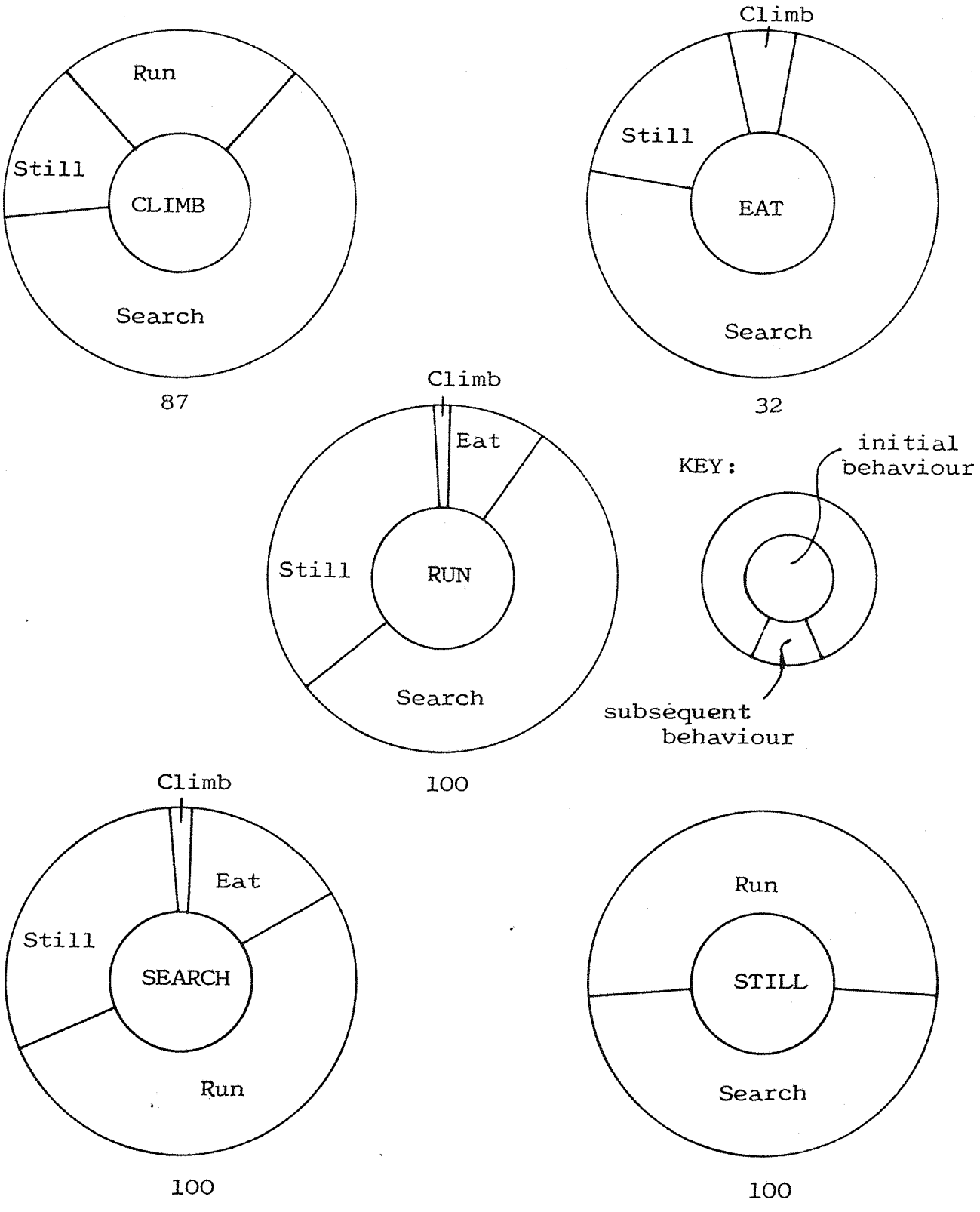
If possible 100 recordings of the initial behaviour with its different subsequent behaviours were extracted from the results. This was not possible in all cases as in total only 32 captures and 87 climbs were observed. The initial and subsequent behaviours are shown as "pie charts" with the angle subtended being directly proportional to the frequency of the subsequent behaviour (Fig. 19).

Of the five behaviours, Climb, Eat, Run and Still were all followed by Search most often, with the frequency of searching being highest after eating. Search was most often followed by running behaviour. All of the three behaviours that could lead to climbing (A. dorsale could obviously not go from Still to Climb) did so only occasionally; no one behaviour commonly led to climbing suggesting that climbs were made at random rather than as a result of a specific behavioural sequence.

A major difference between the early and late season trials was that in the early season trials captures of aphids did occur on the plants, this led to the respective climbs being longer but not higher. More detailed examination of data collected on climbs, both with and without capture of aphids, shows the reason for this and provides further evidence that A. dorsale is not adapted to finding cereal aphids on wheat.

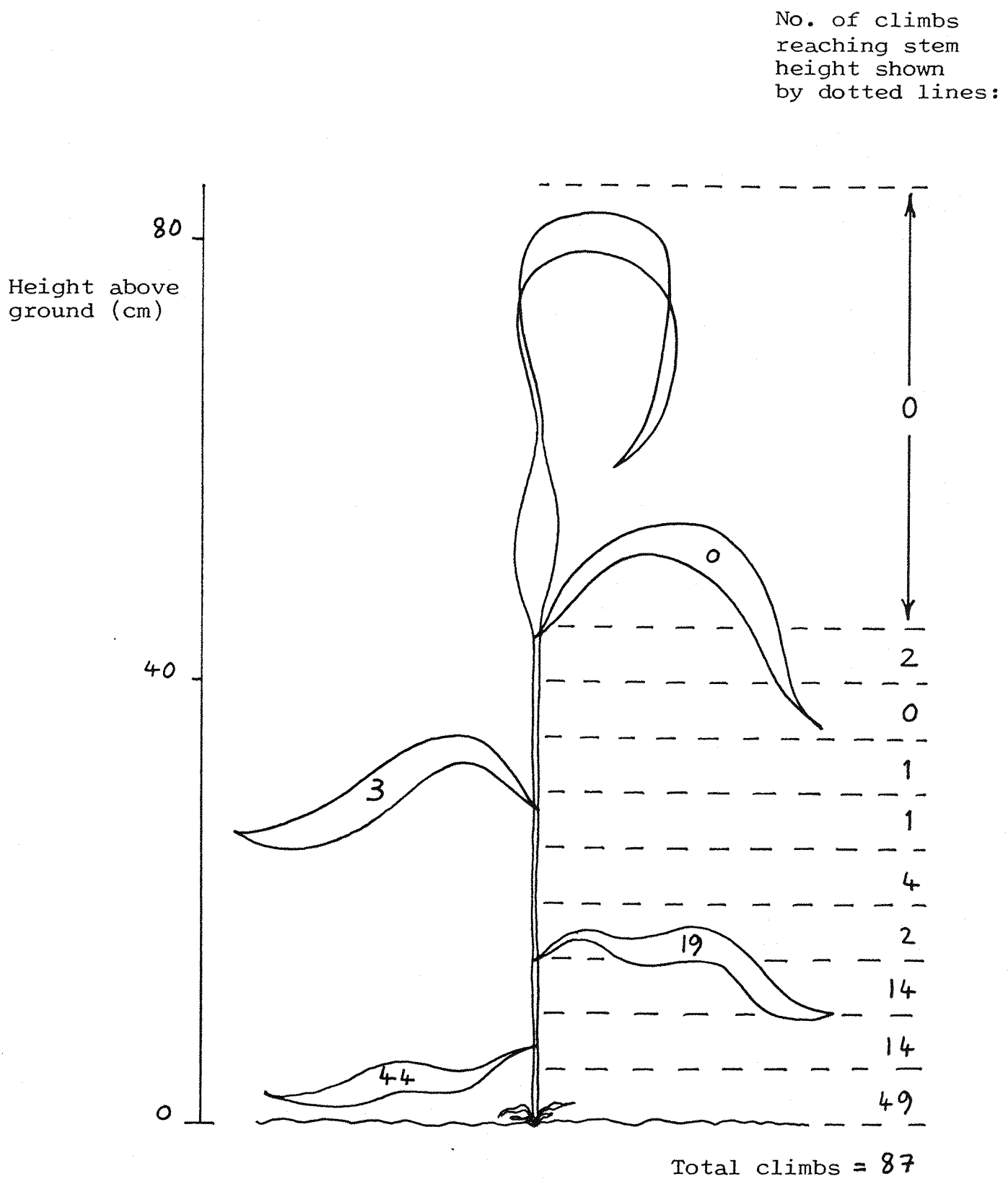
A frequency distribution of the stem height reached by all observed climbs and of which leaves were visited during the climbs is given in Figure 5.20. Nearly all climbs (90%) reached a height of only 15 cm or less and about 95% of visits to leaves were made to the lowest two leaves. A. dorsale will only encounter, and hence capture, aphids if the aphids are distributed on the lower parts of the wheat (as in the early but not the late season trials).

Fig. 5.19 Pie charts to show the frequency with which each of the major behaviours follows the others.



Numbers below pie charts show the number of observations on which the charts are based.

Fig. 5.20 The frequency distribution of heights of climbs up wheat stems and climbs onto leaves.



Numbers on leaves show frequency of climbs onto those leaves.

The early season trials showed that capture of aphids on plants by A. dorsale led to longer but not higher climbs. Close observation of A. dorsale on the plants before and after capture of aphids showed that this was because the beetle showed the same area restricted search pattern as described in Chapter 4.4 The beetle slowed down and turned frequently in the area of the capture, whether on stem or leaf. A comparison of the length of stem or leaf searched per second before and after an aphid capture, showed that it dropped significantly from about 0.75 cm/s to about 0.2 cm/s (Wilcoxon matched-pairs signed-ranks test, Siegel 1956). This behaviour led to A. dorsale searching the lower areas of the wheat vigorously after capturing an aphid but not climbing further up the stem.

In addition, as the lower leaves in early season trials were green while those in the late season trials had senesced (but were still structurally sound), it was possible to test whether A. dorsale could discriminate between these two types of leaf (aphids cannot feed on senesced leaves and hence are rarely found on them). A. dorsale visited both types with equal frequency (Mann-Whitney U-test, Siegel 1956), the number of visits per beetle that climbed being 4 to senesced leaves and 2.7 to green leaves. This lack of discrimination between healthy and dead leaves suggests again that A. dorsale is not specifically adapted to finding aphids.

Finally, observation of aphid captures showed that searching on the wheat introduced new factors which lowered the success rate with which A. dorsale caught aphids. These seemed to be a combination of A. dorsale knocking aphids off the plant and walking over the top of aphids. Success rate on the ground was similar to that found in the functional response experiment of Chapter 4:

$$\% \text{ successful encounters} = \frac{\text{no. aphids eaten/captured}}{\text{no. aphids encountered}}$$

$$\text{On the wheat} \quad \frac{10}{21} = 48\%$$

$$\text{On the ground} \quad \frac{20}{24} = 83\%$$

The lower capture success rate suggests that A. dorsale is not adapted to catch cereal aphids on the curved and angled surfaces presented by the wheat.

In summary, A. dorsale seems to adopt a general predator's strategy of searching the immediate area where it finds prey. There was no suggestion that finding aphids on the ground caused A. dorsale to climb and search the wheat. Search patterns on the wheat suggested that A. dorsale searched only the immediate area of a prey capture and was not stimulated to search further up the wheat (S. avenae is usually found on the flag leaf and ear in the field). Searching was concentrated on the ground with only occasional climbs on to the wheat. This, combined with the low height of climbs, suggests that A. dorsale will only encounter aphids on the wheat in the early season (mid May) when the aphids are distributed on leaves close to the ground.

5.7 Discussion

The adaptations shown by predators to finding their prey reflect both the mobility of the predator and the spatial and temporal behaviour of the prey population. A stable prey population (one that is evenly distributed through a habitat and present throughout the active life of the predator) gives the predator the opportunity to become highly adapted to catching that type of prey. An unstable prey population (one that is patchily distributed in a habitat and present only spasmodically) presents the predator with two options:

The predator could be highly mobile with sophisticated sensory adaptations to enable it to find the patches of prey within the habitat (or undergo migration when the habitat contained no prey patches).

Alternatively, the predator could be less mobile and less well adapted and could feed off alternative prey when the primary prey was absent or could not be found in the habitat.

A. dorsale, if it genuinely prefers cereal aphids (see Section 5.1, Introduction), has a primary prey which is unstable in space and

time. The advantage of feeding on cereal aphids is, that while present, they are highly aggregated on the wheat plants (Vickerman & Wratten 1979). Thus once an aggregation has been found they represent a highly abundant and easily captured (Chapter 4) source of prey. The disadvantage is that A. dorsale, like many carabids, is flightless (Thiele 1977) and so must travel from aphid patch to aphid patch on the ground. Given this, A. dorsale must be highly mobile and able to detect aphid aggregations from the ground (random climbing of stems to find aphids would be very inefficient). A summary of a gradient of possible adaptations which A. dorsale could show to enable it to detect and find cereal aphid aggregations is given in Table 5.6. The differences between adaptations would probably be small in terms of predator behaviour in the field but they do represent a changing overall efficiency, e.g. honeydew detection is less efficient than detection of kairomones released directly by the aphids because honeydew can persist after the aphids have gone.

In the Introduction to this Chapter it was shown that although A. dorsale is polyphagous it seems to show a preference for cereal aphids; this implies that it should show some level of adaptation for detecting cereal aphids (Table 5.6). It was also discussed how the most advantageous of these adaptations, long-range detection of aphids by air-born kairomones, was unlikely to be effective because of the wind profile in cereal crops. Experiments (Sections 5.2/5.3) showed that A. dorsale did not respond to the presence of aphids or honeydew, the most feasible sources of such kairomones, suggesting that as predicted the beetle had not developed an adaptation for long-range detection of aphids.

Short-range detection of aphids either by detecting kairomones from aphids, honeydew or aphid exuviae, or by coming into physical contact with honeydew or aphid exuviae also did not occur (Sections 5.2/5.3). In terms of Table 5.6 this now limits A. dorsale to short-range detection of aphid patches by physical contact with aphids (but no perception of aphid distribution within the patch) or random foraging.

Table 5.6 The different levels of adaptation that A. dorsale could show for the detection and locating of cereal aphids

Level of Adaptation	Distance of prey detection	Level of predator sensitivity	Predator behaviour	Underlying mechanism
HIGH	LONG RANGE	PREY PATCH AND DISTRIBUTION WITHIN PATCH	Detects patch at long range and then homes in on individual prey within patch.	Kairomone detection followed by anemotaxis to the patch. At the patch the kairomone concentration gradient leads to individual prey.
		PREY PATCH	Detects patch at long range, then searches randomly for prey within it.	Kairomone detection followed by anemotaxis to the patch.
	SHORT RANGE	PREY PATCH AND DISTRIBUTION WITHIN PATCH	Searches randomly until close to patch, then homes in on prey	Finds patch by local detection of kairomones (including honeydew) or exuviae or aphids on the ground. Then uses a kairomone concentration gradient to find prey.
		PREY PATCH	Searches randomly until close to patch, then searches randomly within the patch area.	Finds patch by local detection of kairomones (including honeydew) or exuviae or aphids.
LOW	INSENSITIVE TO DISTRIBUTION	PREY	Discovers prey completely randomly.	Environmental factors, availability of alternative prey, temperature, etc.

If A. dorsale responded to contact with aphids on the ground by climbing surrounding wheat stems this would give it the ability to detect aphid patches, although search within the patch (i.e. choosing the right stem to climb) would be random. Experiments to show this response on seedlings failed because the structure of the plants made it difficult for A. dorsale to climb and find aphids on the seedlings (Section 5.5). The stem and leaf structure close to the ground of mature plants, however, was shown not to influence the climbing frequency and behaviour of A. dorsale (Section 5.4). This meant early (aphids on lower leaves) and late season (aphids on upper leaves/ears) wheat field distributions of aphids could be simulated in the laboratory. This was done using plants at the same growth stage but partially burying some to bring leaves with aphid infestations closer to the ground and so simulate early season conditions. These experiments (Section 5.6) showed that A. dorsale did not respond to the presence of aphids on the ground by climbing the wheat more often. Furthermore, although A. dorsale did capture aphids while on the wheat, and though this did stimulate the beetle to spend more time searching there, it was not stimulated to climb higher up the wheat (where most aphids would be aggregated) or subsequently to climb more frequently. Searching for further aphids occurred only in the area of the original encounter. The results were consistent with a general predator which although capable of preying on aphids, would be unable to detect the distribution of the aphids either across the field or on the wheat plants.

The brief survey of the Carabidae family (using Thiele 1977; Erwin et al. 1979; Crowson 1981) and their characteristics showed no known examples of sophisticated adaptations (e.g. kairomone detection) to prey detection and capture. A. dorsale proved to be no exception; there were no responses to any of the cues most likely to be used by a predator to catch aphids. These results imply that A. dorsale is unlikely to be useful in controlling cereal aphid populations; if there is no obvious adaptation for detecting aphids, how can the beetle find aphids when the aphids are at low field densities and why should it "choose" aphids rather than other prey?

Despite these results, previous field-based work (Sunderland 1975; Sunderland & Vickerman 1980) does suggest that A. dorsale "prefers" aphids. In addition, sampling in this project (Chapter 7.3) showed that even when aphids were at field densities as low as 30 per m^2 (equivalent to about 0.05 aphids per tiller) about 10-15% of beetles contained aphid remains. The results of these field samples are difficult to explain if A. dorsale has no adaptation to finding cereal aphids.

It may be that A. dorsale uses a less specific adaptation to catch prey, e.g. the beetle "optimally forages", and that aphids are the most profitable prey, or habitat factors may combine to make aphids the most available prey. The next Chapter looks more generally at the way in which A. dorsale "chooses" prey that it would encounter in the field.

C H A P T E R 6

CHAPTER 6

THE BASIS OF PREY CHOICE BY A. DORSALE

(See Chapter 2.6 for material and methods)

6.1 Introduction

In the previous Chapter the hypothesis that A. dorsale had adapted to feed mainly on cereal aphids was investigated. The general conclusion was that A. dorsale did not show any finely-tuned adaptations for predation of cereal aphids and that its behaviour was typical of a general or opportunistic predator. If A. dorsale is truly a generalist predator it may concentrate on aphids for one of two reasons. A. dorsale may be optimally foraging (maximising the net rate of food intake) and aphids may be the most appropriate prey for this. Alternatively, the beetle may be incapable of distinguishing between the prey types available and it catches mostly aphids because they are the most common, the least able to escape and so on.

If A. dorsale was optimally foraging, how would this fit in with the current theories of foraging and the likely conditions of prey availability in a wheat field? Modelling has indicated which would be the most important variables for a predator to assess to forage optimally.

Estabrook & Dunham (1976) showed how three major prey variables were different in their ease of assessment by a predator. Their findings are summarised in Table 6.1. Essentially they argue as follows. A predator like A. dorsale could optimally forage using the absolute abundance of prey; when abundance was high the predator would be less hungry and could afford to choose profitable prey types; as abundance decreased the predator would become hungry and cease to be selective of prey. Alternatively, in a habitat where total abundances of prey items were more constant the predator would have time to develop a search image for those prey with a high net food value. In both these cases

Table 6.1 Prey parameters and their ease of evaluation by predators (after Estabrook & Dunham 1976)

Variable	Importance in model	Rate of change in nature	Ease of evaluation by predator
Absolute abundance of prey types	Highest	Moderate-high (e.g. weekly)	Easy; hunger state of predator used
Net food value of prey types	High	Very slowly (e.g. monthly)	Easy; search image of predator used
Relative abundance of prey types	Low	Very high (e.g. daily)	Hard; mechanism not clear

the variable assessed would change sufficiently slowly for the mechanism used by the predator to be effective. The relative abundance of prey types is always likely to change the most rapidly (even small changes in absolute abundances or net food values of prey types can produce large changes in relative abundances). This could make continuous sampling of prey necessary if the predator were to forage optimally. In the wheat field, abundances of prey are never very constant, making it unlikely that A. dorsale could develop efficient search images based on relative prey abundances or net food values. If A. dorsale were to forage optimally it should use the absolute abundance of prey to guide its strategy.

Other works give further clues as to how A. dorsale should behave in selecting its prey. It may be that cereal aphids offer a particular quality, such as nutrients, rather than high net food intake. This may cause A. dorsale to prefer them even at some energetic cost (Pulliam 1975); even so if the abundance of this preferred prey declines too much a more general strategy of taking any prey available should prevail (Cody 1974). This is particularly relevant to A. dorsale which may be confined by lack of mobility to single fields where the abundance of cereal aphids will be unpredictable. The taking of less profitable (or preferable) prey in conditions of general prey scarcity has also been predicted by Emlen (1966) and Stenseth & Hansson (1979): either prey are so widely spaced that the energetic costs of ignoring any prey encountered are prohibitive, or at low prey densities the predator rapidly over-exploits the optimal prey and is forced to take the less profitable types. Hughes (1979) has shown that even when prey is abundant, a predator may not select the most profitable prey because the differences in value of the various prey types may be too slight for the development of an optimal foraging technique to be profitable. Erichsen, Krebs & Houston (1980), as a corollary of Hughes' work, have shown that selection of these less profitable preferred prey can also occur in conditions when the predator takes some time to recognize prey (either because the prey is cryptic or because the predator lacks the sensory equipment to distinguish the prey). Clearly it is important to establish whether A. dorsale exists in a habitat with an abundance of prey and also what its capacity for recognizing the value of prey types is.

How likely is it that an invertebrate predator such as A. dorsale can show complex foraging behaviour? The work of Griffiths (1975) suggests that invertebrates (and some larval vertebrates) will take prey as it is encountered (number maximizers) while vertebrates will select profitable prey (energy maximizers); his reasoning for this was as follows. A number maximizer merely catches prey as it encounters them but an energy maximizer must integrate information on size and abundance of prey. To cope with this a predator must either have a complex neural system to learn and adjust to short-term changes in prey abundances or be sufficiently long lived to allow time for a slower rate of learning and adjustment. Both these requirements make it unlikely that an invertebrate could be an energy maximizer. Griffiths compared the food profiles predicted for either a number or an energy maximizer with the prey profiles observed by other workers for a range of predators. He found that as predicted, invertebrates (and larval vertebrates) fed as number maximizers while vertebrates fed as energy maximizers. Hughes (1979) proposed a different underlying cause for this division between invertebrates and vertebrates. The model he used showed that predators would feed as number maximizers whenever recognition times were large or there was a high probability of misidentifying prey. Many invertebrate predators do not use sight to identify prey; the consequential reliance on tactile or chemical identification may increase recognition times and misidentifications sufficiently to preclude identification of prey before consumption. A. dorsale is an invertebrate and a non-visual (tactile) hunter suggesting that it is likely to be a number maximizer rather than an energy maximizer; it will not be an optimal forager.

The models discussed up to this point have really applied to predators in "equilibrium" with their environment; the predator has already encountered and assessed the prey and patches in the habitat. If the predator finds itself in a new habitat or the prey change rapidly in the habitat how much time should it spend sampling? This is an important question in the life of A. dorsale which has firstly to enter a cereal crop containing prey of unknown quantity and quality and then exist in this habitat of rapidly changing prey types and abundances. Cowie & Krebs (1979) used a model in which the amount of

sampling necessary was essentially decided by the difference in value between the prey types or patches and the available resources that could be devoted to sampling. If there is a big difference between the prey or patches available only a small amount of sampling will be needed to show this. If the predator has only a limited resource it pays to use this to catch any prey encountered rather than incur the expenses of sampling from which no future benefit can acrue. In addition, if the habitat changes rapidly, extensive sampling becomes inefficient because prey availability changes too rapidly for the predator to benefit. A. dorsale is a tactile predator and its relatively poor discriminatory powers will in effect reduce the differences between prey types. The beetle's low mobility limits its resources (particularly time) for sampling and its habitat is one of rapidly changing prey abundances. With these constraints it seem unlikely that A. dorsale will devote much if any time to sampling. As "Sampling is an implicit necessity of optimal foraging models" (Krebs, Kacelnik & Taylor 1978) the beetle is probably not an optimal forager.

True optimal foraging implies that a predator changes its strategy as conditions change; models have framed this in terms of the predator having to assess its average net intake of food and because no simple mechanism for acquiring this information has been specified, foraging has come to be associated with vertebrates. There are, however, examples of optimally foraging invertebrates. Elner & Hughes (1978) showed that the shore crab takes mussels so as to maximize its energy intake, but the same crabs attacking dogwhelks (Hughes & Elner 1979) attacked all sizes, although in the laboratory a clear optimum size was demonstrated. The crabs seemed unable to determine the yield of dogwhelks; this demonstrates that invertebrates may have the neural apparatus to forage optimally but that this may be restricted to perhaps only one commonly encountered prey type. Forms of optimal foraging have been shown for other invertebrates; for hymenopterous parasites (Cook & Hubbard 1977; Hubbard & Cook 1978), for a ladybird and water boatman (Cook & Cockrell 1978) and for bumblebees visiting flowers (Pyke 1978). A failing of some of these studies is that the models with which the real data are compared imply that the invertebrates would have to be capable of learning and of calculating net food intake.

The study of the parasitoid Nemeritis canescens by Waage (1979) accounted for its ability to optimally forage with a simple innate behavioural mechanism. The inflexibility of this mechanism means that the parasitoid does not always forage optimally but this is more than compensated for by allowing the parasitoid to exploit patches immediately without first using a time-consuming sampling program of the environment. As Cowie & Krebs (1979) point out, birds face a wide range of conditions in their lifetime and so need to be able to adjust accurately to them. Foragers such as insect parasitoids, are confronted with a less variable environment (they may use only one host species for instance) and simple, albeit inflexible, innate responses cope adequately with this.

In summary, it seems that A. dorsale is most likely to respond to the cue of prey abundance when optimally foraging. In conditions where prey are scarce or hard to recognise or differences between prey types are small, it is unlikely that the beetle will optimally forage. The beetle is more likely to show a fairly simple strategy of foraging applicable to the short period it spends in the crop, rather than the more flexible/adaptable strategies of some longer-lived vertebrates.

As in the last Chapter, it should be possible to distinguish various levels of adaptation shown by A. dorsale; these would point to differing levels of sophistication in foraging. In essence the approach of this Chapter is to establish the size range of prey taken by A. dorsale and then to ask the following questions which infer a successively decreasing level of adaption:

Can A. dorsale distinguish between cereal aphid species?	High level of adaption, sophisticated foraging technique; energy maximizer.
Can A. dorsale switch between two prey types commonly encountered?	
Can A. dorsale distinguish between any prey types encountered?	
Does A. dorsale catch prey in the ratio available to it?	Low level of adaption, catch prey as encountered; number maximizer.

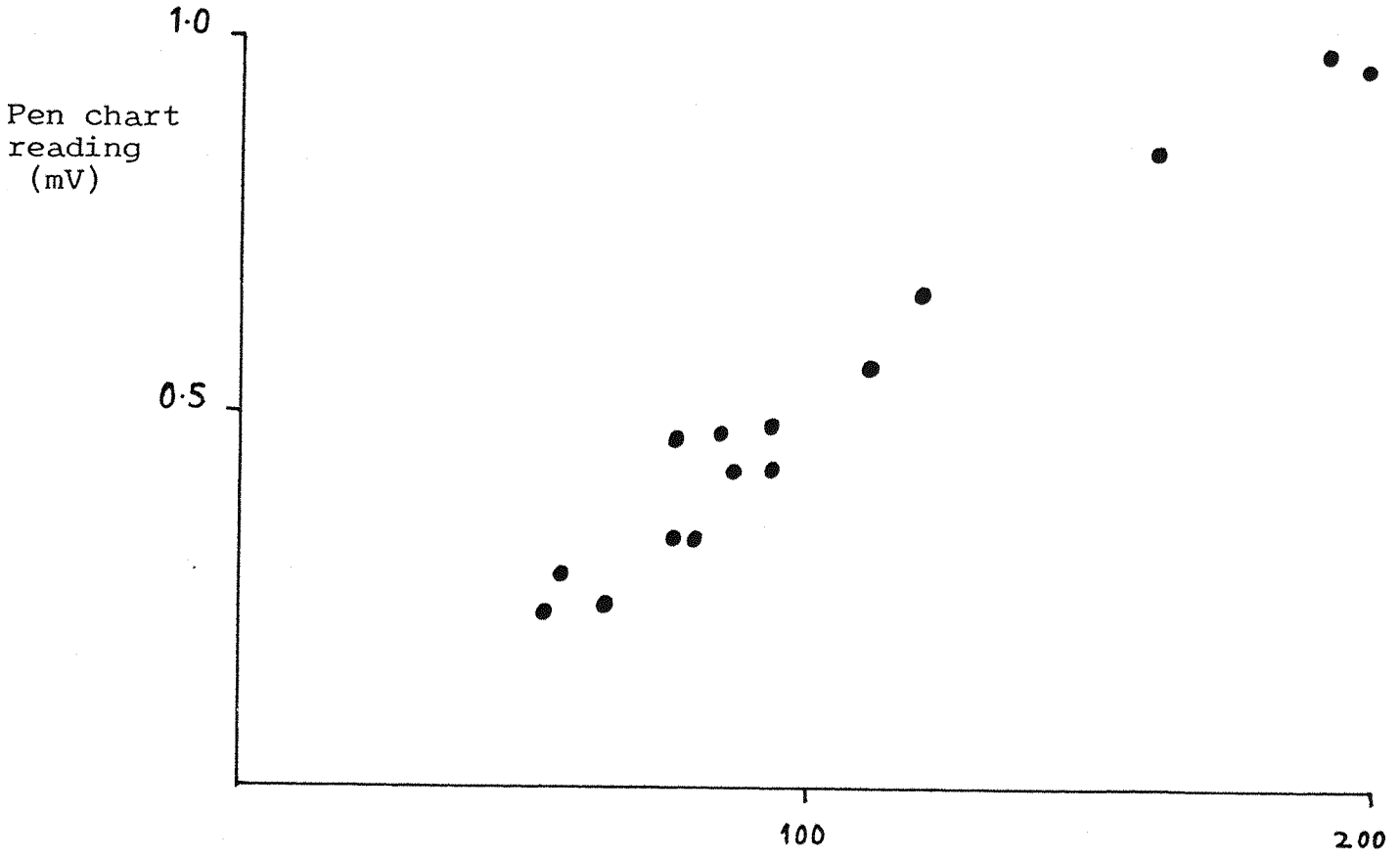
6.2 Micro-bomb calorimetry of prey types commonly found in wheat fields

Studies on optimal foraging require that the energy yield of the prey available is known in some detail; this information is then combined with factors such as prey handling times to give an estimation of the net energy yield of the prey to the predator. The calorific content of prey likely to be taken by A. dorsale was measured using a micro-bomb calorimeter (Phillipson 1964) which allows the estimation of the energy content of very small amounts of material.

The bomb calorimeter does not have a direct calory read-out but must be calibrated so that the output in mV can be converted to calories of energy released by the combustion of the prey. The calibration is achieved by combusting known amounts (and hence known calories) of benzoic acid and plotting these against the resulting readings in mV from the recorder. The resulting calibration curve (Fig. 6.1) is a straight line passing through the origin; the gradient of this line represents the conversion factor for changing mV readings into calories; that is 0.00496 mV = 1 calorie. The relationship was a very strong one implying that variation in later readings for prey types originated from the material combusted rather than inherent variation in the method itself. This was important because only a few firings were possible for each prey type as each firing required the freeze-drying and individual sorting of large numbers of prey. Hence any variability in the method itself would have added a large component of variation to results.

As sorting of prey was very labour-intensive, firings for different sizes of the same prey type could only be attempted in a few instances i.e. aphids (the different sizes used for functional responses in Chapter 4.5) and the Diptera (Nematocera were separated from other Diptera both because they were commonly eaten by A. dorsale in the field and because they have a very different body shape). The results for the aphids (S. avenae) were compared with data for the lime aphid (Eucallipterus tiliae) obtained by Llewellyn (1972). When the data are plotted on a relative scale (calories/mg of aphid) for easy comparison, the trends for the two aphids are very similar (Fig. 6.2). While not proof, this strongly implies that even with

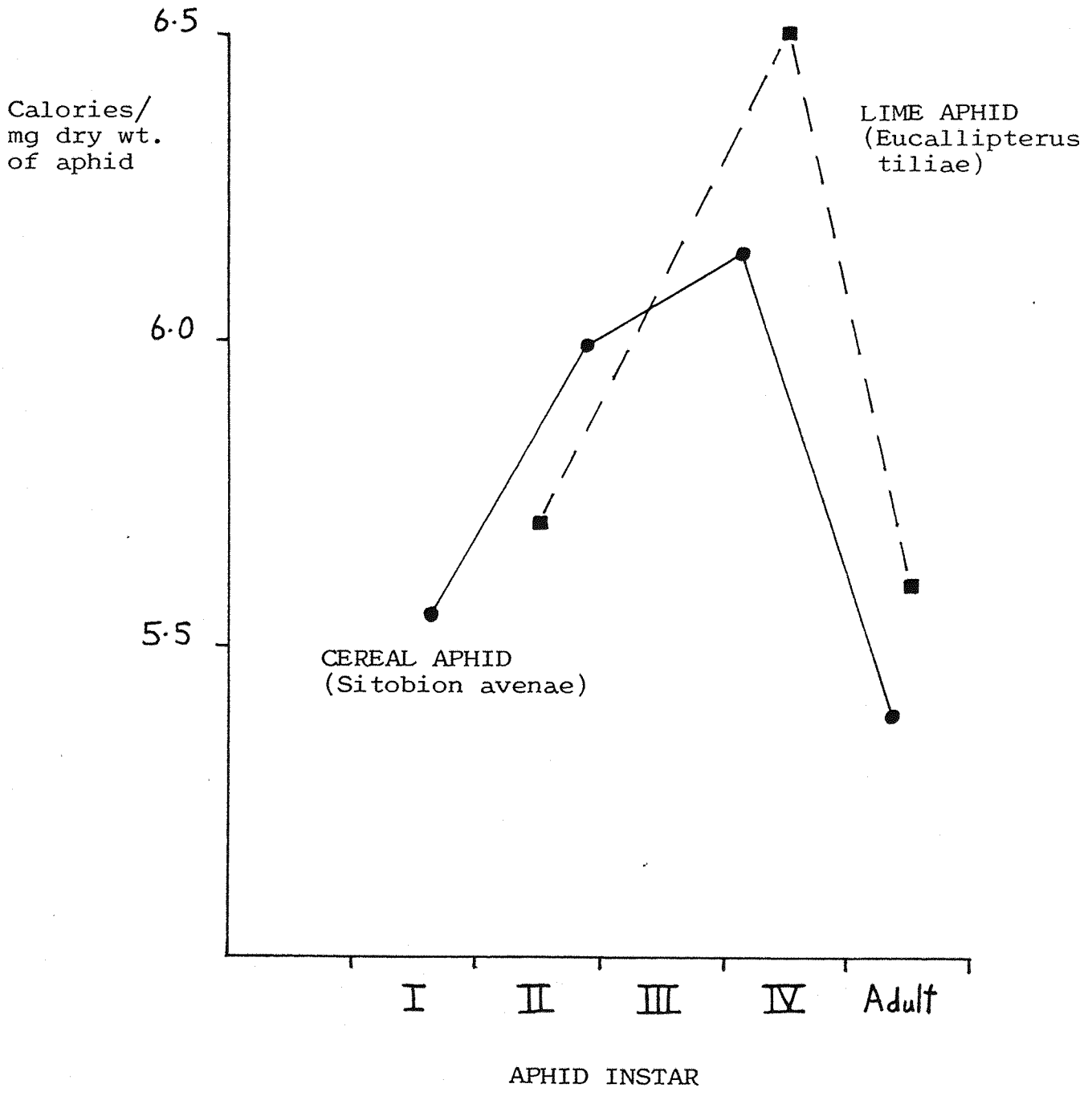
Fig. 6.1 The calibration curve for the bomb calorimeter using benzoic acid of known calorific content for the calibration.



	Mean	Standard error
Intercept	-0.006	0.0389
Slope	0.00496	0.000347

F-ratio = 284.3 with 1 & 13 d.f.

Fig. 6.2 The relative calorific contents of different instars of the lime and cereal aphids(Lime aphid data from Llewellyn 1972).



only a few firings (3-5) per prey size, or type, the results can be taken to be of low variability. (This is as expected as there are two main sources of variation; the methodology itself and variability of the prey. The first has already been shown to be minimal and the second is likely to be small because each firing was made with a pellet composed of many individuals of each prey type).

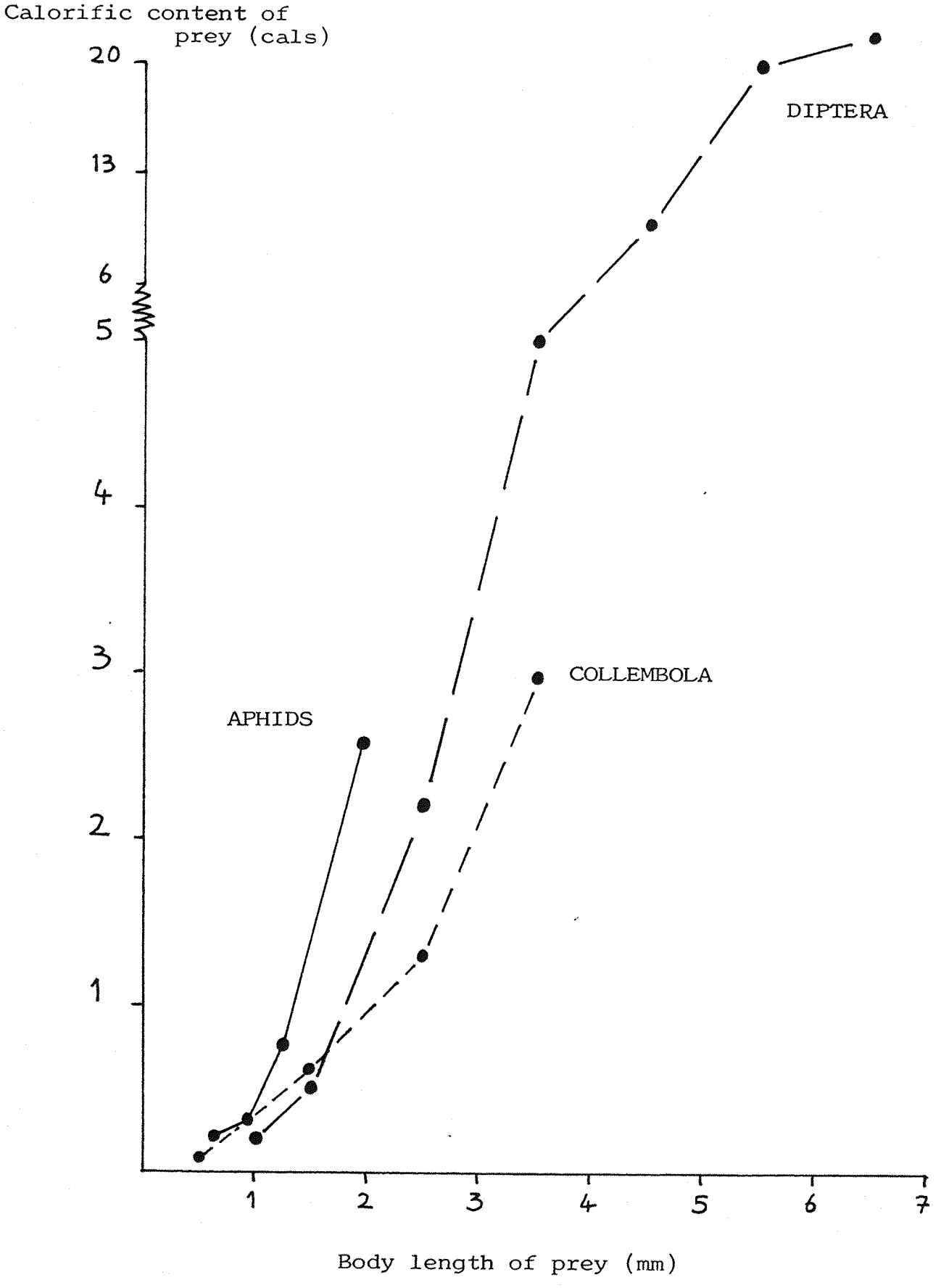
An average value of calories/mg dry weight of prey was calculated for the seven prey types tested. These are given below; there is no clear trend as to which families/orders give the highest values but aphids gave the highest calories/mg.

Prey Type	Calories/mg.
Aphids	5.92
Diptera	5.36
Thysanoptera	5.22
Parasitic Hymenoptera	4.80
Collembola	4.49
Acarina	4.27
Nematocera	4.13

These values were multiplied by the dry weights of the different size classes of prey to show how many calories the different prey would contain. In measuring the dry weights, allowance was made for prey that were not usually completely consumed. It was noticed at the end of the feeding trials of Section 6.3 that in general the whole prey were consumed. For some prey (especially the Diptera) A. dorsale either dropped accidentally or discarded the legs and wings. In some cases these appendages accounted for about 10-15% of the total dry weight of the prey; this figure was deducted in calculating the total calorie yield of prey.

Field data (Chapter 7.3) showed that the most common prey were aphids, Collembola and Diptera (including Nematocera). The results from Section 6.2 suggest that these are also the prey most commonly taken by A. dorsale. The calorific content of these prey types was

Fig. 6.3 The calorific content of different sizes of the commonly available prey in wheat fields.



calculated and plotted for the different size classes of prey (Fig. 6.3). Aphids have the highest calorific content for prey between 0 and 2 mm long, followed by Collembola and the Diptera (mostly Nematocera at this size). Above 2 mm long the Diptera have the highest calorific content. With differences of up to two times in calorific content between prey types of the same size, this should be an important factor for a predator that optimally forages.

N.B. The calorie content of prey referred to in this Chapter came from this work rather than from the literature.

6.3 The selection of dead and live prey commonly found in cereal crops by A. dorsale

Studies on the diet of carabids living in crops have shown that they consume a wide variety of prey (see Thiele 1977 for a review). Most of the carabids were found to be polyphagous carnivores and A. dorsale was no exception. These studies showed that A. dorsale would eat representatives from most of the invertebrate orders present in the crop system, although in many cases the larval stages were consumed rather than the adults.

In order to study the foraging strategy of A. dorsale and account for the variations in prey taken the range of prey available was assessed. There were two stages to this: first A. dorsale was presented with a wide range of cold-killed prey taken from field samples and a record made of which prey were eaten. The same range of prey was then presented live to show how prey activity would limit their availability to A. dorsale. Cereal aphids were included in these trials. The numbers presented of each prey type were adjusted so that A. dorsale was always given the same total dry weight of prey regardless of type or size. (Thus the later use of percentage of prey eaten has a comparable meaning in dry weight consumed between prey classes).

The range of prey collected from the field is shown in Table 6.2 together with the approximate size ranges of the prey and the

Table 6.2 The size ranges (mm) of invertebrates commonly caught in wheat fields

	PREY SIZE RANGE		
PREY TYPE	SMALL < 3 mm	MEDIUM 3 - 6 mm	LARGE > 6 mm
ACARINA	½ - 1		
ARANEAE	2 - 3	4 - 5	7 - 9
COLEOPTERA	Coccinellidae Carabidae Staphylinidae 2 - 3	Coccinellidae Carabidae Staphylinidae 4 - 6	
COLLEMBOLA	Entomobryoidea 1 - 2	Entomobryoidea 4 - 5	
DIPTERA	Nematocera Sepsidae 2 - 2.5	Stratiomyidae Muscidae Sepsidae Lonchopteridae Syrphidae 3 - 5	Syrphidae Tipulidae Muscidae 9 - 10
HEMIPTERA	Cercopidae Pentatomidae Miridae 2 - 3	Cimicidae Delphacidae Miridae 4 - 5	Anthocoridae Delphacidae 7 - 9
THYSANOPTERA	1 - 2		
APHIDIDAE	1.5		

N.B. A rough size range of prey is given in mm; all measurements were body length excluding antennae, mouthparts, legs or other extremities.

representative families. Where several families are shown for a particular prey size and type, a mixture of the families was presented to A. dorsale.

The range of prey offered and the range of prey eaten when presented dead or alive is summarised in Figure 6.4. The Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to show whether the number of prey consumed was significantly different when presented live or dead or significantly different from zero for each prey type/ size category. Clearly the range of prey taken by A. dorsale is strictly limited by prey activity.

When all the prey are grouped into size classes and the average percentage of prey eaten calculated for each size class two bar charts can be drawn to show the sizes of dead and live prey taken by A. dorsale (Fig. 6.5). Prey below 1 mm or above 6 mm in length were not eaten in any significant numbers by A. dorsale whether dead or alive. The 1- to 2-mm size range was taken most often and a large proportion of these were aphids. The percentage taken of this size range remained high for dead and live prey, whereas the percentage eaten for other sizes was substantially reduced.

The proportions of prey eaten for each size were combined with the maximum field density (nos. per m^2) of those prey (from 1979 and 1980 field data, Chapter 7.3) during the field-active period of A. dorsale to show which prey types have the potential to be prominent in the diet of the beetle. These calculations are shown below:

Fig. 6.4 The range of prey eaten by A. dorsale when offered dead or live prey.

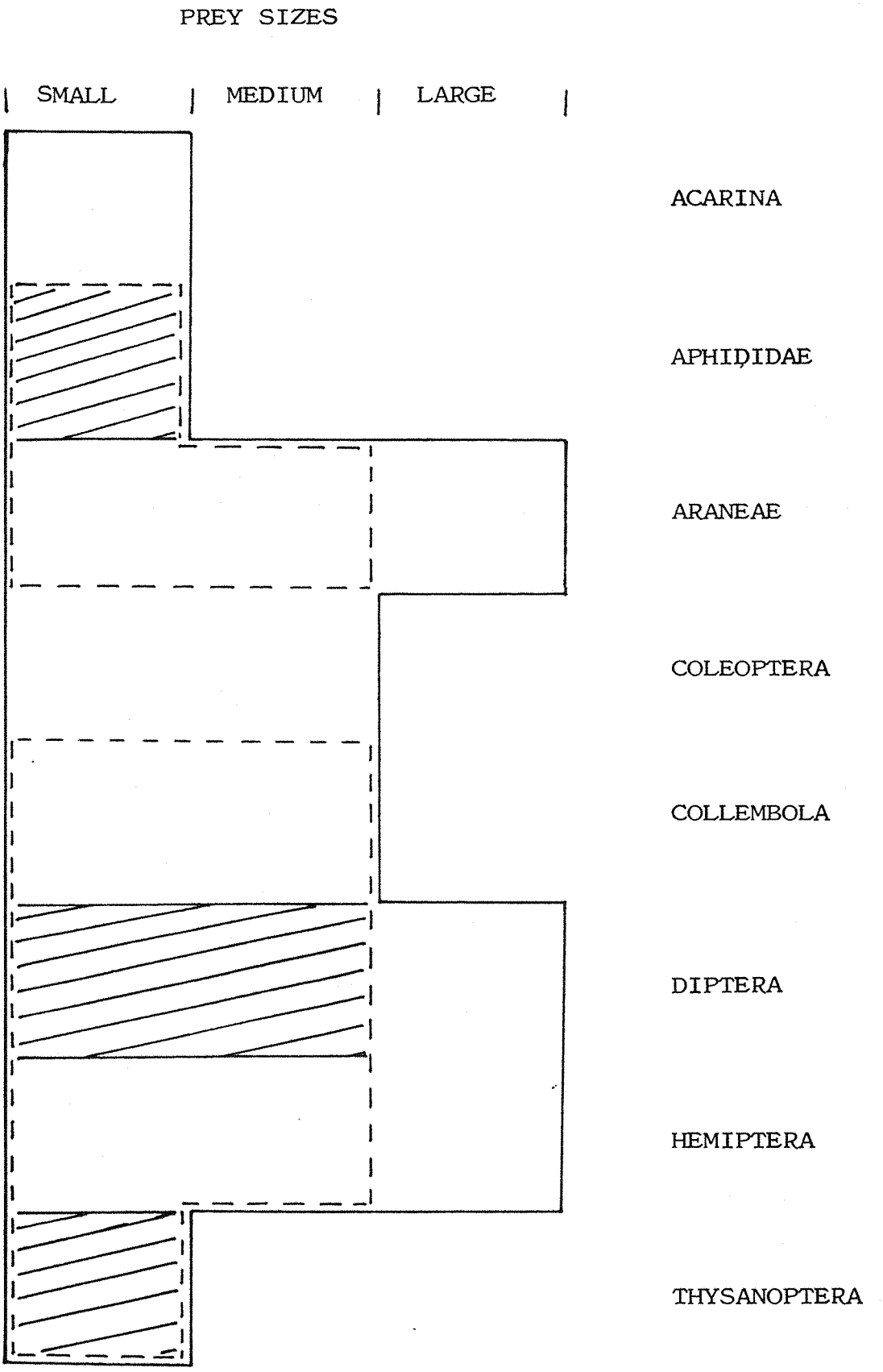
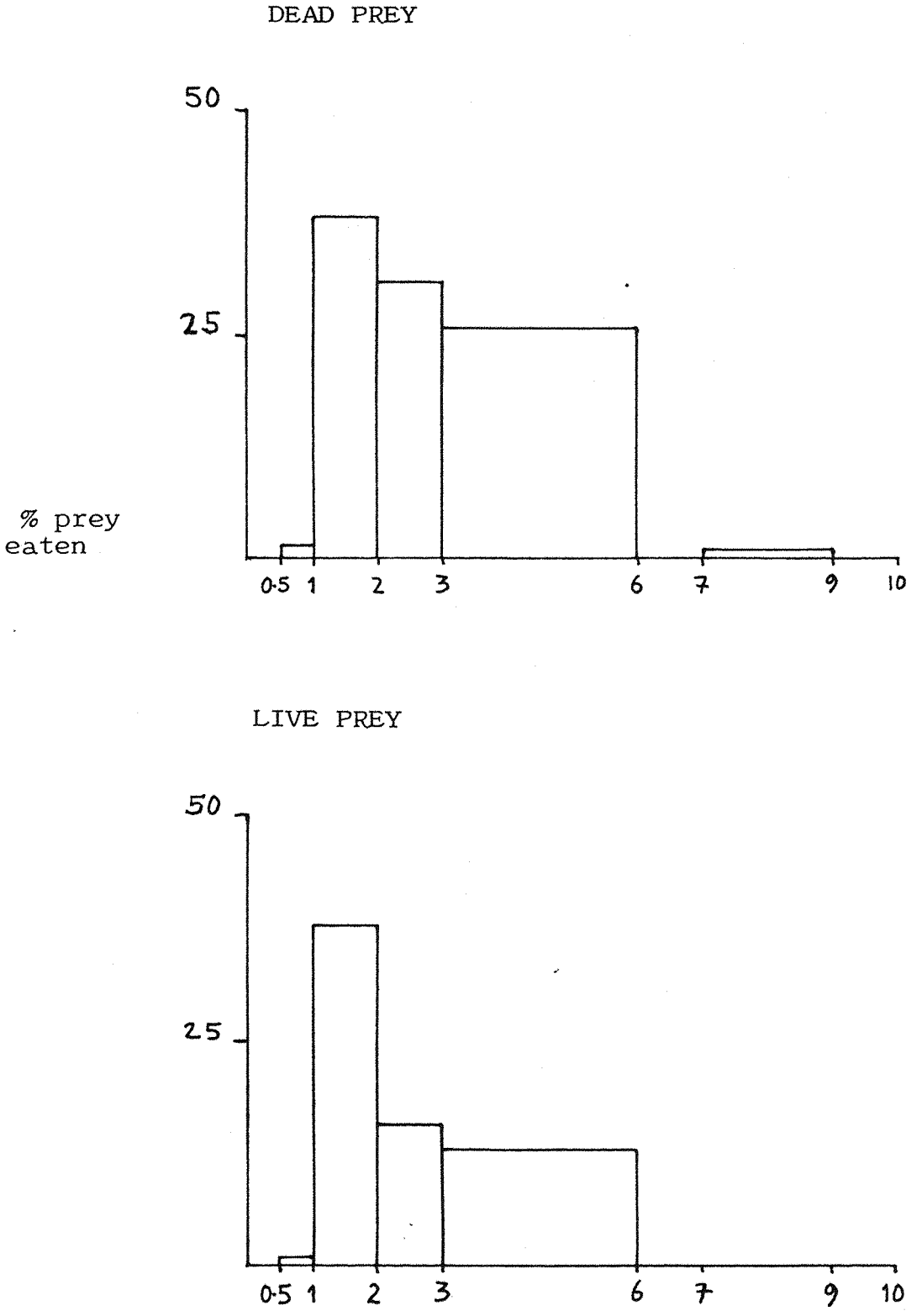


Fig. 6.5 The average percentage of prey eaten in each size class offered for dead and live prey.



	Dead Prey		Live Prey	
	(Density x proportion)			
Acarina	96 x 0.014	= 1.3	96 x 0.0095	= 0.9
Aphididae	224 x 0.65	= 146	224 x 0.90	= 202
Avaneae	18 x 0.198	= 3.6	18 x 0.023	= 0.4
Coleoptera	55 x 0	= 0	55 x 0	= 0
Collembola	305 x 0.298	= 91	305 x 0.027	= 8
Diptera	647 x 0.392	= 254	647 x 0.398	= 258
Hemiptera	12 x 0.176	= 2	12 x 0	= 0
Thysanoptera	116 x 0.035	= 4.1	116 x 0.036	= 4.2

Aphids, Collembola and Diptera are clearly the prey most likely to be prominent in the diet of A. dorsale.

Observation during trials showed the underlying reasons for differing percentages of prey eaten. At the lower end of the size range the Acarina were not detected by A. dorsale; the predator simply walked over the top of the mites. While at the upper end of the size range the prey seemed either too hairy (large Araneae/ Diptera) or had too strong a cuticle (large Hemiptera and all Coleoptera) for A. dorsale to use its mandibles effectively. Of the live prey only aphids, flies and thrips were sufficiently inactive in the dark of the experiment for A. dorsale to catch them successfully.

In summary, diet in the field is likely to comprise mainly the aphids, Collembola and Diptera within the size range of 1-6 mm. Only these prey showed the combination of high average abundance in the field and availability from the laboratory studies to be commonly included. Within this size range, prey between 1 and 2 mm were taken most often and of these aphids had the highest calorific content (Section 6.2). Tests of optimal foraging should concentrate on these prey as it is likely that A. dorsale will have adapted, if at all, to forage off the prey most available to it.

6.4 Selection between the cereal aphid species Sitobion avenae and Metopolophium dirhodum by A. dorsale

The conclusion of Chapter 5 was that A. dorsale did not show any obvious and specific adaptation for finding and catching cereal aphids even though they formed a disproportionately large part of the diet. There are two possible explanations for this: environmental factors may combine to make cereal aphids the most available prey or A. dorsale may be showing optimal foraging i.e. aphids give the biggest net energy intake of the available prey. These two possibilities are investigated in this Chapter by a series of experiments progressing from the hypothesis that A. dorsale is capable of fine discrimination between prey to the hypothesis that A. dorsale cannot discriminate and takes prey in the ratio presented to it.

If A. dorsale was capable of fine discrimination between prey items it should be evident for aphids, the prey with the highest calorific content in the most available prey size range i.e. 1-2 mm (Section 6.2). For this experiment A. dorsale was offered a choice between the two aphid species Sitobion avenae and Metopolophium dirhodum, which have the same size range and body form. These aphid species were used because early observations showed that A. dorsale caught these species with differing degrees of success. M. dirhodum was more active than S. avenae and often escaped capture by walking quickly away from the beetle after the initial contact, leading to a lower capture rate (Table 6.3). Comparison of numbers of the two aphids eaten over a period of 24 h at different densities (Fig. 6.6) showed no significant differences (Wilcoxon matched-pairs signed-ranks test; Siegel 1956) either for the number of "nymphs" (I & II instar aphids) or "adults" (IV & adult aphids) eaten between the two species. Observations during these trials also showed no significant differences between handling times for nymphs or adults of the two species (Wilcoxon matched-pairs signed-ranks test; Siegel 1956); see Table 6.3). The aphid species differed only in how successfully A. dorsale could capture them so optimal foraging decisions by the beetle should be directly related to this variable.

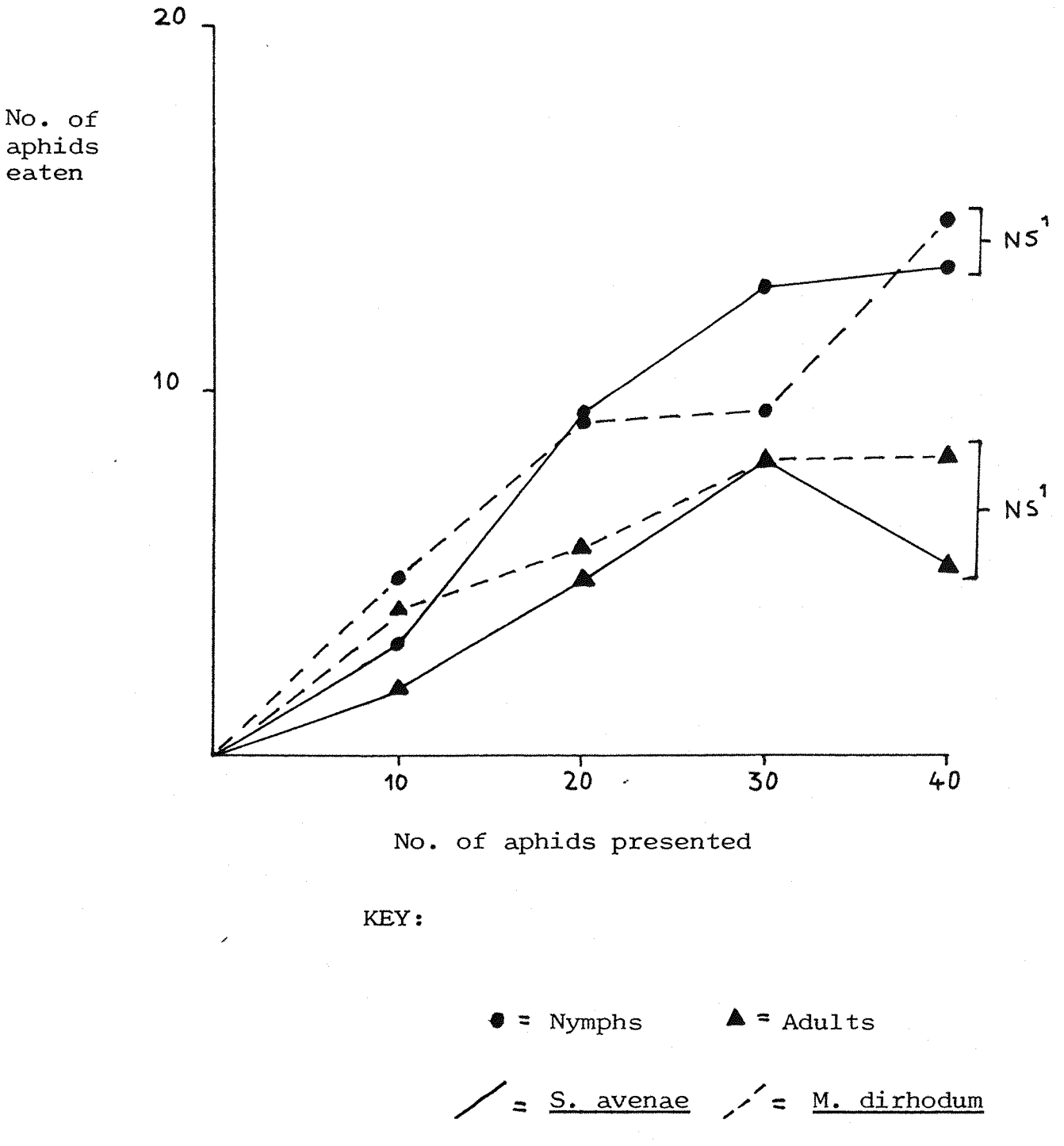
Table 6.3 Percentage capture efficiency and handling time(s) for nymph and adult S. avenae and M. dirhodum

Variable	Aphid size	S. avenae	M. dirhodum	Significance of difference between species
Capture efficiency	Nymph	51	41	NS
	Adult	76	50	$p < 0.01$
Handling time(s)	Nymph	58	44	NS
	Adult	297	329	NS

Table 6.4 The size, calorific content, handling times and capture efficiencies of the two prey types, aphids and Collembola

Prey Type	Body length (mm)	Calories/individual	Handling Time (s)	Capture Efficiency (%)
Aphids	1.5 - 2.0	2.12	210	75
Collembola	3 - 4	2.96	134	20

Fig. 6.6 The change in the numbers of S. avenae and M. dirhodum (nymphs and adults) eaten by A. dorsale with changing aphid density over 24 h.



[1] Wilcoxon matched-pairs signed-ranks test

N.B. Capture efficiencies are referred to throughout this Chapter and the term was defined by:

$$100\% \times \frac{\text{No. of prey eaten of those encountered}}{\text{Total no. of prey encountered}}$$

An encounter was recorded when A. dorsale physically touched a prey item regardless of whether it appeared to detect the prey or not. Prey were considered eaten if the beetle killed them regardless of whether it subsequently consumed them; in practice almost all prey killed were eaten as well.

Handling time was the time from when A. dorsale first touched a prey item to the time when it moved off having completely consumed that prey item. Prey items dropped or only half consumed were not included in estimates of handling time; however, these events happened only rarely.

To test how A. dorsale would select between these two aphid species, the beetles were presented with the aphids in four different ratios. These were:

S. avenae	:	M. dirhodum
1		4
2		3
3		2
4		1

In all cases a total of 100 aphids were presented to beetles; this number was chosen to give the high density of about one aphid per 2 cm^2 for two reasons. Previous feeding trials over the same 1 h time period (Chapter 4.5) suggested that depletion would be minimal (10% or less) at this prey density. Optimal foraging theory predicts that animals will be likely to select optimally only when prey are abundant (this prediction was taken into consideration for all the experiments of this Chapter).

Although the percentage of successful encounters with prey (Table 6.3) was significantly different between the "adult" classes

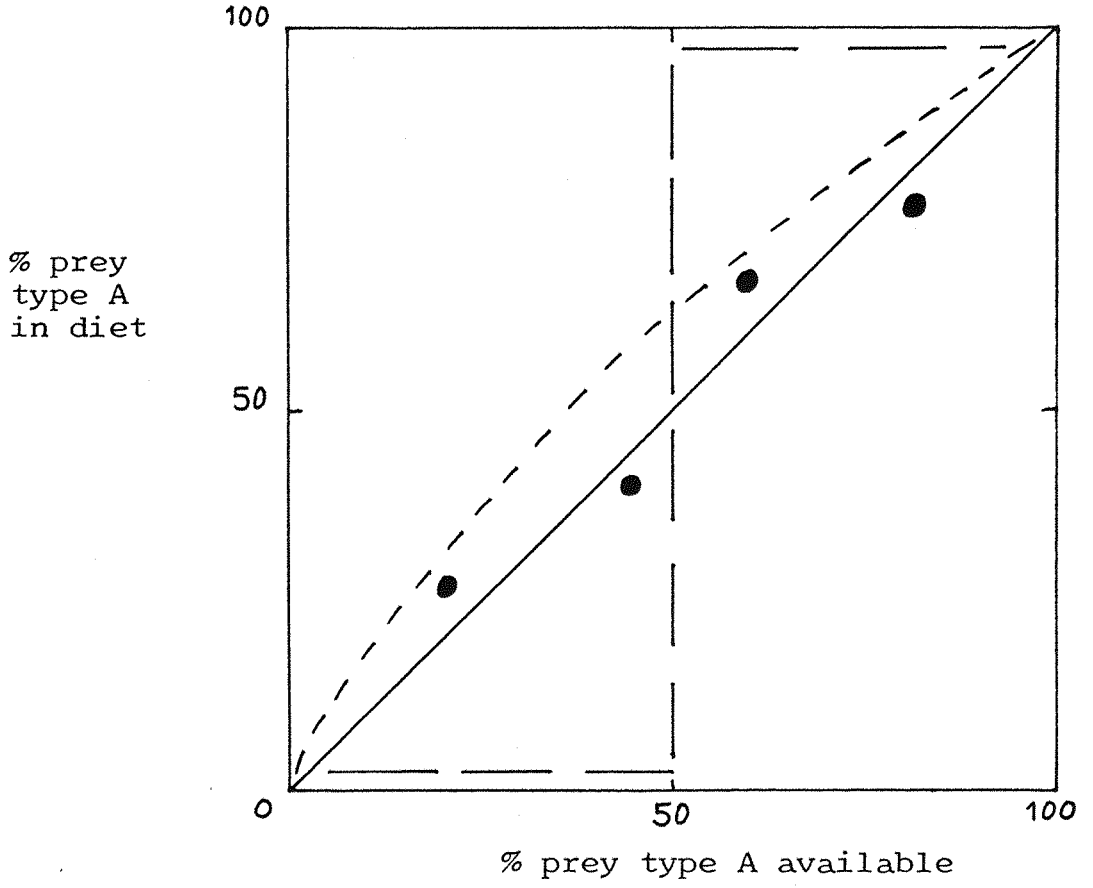
of the two aphid species, the obtained percentages were used unaltered to predict the various ways in which A. dorsale could take the aphid prey. The results are presented in the familiar graph of "% of prey type A available vs. % of prey type A in the diet" (see Hassell 1978). Each group (Figs. 6.8 and 6.9) also shows three predictive lines, Figure 6.7 explains what these predictive lines represent.

The predicted values for no preference but with the capture efficiences taken into account were calculated as below (in this case for the ADULT aphids in the ratio 4 S. avenae : 1 M. dirhodum):

	S. avenae		M. dirhodum
Presented ratio	4	:	1
x (capture efficiency)	x 0.75		x 0.50
= predicted ratio in the diet	3	:	0.5
predicted ratios as percentages for plotting on graphs.	86	:	14

The prediction for an optimally-foraging predator was based on the same principles as those for birds foraging in an artificial laboratory arena on two patches of different reward status which are not depleted and do not change in quality (Krebs 1978). Once the predator has detected the patch (in this case the aphid species are equivalent to the patches) with the higher reward rate it should switch to feed on this patch all the time. The switch point between the two aphid species is the presented ratio at which A. dorsale will capture equal numbers of the two species. This was calculated as follows (for ADULT aphids in this case):

Fig. 6.7 Guide to predictive lines used for comparisons with the real data in Figures 6.8 & 6.9.



● = The mean values of the observed data.

/ = The predicted values if there was no difference in capture efficiency and no preference for either prey.

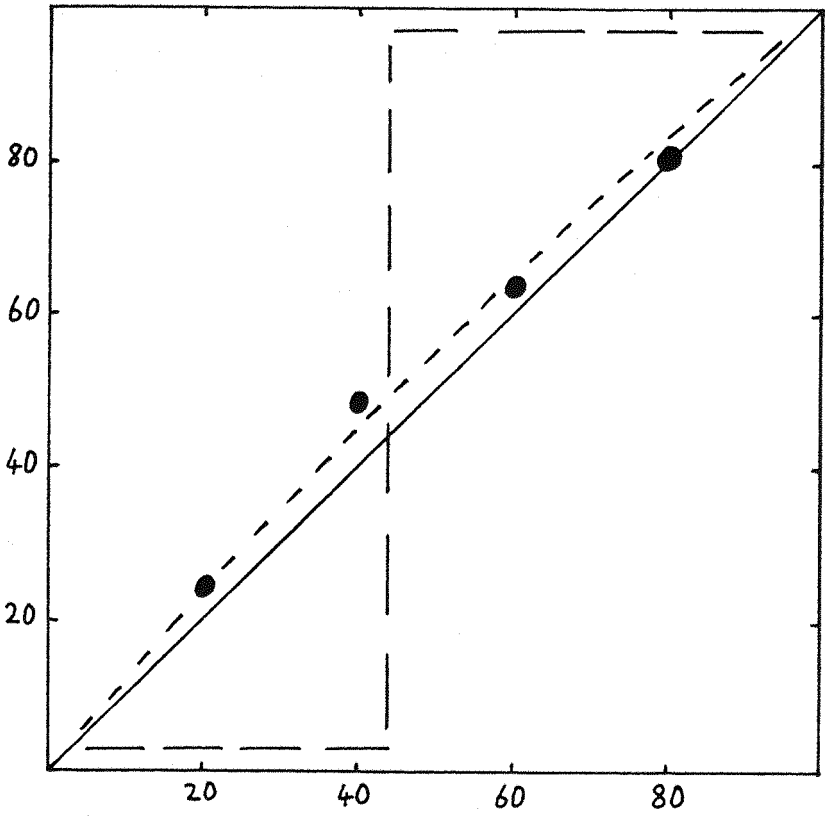
= The predicted values if there is no preference for either prey but the higher capture efficiency for prey type A is taken into account.

= The predicted values if prey are not depleted, the higher capture efficiency for prey type A is taken into account, and the predator forages optimally (after Krebs 1978).

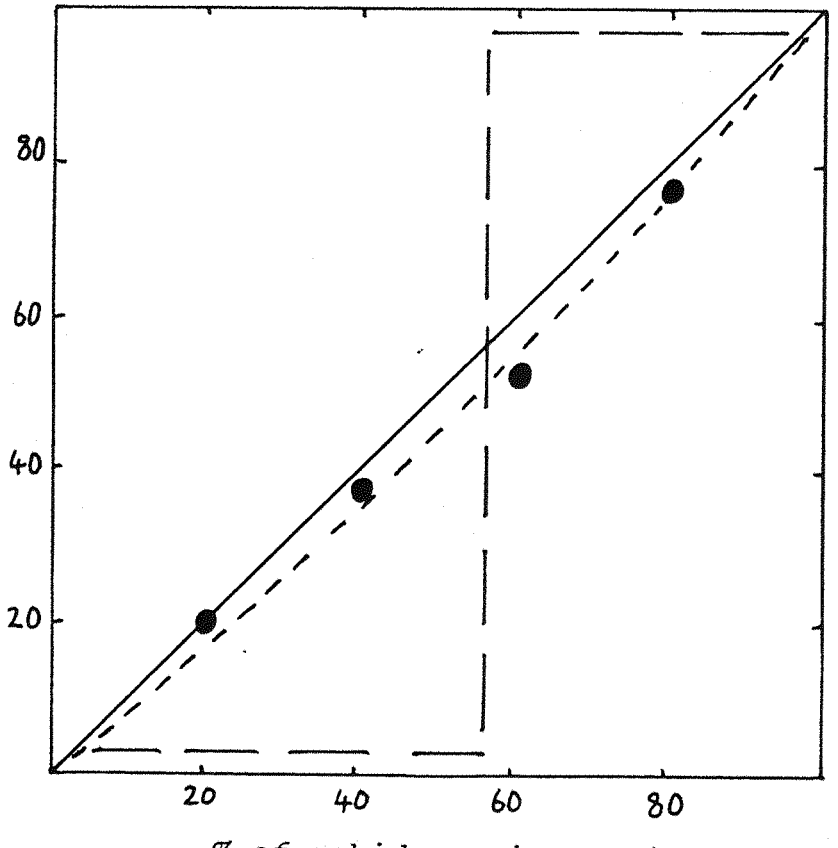
Fig. 6.8 The change in the percentage of total captures of one aphid species with the change in availability of that species.

NYMPHS

S. avenae



M. dirhodum



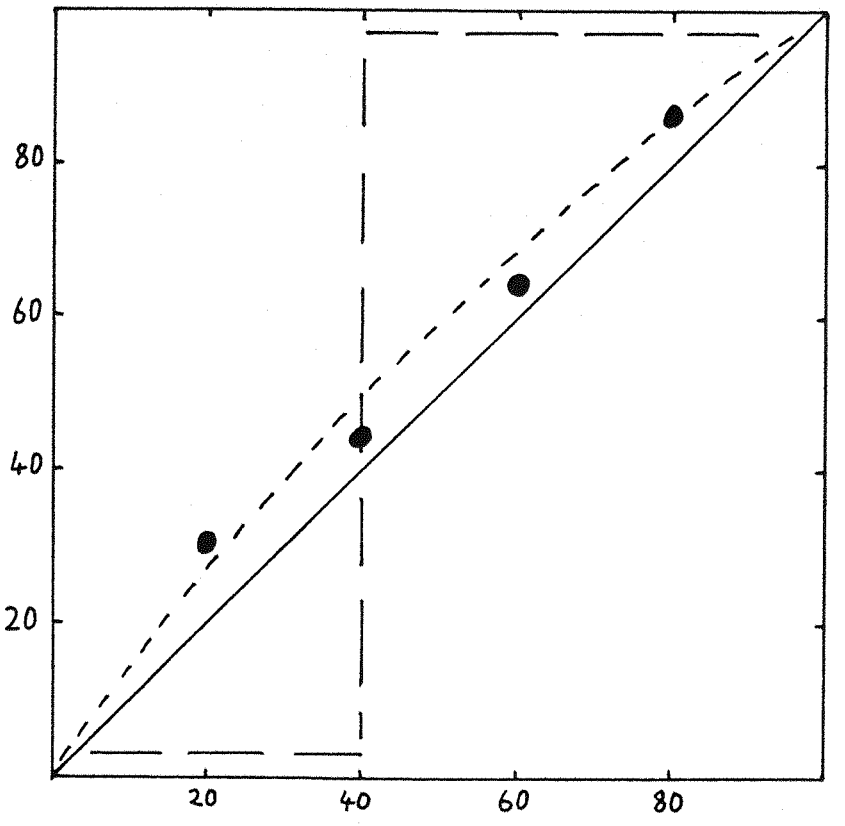
% of aphid species in total captures

% of aphid species available

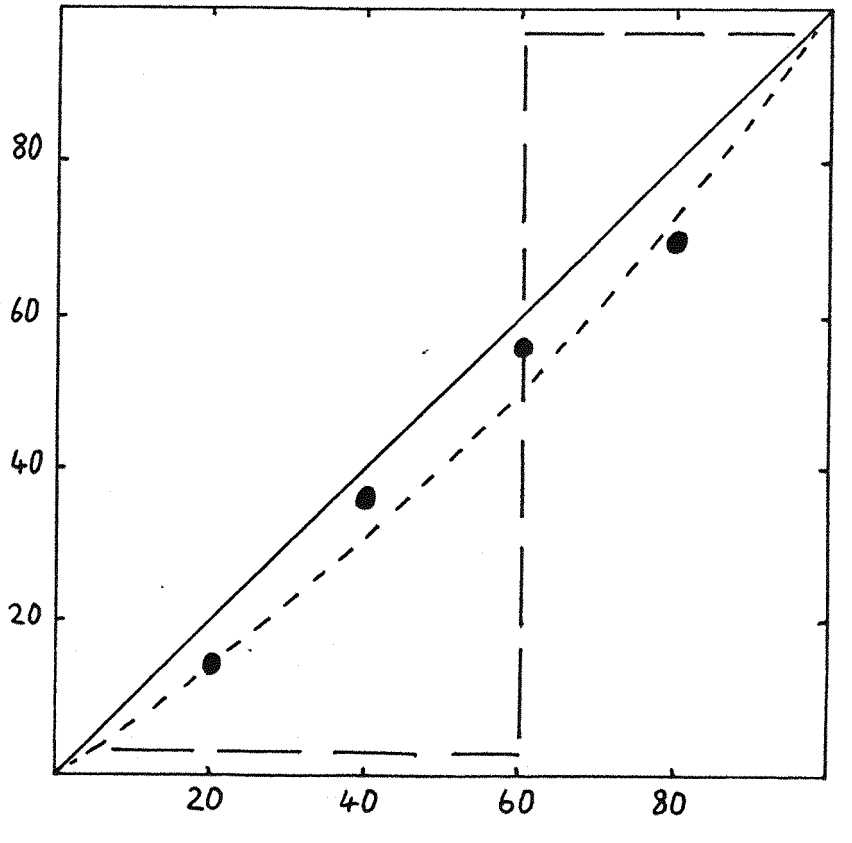
Fig. 6.9 The change in the percentage of total captures of one aphid species with the change in availability of that species.

ADULTS

S. avenae



M. dirhodum



% of aphid species in total captures

% of aphid species available

	S. avenae	M. dirhodum
Capture efficiencies	0.75	0.50
Ratio of captures	1.5	1
Reciprocals of capture ratios (i.e. ratio x reciprocal = 1)	0.67	1
Reciprocals as percentages, corresponding to the switch points for an optimal forager	40	60

The four sets of observed mean points were compared with the corresponding points for each of the three predicted types of prey selection using the Kolmogorov-Smirnov one-sample test (Siegel 1956). The tests were made using the actual mean numbers of individuals eaten for each aphid size/species; the predicted number of nymphs or adults eaten was generated from the average total number of aphids eaten over the four different ratio trials multiplied by the appropriate correction factor for the prediction model in question (see earlier calculations). In all four cases (Figs. 6.8 and 6.9) there was no significant difference between the observed values and either the model for "no preference/no allowance for capture efficiency" or the model for "no preference/capture efficiences allowed for". In no case did the optimal foraging model fit the data.

Examination of Figures 6.8 and 6.9 suggests that the observed points are best fitted by the model which takes into account the observed difference in capture efficiencies. There is no suggestion that A. dorsale showed a preference for either aphid species as would be expected if it were optimally foraging. It must be concluded that A. dorsale is not capable of the discrimination necessary to forage optimally when prey differ only in their capture efficiencies. The next Section examines selection by A. dorsale between prey differing not only in the beetle's capture efficiency of them but also in their

size, shape and net calorific yield (as defined by calorific content divided by handling time).

6.5 The effect of previous prey experience on prey choice

The previous Section showed that A. dorsale could not distinguish between two prey species that differed only in capture efficiency. A. dorsale may need less subtle differences to enable it to pick the most profitable prey. Accordingly the next step was to offer the beetle a choice between prey differing in size, shape and net calorific yield as well as capture efficiency. Optimal foraging principles imply that a predator is most likely to have developed the necessary discriminatory skills for prey that it commonly encounters. Section 6.3 showed that these prey types are likely to be aphids, Collembola and Diptera. Preliminary trials showed that aphids and Collembola were easy to manipulate experimentally and also differed in each of the four required categories. The aphids used were IV instar to adult S. avenae, while the Collembola used belonged to the Entomobryoidea group and were selected to be 3-4 mm long.

Capture efficiencies and handling times were measured for aphids and Collembola separately during the "training" period of the experiment. Calorific content was assessed by micro-bomb calorimetry (Section 6.2). These data are summarised in Table 6.4.

There are several mechanisms by which a predator may choose, or switch between prey types. The sophisticated predator may form a mental image of a common/profitable prey type which leads it to selectively concentrate on this prey and ignore less common/profitable prey (Holling 1959; Cornell 1976). Switching can occur at a less sophisticated level if the predator has different hunting methods for different prey. The predator would appear to concentrate on the more common type because the hunting method used prevents encounters with other prey (Akre & Johnson 1979). Alternatively, if different prey types lived in different areas of the habitat the predator could switch by changing the time spent searching in each of these areas (Hassell 1978). The latter possibility has been discounted with aphids as prey because A. dorsale did not switch between the ground and wheat in response to changing aphid distributions (Chapter 5.6).

A. dorsale individuals were fed on a diet of aphids or Collembola for 2 wk prior to trials. If they were capable of developing a search image for either prey type it should be formed within this time because A. dorsale is active in the field for only 6 wk (Chapter 7) so to be adaptive the image must develop within days. In addition work by Lawton, Beddington & Bonser (1974) showed that the image forming process for the invertebrate Notonecta occurred in about 10 days.

After this initial "training" period all beetles were presented with a numerically equal (20:20) mixture of aphids and Collembola. The numbers of each prey eaten per day were monitored for 10 days with the original prey ratio being maintained by daily replacing those eaten. Observations were also made of some of the beetles encountering prey on each of the 10 trial days to obtain measures of capture efficiency.

The purpose of the training period was to allow the beetles time to develop a search image; monitoring of the numbers of prey eaten and the capture efficiencies when the prey mixture was first presented would show whether this search image had been developed. Further monitoring of numbers eaten and capture efficiencies was used to show whether, if A. dorsale could not be preconditioned to prey by developing a search image, it could respond directly to the prey mixture (e.g. by different hunting methods for different prey) and switch within the 10 days of the trials.

(i) Analysis of training period results

A normal analysis of variance (Snedecor & Cochran 1967) showed that there was no significant difference between beetles, within the aphid- or the Collembola-fed groups, in the numbers of prey eaten during the 2 wk training period. Normal regression analysis showed that there was no significant upward or downward trend for the numbers of prey eaten in either group over this 2 wk period.

On average, each beetle ate 6.3 aphids per day or 4.4 Collembola; data from Section 6.2 allow these figures to be converted to mg dry weight eaten per day or calories eaten per day. It is essential if

predictions about foraging method are to be accurate that the "currency" a predator works in is known. This was tested by comparing the 13 pairs of mean numbers of prey eaten (aphids vs Collembola) during the training period with dry weight and calorie conversions (Wilcoxon matched-pairs signed-ranks test; Siegel 1956). Three comparisons were made:

the numbers of prey eaten
the dry weight of prey eaten
the calories of prey eaten

The comparison showing the least significant difference between aphids and Collembola would strongly indicate which of the above three variables A. dorsale was using to measure its daily intake of food. The comparisons showed that a conversion to calories accounts almost completely for the difference in numbers of aphids and Collembola eaten per day (Table 6.5). This is illustrated in Figure 6.10 where the numbers eaten and the calorific intake of aphids and Collembola are shown.

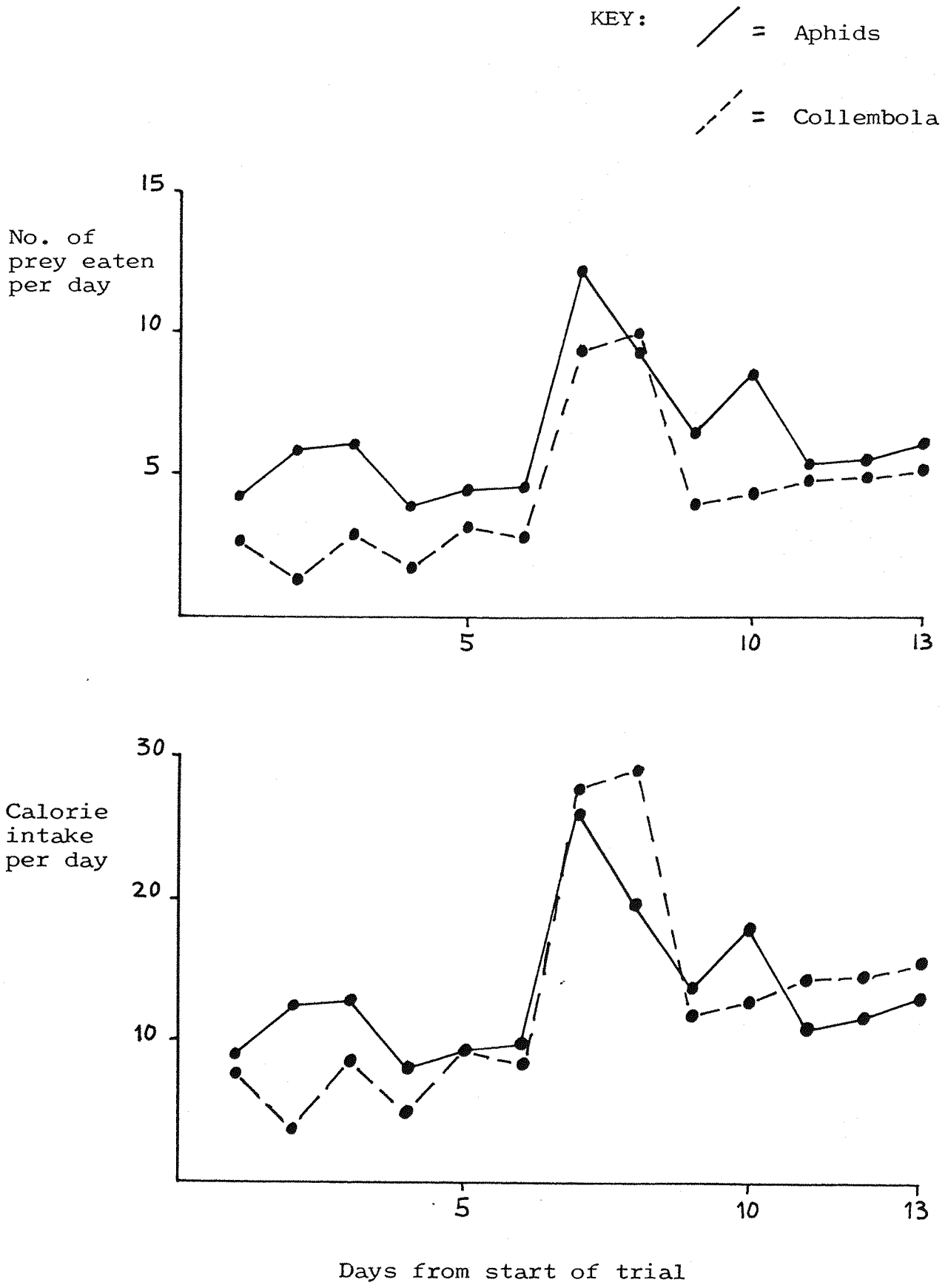
During the training period the relative capture efficiencies of the two prey types did not affect the number of prey eaten. This was achieved by presenting prey to the beetles at such a high density that they could daily eat until satiated. When a mixture of prey types is presented, however, the capture efficiency will directly affect the ratio in which those prey types are taken. It is possible to calculate, taking into account capture efficiency, handling time and calorific content (Tables 6.4 & 6.5), the ratio that the aphids and Collembola should be taken in if A. dorsale acts as a random predator:

(The corrected ratios are presented as the numbers of aphids and Collembola consumed if a total of 100 prey were eaten).

Table 6.5 Comparison of numbers, dry weight and calories of prey eaten daily over about 2 wk by A. dorsale

Variable (intake per day)	Aphids ($\bar{x}$ for 13 days)	Collembola ($\bar{x}$ for 13 days)	Significance of difference
Number of prey	6.29	4.36	$p = 0.0013$
Dry weight of prey (mg)	2.25	2.86	$p = 0.032$
Calories of prey	13.3	12.9	$p = 0.337$

Fig. 6.10 The number of prey (aphids or Collembola) eaten or the corresponding calorie intake per day by A. dorsale over a period of 2 weeks.



	Aphids		Collembola
Ratio in which prey were presented	50	:	50
	(x 0.75)	Table 4	(x 0.20)
Effect of capture efficiencies on ratio	79	:	21
	(÷ 210)	Table 4	(÷ 134)
Effect of handling times on ratio	71	:	29
	(x 2.12)	Table 4	(x 2.964)
Effect of calorific content on ratio	64	:	36
		(FINAL RATIO)	

(ii) Analysis of the mixture trials

A nested analysis of variance (Snedecor & Cochran 1967) showed that there were no significant differences between sexes or individuals in the daily numbers of aphids, or Collembola, eaten (individuals were dissected at the end of the trial to assess their sex and reproductive status). In addition all individuals were of reproductive status 1 (immature), so no allowance for sex or correction for reproductive status was necessary in the following analyses of results.

The results have shown that, given a numerically equal mixture of aphids and Collembola, of the prey that A. dorsale catches 64% should be aphids. If the percentage is higher then A. dorsale is showing a preference for aphids and if lower a preference for Collembola. The 64:36 ratio also shows that aphids are the most catchable/profitable prey and to forage optimally on encountering a 50:50 mixture of aphids and Collembola A. dorsale should feed exclusively on the aphids. Essentially, although the Collembola have a higher calorific content (Table 6.4) than the aphids A. dorsale is much less successful at catching them (Table 6.4) and should concentrate solely on the aphids.

Using the above information it is possible to indicate on a graph of "time from start of trial" vs "percentage of aphids in diet" where the values for the percentage of aphids eaten on each day of the mixture trial should lie. This will vary according to whether the beetles were aphid- or Collembola-trained and whether they are assumed to forage optimally or not. (This analysis is for aphids only; as the results are percentages the analysis for Collembola is exactly the reverse and so is not included.) The graph can be divided into eight areas (Fig. 6.11) on the following basis. If the points are above the 64% line then A. dorsale is showing a preference for aphids (as predicted by optimal foraging theory) and if below a preference for Collembola. If Collembola-trained A. dorsale had formed a search image for their prey and then during the course of the 10 day trial switched to feed on aphids, then the points should generally go from the bottom left to the top right corner of the graph, e.g. the dashed "switching" line in Figure 6.11. If the beetles showed no preference for the aphids or Collembola (i.e. behaved as random foragers) then points should be scattered equally above (up to 100%) and below (down to 28%) the "no preference" or 64% line. Hence with the 64% line, the two lines necessary to delineate the bottom left and top right quadrants and the lower boundary to mark equal scattering of points above and below the 64% line the area of the graph becomes divided into eight.

There are four main strategies that can be pursued by A. dorsale; these are shown in Figure 6.12 and are now briefly summarised.

The Optimal Forager

In this strategy it is assumed that A. dorsale can detect instantaneously which of two prey offered is the more profitable and concentrate on this prey type exclusively regardless of previous prey experience (in this case if should always concentrate on aphids).

The Learner

Here A. dorsale is assumed to have learnt to concentrate exclusively on the prey type it had previously fed on. If then presented with a mixture of prey containing another more profitable prey type it should

Fig. 6.11 The division of the "time vs. percentage aphids in diet" graph into eight areas to indicate where data points should lie for the various predation strategies.

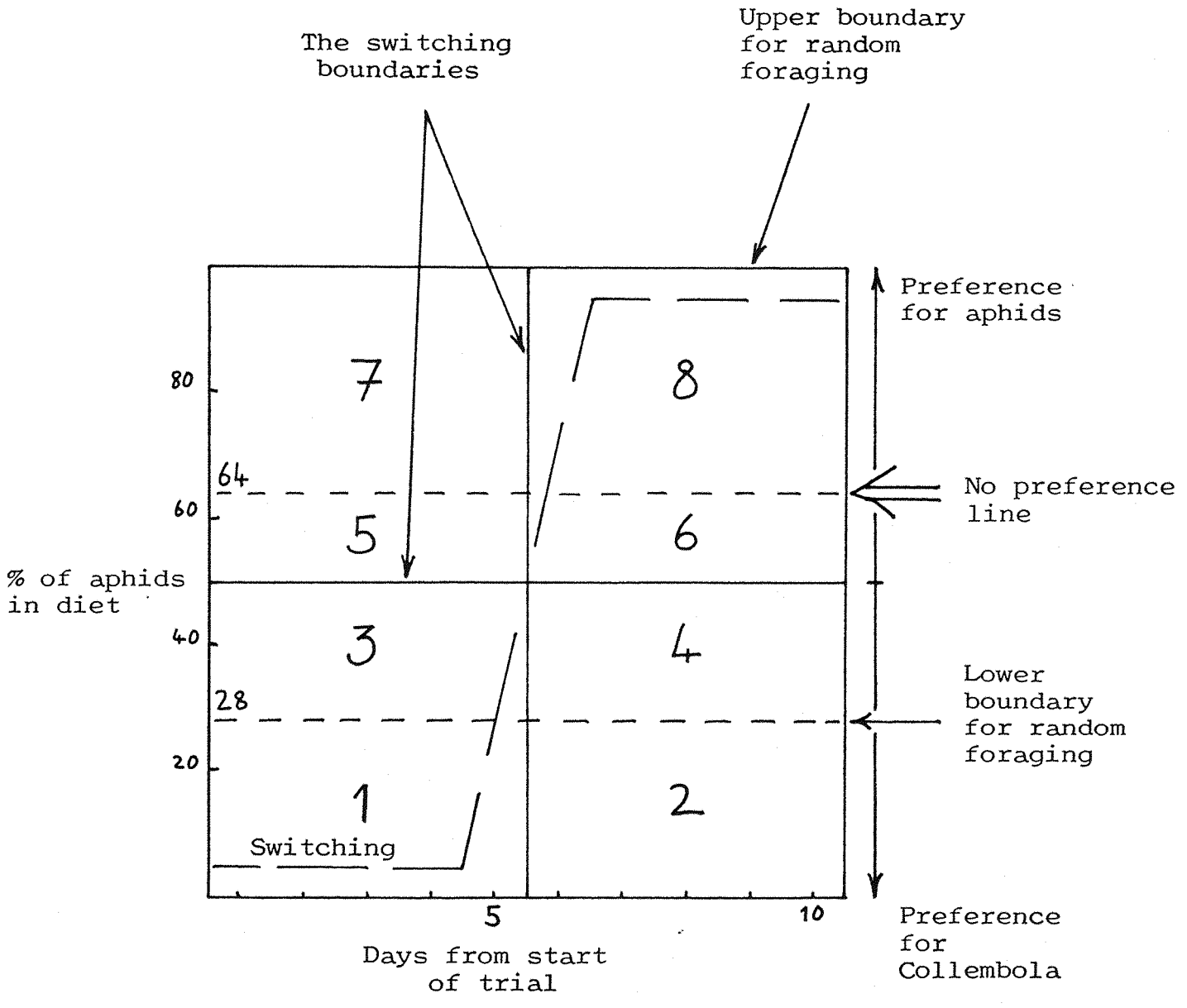
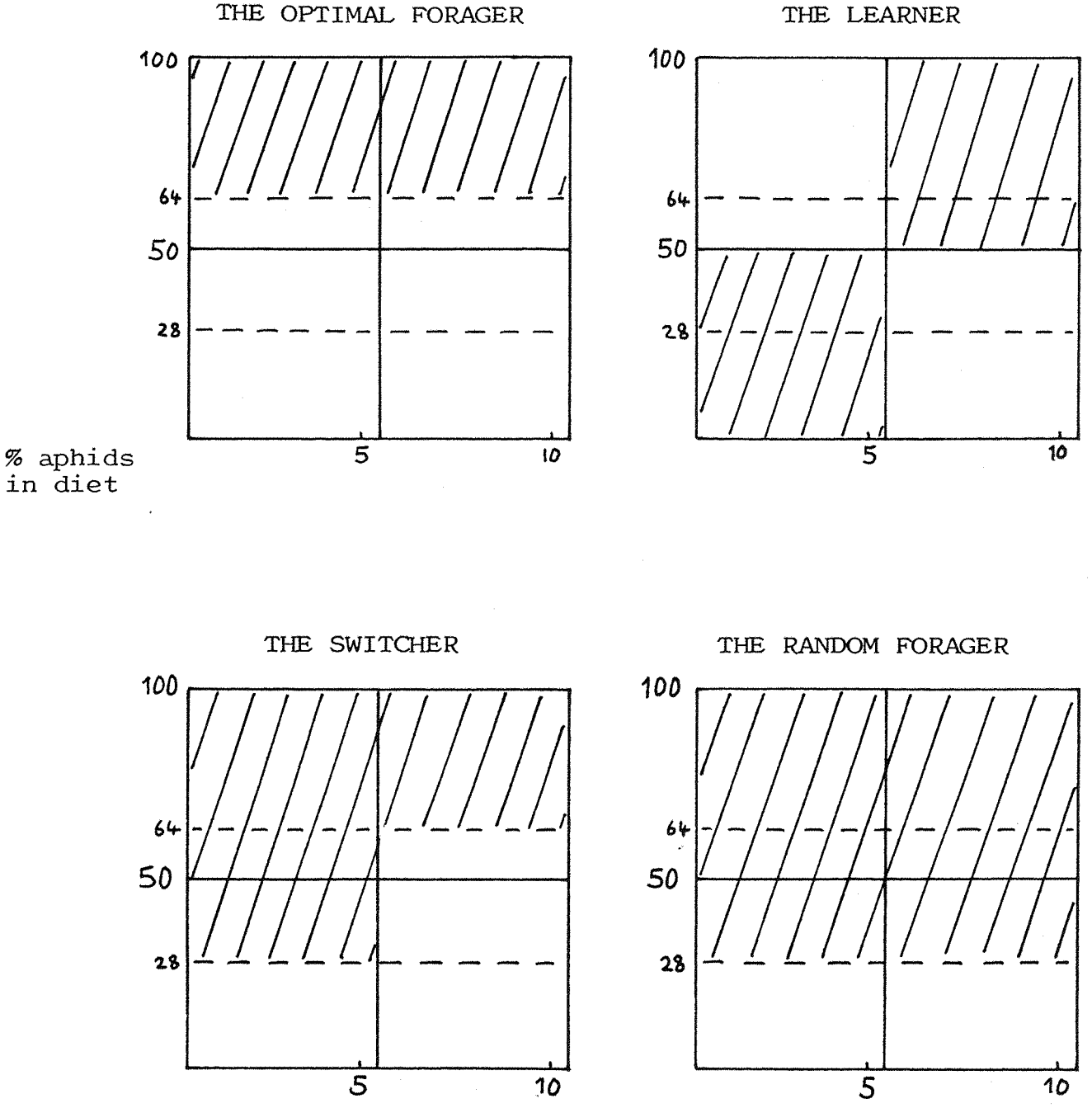


Fig. 6.12 The distribution of points on the "time vs. % aphids in the diet" graph if A. dorsale pursues one of four predation strategies.

(The shaded areas indicate where data points should lie if A. dorsale pursues the indicated foraging strategy)



gradually switch over the 10 days to feed off the more profitable prey (aphids). In the case where the predator had already learned to concentrate on the more profitable prey (as when A. dorsale was trained on aphids) it should follow the same course as the Optimal Forager and concentrate exclusively on this prey.

The Switcher

A. dorsale is assumed not to be able to learn to concentrate on a prey type but when confronted with two prey of differing profitability can gradually concentrate on the more profitable one by some innate functional difference in the way it catches prey. For instance it could have a particular hunting method that is triggered by encountering the more profitable prey but which excluded encounters with the less profitable prey.

The Random Forager

In this case A. dorsale is assumed to show no choice between the two prey types; prey are eaten in the calculated "no preference" ratio (64 aphids:36 Collembola).

The fit of these models to the observed data (Fig. 6.13) can be tested using the Kolmogorov-Smirnov test (Siegel 1956). A cumulative frequency distribution is constructed of the proportions of the points that should lie in the eight sections of the graph. The eight cumulative frequency sections of each model are then sequentially compared with the eight cumulative frequencies of the real data and the size of the largest difference between the two used to test the goodness of fit of the model. This process is summarised in Table 6.6 together with the goodness of fit of each model.

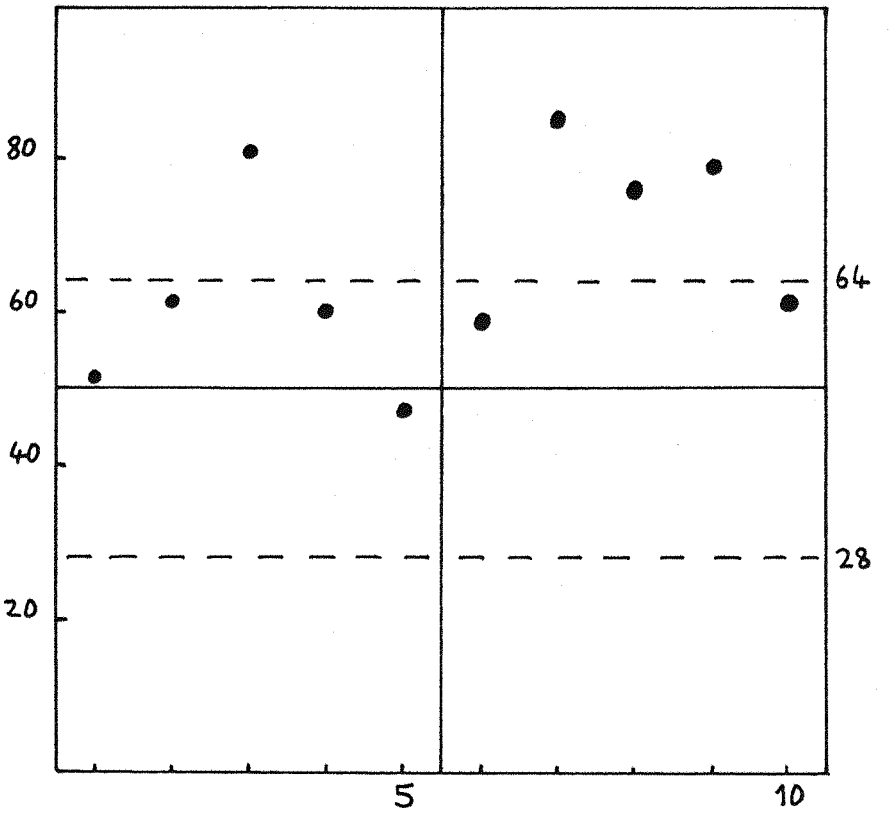
The only model adequately describing the distribution of data points on the graph was the "Random Forager". The predictions of all the other models were significantly different from the observed data at the 0.01 level of probability and grew progressively worse from the "Switcher" to the "Optimal Forager" model. The more "knowledgeable" the model assumed that the predator was about the prey the less good the fit to the data was. This is reinforced by the way in which the

Fig. 6.13 The distribution of observed mean points on the "time vs. % aphids in diet" graph for A. dorsale feeding on a mixture of aphids and Collembola.

Aphid-trained A. dorsale:

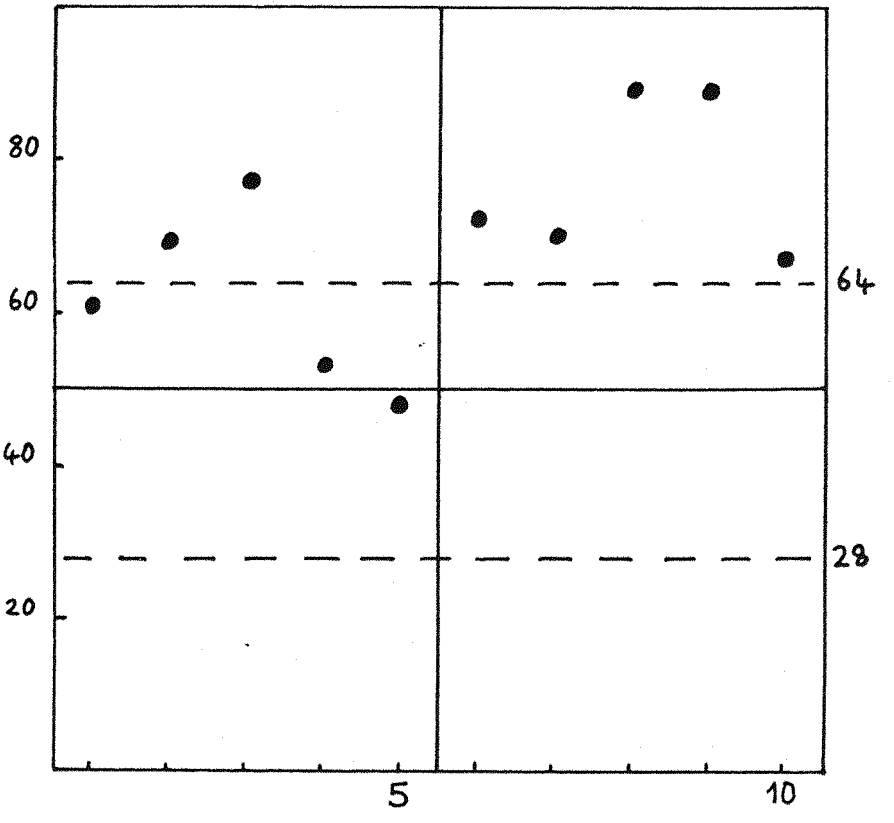
KEY:

● = mean value of 10 data points



Collembola-trained A. dorsale:

% aphids in diet



Days from start of trial

Table 6.6 The observed and expected cumulative proportions of data points in the eight sections of the "time vs percentage aphids in diet" graphs

MODEL OR DATA SET	GRAPH SECTION 1	2	3	4	5	6	7	8	Significance of difference between model and data set
OPTIMAL FORAGER	0	0	0	0	0	A C 0	0.5	1.0	p < 0.01 p < 0.01
LEARNER	0.28	0.28	A C 0.5	0.5	0.5	0.64	0.64	1.0	p < 0.01 p < 0.01
SWITCHER	0	0	0.153	0.153	0.25	A C 0.25	0.5	1.0	p < 0.01 p < 0.01
RANDOM FORAGER	0	0	C 0.153	0.306	0.403	0.5	A 0.75	1.0	p > 0.20 p > 0.20
APHID-TRAINED A. DORSALE	0.01	0.05	0.20	0.27	0.41	0.45	0.65	1.0	(Upper p-value is for aphid-trained data set,
COLLEMBOLA-TRAINED A. DORSALE	0.07	0.10	0.26	0.34	0.37	0.44	0.68	1.0	the lower for Collembola-trained)

N.B. The suffixes 'A' and 'C' in the table show in which sections the biggest differences between model and data occur for aphid-trained or Collembola-trained A. dorsale respectively.

largest differences between models and data were in the same sections of the graph whether A. dorsale had been trained on aphids or Collembola (Table 6.6). This broke down only for the "Random Forager" model where the sizes of the differences between model and data were similar for all sections so some randomness would be expected.

More powerful parametric analysis was used to confirm that there were no differences in prey eaten between the aphid and Collembola trained beetles and that the "Random Forager" model best explained the data.

A nested analysis of variance (Snedecor & Cochran 1967) showed that there were no significant differences in the daily number of aphids eaten either between the aphid- and Collembola-trained groups or between individuals within those groups. The same analysis was used to show that there were no significant differences in the daily number of Collembola eaten between the two groups or the individuals within the groups.

Normal regression analysis (Snedecor & Cochran 1967) showed that for both aphid- and Collembola-trained groups there was a small but significant decrease in the numbers of aphids, Collembola and hence total prey eaten over the 10 day trial. In effect this meant that average number of prey eaten declined from 10 to 5 per day representing a decrease in calories consumed from 24 to 12 per day. There were no obvious reasons for this and as this range of calories eaten per day was well within that observed during the training period (Fig. 6.10) and was shown in both groups of beetles it was not considered to affect the interpretation of results.

Normal regression analysis, after angular transformation (Snedecor & Cochran 1967), showed that there was no significant upward or downward trend in the daily percentage of aphids (and hence Collembola) in the diet over the 10 days of the trial. The mean daily percentage of aphids in the diet for the aphid trained (65.3) and the Collembola trained (64.8) beetles were remarkably close to the calculated "no preference" line of 64 per cent.

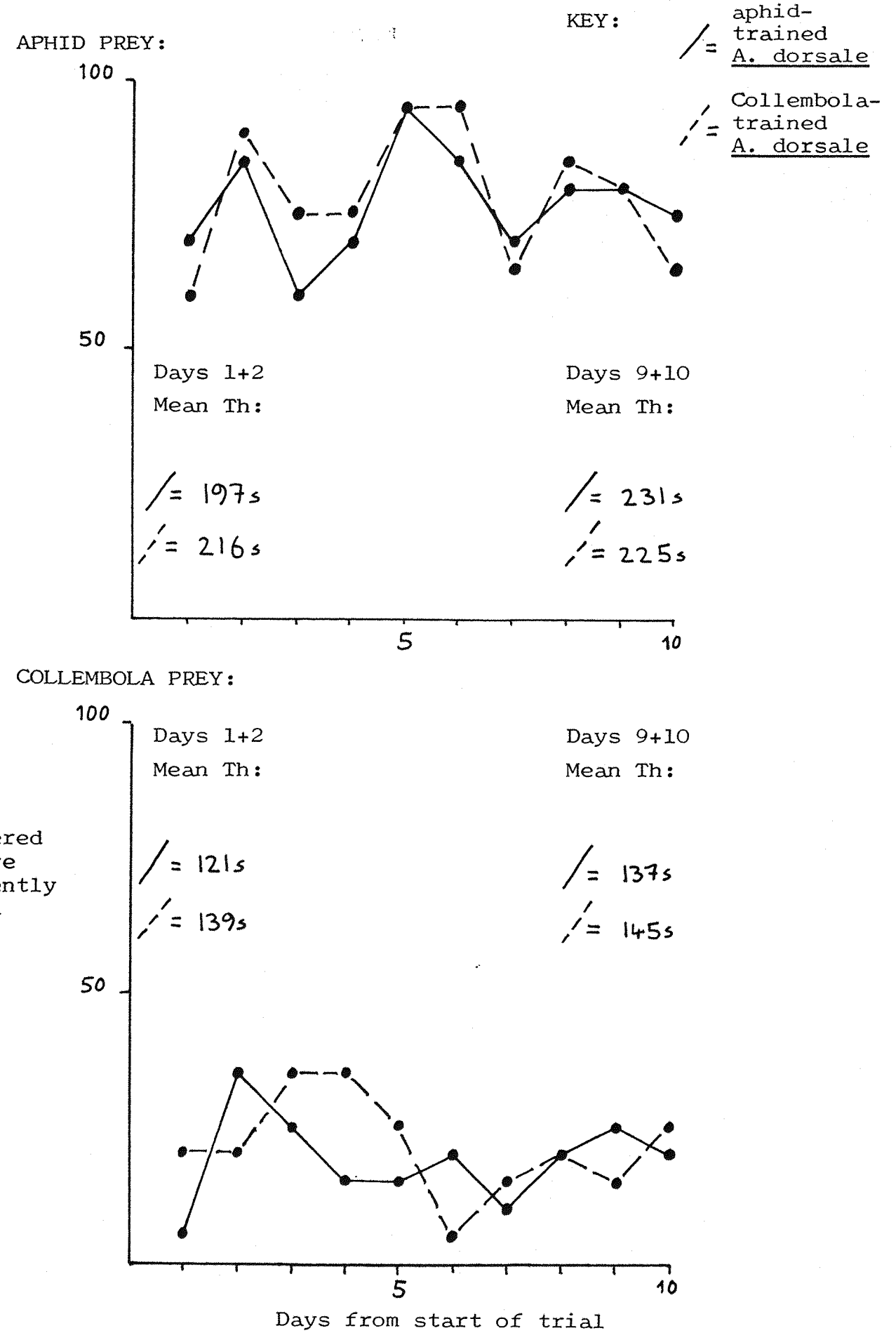
During the 10 days of the mixture trials the capture efficiencies of aphid- and Collembola-trained beetles for both prey types were recorded (Fig. 6.14). In addition, measurements of handling times were made on each of days one and two and nine and 10 of the trials for both prey types in both groups of beetles (Fig. 6.14). Regression analysis showed that for both groups of beetles the average capture efficiency for aphids was about 75% and that there was no significant upward or downward trend in this over the 10-day trial. Similarly the capture efficiency for Collembola for both groups was about 20% and did not change over the 10 days. The Mann-Whitney U-test (Siegel 1956) showed that handling times for aphids (about 200 s) or Collembola (about 120 s) were not significantly different within the aphid- or Collembola-trained groups when comparing the times for the first two days with the last two days of the trials.

The Mann-Whitney U-test (Siegel 1956) for unmatched samples was used again this time to compare the capture efficiencies and handling times for both prey types with the values obtained for these variables during the training period. There were no significant differences between either the aphid- or the Collembola-trained group and the values obtained in the training period.

In summary there was no evidence to suggest that A. dorsale of either sex selected prey in a way compatible with optimal foraging. Nor did the beetle either learn to or innately change its hunting methods to concentrate on the more profitable prey type. In general, the more "knowledge" of, or adaptation to the prey, the foraging model assumed for A. dorsale the less well the model explained the observed data. There were no changes in capture efficiencies or handling times during the two-prey trials confirming that A. dorsale was not adjusting its foraging strategy. The beetle took prey in the ratio predicted from independent measurements of capture efficiencies, handling times and calorific content of the aphids and Collembola. A. dorsale behaved as a random forager.

Aphids and Collembola are amongst the most common prey in a wheat field and if A. dorsale could not optimally forage on these it is unlikely

Fig. 6.14 The capture efficiencies and handling times of aphid- or Collembola- trained A. dorsale when fed a mixture of aphids and Collembola.



that it is adapted to do so on less common prey types. However, this needs to be tested and the next Section assesses whether A. dorsale always behaves as a random forager when offered the choice between aphids and other prey available in the wheat field.

6.6 The preference of A. dorsale for cereal aphids versus other common wheat-field prey types

So far experiments have shown that A. dorsale does not discriminate between prey types differing only in their capture efficiency nor does it discriminate between prey that in addition differ in size, shape and calorific yield. This suggests that A. dorsale either optimally forages using only extremely crude cues or that it forages randomly, i.e. a number maximizer. In the latter case it should take any prey it encounters until it has achieved the necessary calorific intake for the foraging period. This experiment is designed to test whether A. dorsale has any crude preferences for the more common wheat field prey types that cannot be explained by correcting the numbers eaten for the calorific content of the prey. For these experiments prey were freeze-killed so that the added complication of capture efficiencies was excluded.

The prey were placed in rough taxa and size (body length) classes and presented two at a time to individual A. dorsale in equal numbers (10 of each). After 1½ h the number of each prey type eaten was recorded and used to calculate a measure of preference which allows for depletion of prey. This measure is the β index of Manly, Miller & Cook (1972) and its advantages and disadvantages are reviewed more fully in Cook (1978). The main disadvantage is that for the estimation of preference to be good the total prey presented should be 20 or more, otherwise attaching accurate confidence limits to the index is not possible. The index has the main advantages that it has a finite symmetrical scale and it allows for exploitation. The range of the scale for a prey type is:

	Negative preference*	No preference	Positive preference	
0	⟵	0.5	⟶	1.0

* i.e. a preference for the other prey type.

The index is calculated in the following way (after Cook 1978):

First the index α' is calculated as an instantaneous measure of preference (i.e. a measure allowing for depletion) which has an assymetric and infinite scale. This is calculated from the expression:

$$\alpha' = \frac{\ln (N'/Ne')}{\ln (N/Ne)}$$

where N,N' = the numbers of prey types I & II initially present

Ne,Ne' = the numbers of prey types I & II eaten at the end of the trial.

This is easily converted to β in the situation where the prey types are presented at equal density (as in these experiments) by the expression:

$$\beta = \frac{N}{(N + \alpha' N')} \qquad \text{(symbols as before)}$$

where β is in effect the probability of the next prey eaten being type I and as such is a measure of preference.

The β index was calculated for each of the 10 individual trials that went to make up one prey type/size comparison. The binomial test (Siegel 1956) was then used to show whether the 10 β-values were consistently above or below the "no preference" 0.5 value (this indicates whether the beetles showed a consistent preference). The mean β values are shown in Table 6.7 together with data to show the difference in body length, dry weight and caloric content of the prey being compared. This information was used to test the hypothesis that the strength of preference for prey types is directly related to their calorific content. This does not imply that A. dorsale chose prey with the highest net energy yield only that the energy content of prey decided the ratio the prey were taken in: A. dorsale has a small and finite energy requirement per day so that if it eats one prey item with a high energy content it will eat less or none of the other prey

Table 6.7 The mean β preference values for, and the difference in body length, dry weight and calorific content between, some prey types commonly encountered by A. dorsale in the wheat field habitat.

Prey types presented		The difference between prey (Type I - Type II) in:				
Type I	Type II	Body length (mm)	Body weight (mg)	Calorific content	Preference value (β) for prey Type I	Significance of difference of β from 0.5 using the binomial test
Small aphids	Small Collembola	-1.7	-0.36	1.45	0.63	NS
Small aphids	Small Diptera	-0.75	-0.14	-0.70	0.22	$p < 0.05$
Small aphids	Large Diptera	-3.35	-1.07	-9.28	0.10	$p < 0.05$
Small aphids	Acari	0.4	0.05	0.41	0.90	$p < 0.05$
Small aphids	Thysanoptera	0	0.10	0.60	0.92	$p < 0.05$
Large aphids	Small Collembola	-1.0	-0.04	0.44	0.45	NS
Large aphids	Small Diptera	-0.05	0.18	1.19	0.29	NS
Large aphids	Large Diptera	-2.65	-0.75	-7.39	0.27	$p < 0.05$
Large aphids	Small Araneae	-2.1	-0.94	-4.59	0.27	$p < 0.05$
Large aphids	Small aphids	0.7	0.32	1.89	0.59	NS
Large Diptera	Small Diptera	2.6	0.93	8.58	0.55	NS

available creating an apparent preference. The way in which A. dorsale eats prey provides a simple mechanism for this. Inspection of the arenas at the end of the trials showed that A. dorsale invariably ate the whole body of prey items attacked. This means that if the beetle is presented with two prey types of difference sizes the following will tend to happen. If the beetle encounters a small prey item first it will eat it but then go on to attack further prey including the larger type. If the beetle encounters the larger prey first this could meet its energy requirement for the day and it would then cease to hunt either prey. Thus the beetle will appear to be exercising a preference for the larger (higher calorific content) prey type.

It seemed likely that β would be related to a simple property of the prey because initial inspection of results (Table 6.7) showed that all positive body length values had preferences of 0.5 and over and all but one (small aphids vs small Collembola) of the negative values had preferences of 0.5 or below. That is, A. dorsale showed a consistent (10 out of 11 cases) tendency to prefer the larger of the prey presented.

The consistent preference for the larger of the two prey presented was tested more rigorously by using the Spearman Rank Correlation Coefficient (Siegel 1956) to measure the association between the significant β values (Table 6.7) and the corresponding difference in body length or body weight or calorific content between the two prey types presented. As only six of the 11 comparisons from Table 6.7 were significant this sample was too small for any of the Spearman rank correlations to be significant:

		Correlation Coefficient
β vs:	Body length	0.757
	Body weight	0.814
	Calorific content	0.814

(If N = 6, for significance at the 0.05 probability level the correlation coefficient must be 0.829 or greater)

Despite the crudeness of the experiment both the intake of dry weight and the calorific content of prey explain a large amount of the variability of the β values for the various prey comparisons. The coefficients are nearly significant at the $p = 0.05$ level and inspection of the data in the Table suggests that calorific content may have been even better correlated if it had been possible to use a more sophisticated type of analysis.

Comparisons were made mainly between aphids and the other prey types. That A. dorsale shows preference for the larger of the two prey presented confirms earlier findings (of this Chapter and Chapter 5) that the beetle is not specially adapted to preying on aphids. Preferences were consistent only with differences between prey in dry weight and calorific content.

Using the data from Table 6.7 it is possible to show how different the prey need to be in body length, dry weight or calories before that difference leads to a consistent preference for the larger prey. Here again there is no suggestion of A. dorsale making a choice between prey, only the principle that if the beetle eats a large/high calorific content prey item it will then eat fewer of the other prey it encounters so appearing to show a preference for the larger prey. The average differences between prey in body length, dry weight and calorific content were compared for when β was significant or not significant (Table 6.7).

	Average difference between prey in variable measured		
Variable measured	β not significant	β significant	% difference
Body length	1.21	1.54	21
Body weight	0.37	0.51	28
Calorific content	2.71	3.83	29

On average the difference between two prey must be about 25% if A. dorsale is to show a clear preference for one of them using any one of the three variables to show the difference. This value seems to represent the difference there must be between prey before the physiology of A. dorsale records that it has eaten a larger prey item.

In other words if all the prey that A. dorsale was exposed to varied by less than 25% for these variables the beetle would be expected to eat exactly the same numbers of each prey (show no preference).

There is nothing to suggest that A. dorsale exercises preference in the sense of "choice" for the prey it encounters. These results suggest that crude differences in dry weight and calorific content determine the numbers of prey eaten (see also Section 6.5). The prey with the higher dry weight and calorific content are apparently preferred because their consumption leads to less of the other prey being taken but not vice versa. This is an effect only of A. dorsale having a limited consumption capacity per day and consuming the whole of any prey it encounters.

6.7 The effect of temperature on the capture efficiency of common prey types by A. dorsale

Chapter 5 showed that A. dorsale is not specifically adapted to preying on aphids. The introduction to this Chapter put forward the hypothesis that A. dorsale is really a general predator without specific adaptation to any one prey type. Two possibilities were put forward as to how as general predators the beetles could come to concentrate on cereal aphids; either A. dorsale optimally forages and aphids are the most profitable prey, or it catches a lot of aphids because habitat factors combine to make them the most available prey. The former possibility has been discounted by the preceding sections of this Chapter; the latter may not be as intractable to test as it sounds.

The previous experiments in this Chapter showed that capture efficiencies (or "how able prey are to escape") created bigger differences between prey types than size, shape, dry weight, calorific content or handling times. Capture efficiencies may be the major factor in deciding the overall availability of prey to A. dorsale. Experiments (Chapter 4.7) showed that the voracity of A. dorsale is markedly affected by temperature; there may be a similar effect of temperature on capture efficiencies. Casual field observations made during autumn collecting of A. dorsale adults from their hedgerow

overwintering sites suggested that on cold mornings (temperature around 5°C) the adults were very sluggish whereas on warmer mornings in the same month the adults were much more active when disturbed. This slowing of activity with temperature could be one mechanism for altering capture efficiencies and hence prey availabilities during the field season.

A temperature-controlled laboratory arena was designed to test the changing capture efficiencies of the prey (Chapter 2.6). The temperature could be varied between about 2°C and 18°C and the interactions between predator and prey observed through an insulating glass and perspex top. The three prey types thought to be most important (Section 6.3) were used; aphids, Collembola and Nematocera (mycetophilids were common in the diet of A. dorsale (Chapter 7.3) and were used throughout this experiment as representatives of the smaller Diptera). The prey types and A. dorsale individuals were placed separately in the arena at different temperatures to record when they became incapable of movement. A distinction was made between voluntary movement and movement forced by deliberately disturbing prey or beetles with the thermistor left in the arena to record temperatures in early trials. The most obvious result was that all the prey species were capable of activity at lower temperatures than was A. dorsale (Table 6.8). The gap in activity seemed to be narrowed at higher temperatures because A. dorsale rapidly became active with increasing temperature.

A methodological criticism is that the predator and the prey undergo rapid changes of temperature when introduced into the arena. There are two aspects to this; the behaviour of the animals may be altered for just a short period by the change in temperature, almost a "shock" effect from which they recover; but also the effect of the change in temperature may be lessened by preceding the test with a period of acclimation to that temperature (as would happen in the field). Both of these possibilities were tested for A. dorsale by recording both the mode of activity (walk or run) shown and estimates of the distance travelled over periods of 5 s (five estimates were made for each of five beetles at each temperature). These recordings were made for groups of beetles that had been acclimated at each of

Table 6.8 The change in locomotion of A. dorsale and some common wheat field prey with changing temperature.

Animal tested	Activity recorded	TEST TEMPERATURE (°C) 2	5	10	15
A. dorsale	Walking	N	V	V	V
	Running	N	N	V	V
Aphids	Walking	F	F	V	V
Collembola	Walking	F	V	V	V
	Jumping	F	F	F	V
Nematocera	Walking	F	F	V	V
	Flying	N	N	N	F

F = forced/prompted movement
V = voluntary movement
N = incapable of movement

the four test temperatures for a period of 5 days (the review by Weiser (1973) suggests that this is sufficient). Recordings were repeated at intervals of 1 h for 5 h at the two lowest test temperatures to assess any "shock" effect of the sudden changes in temperature. Further recordings were not made for the higher temperatures because if there was no effect at the lower temperatures there was unlikely to be one at the higher temperatures.

The Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to compare the average distances travelled for the five acclimated and the five non-acclimated beetles when observed at the beginning of each test. The Friedman two-way analysis of variance (Siegel 1956) was used to analyse the difference in average distance travelled by beetles in the acclimated or non-acclimated groups between the five recordings made at hourly intervals to assess "shock" effect. There were no significant differences between acclimated and non-acclimated beetles at the four test temperatures nor was there any significant "shock" effect in either group (Table 6.9). To extend this and assume that acclimation and shock will not effect the actual predator-prey interactions may not be warranted. So to minimise these sources of error both predators and prey were acclimated to the test temperature for 3-4 days prior to the tests.

Each of the prey types was presented to A. dorsale at test temperatures of 5, 10 and 15°C. All prey were presented at a sufficient density (about 1/2-3 cm^2) to produce a high encounter rate with A. dorsale despite the general decrease in activity at lower temperatures and also so that depletion of prey during trials was negligible. The number of encounters with prey and the outcome of these encounters was then recorded for a period of 30 min for each beetle. Encounters could be divided into several distinct categories with one major division; often A. dorsale touched prey but did not as a result change its behaviour or direction of movement; in this case it was deemed not to have detected the prey; alternatively the beetles responded with a change in behaviour or movement and were deemed to have "Encountered" the prey, i.e. A. dorsale "detected" the prey. Categories of encounters

Table 6.9 The mode and speed of movement shown by acclimated and non-acclimated A. dorsale at four different test temperatures and at hourly intervals during exposure to the two lowest test temperatures.

Initial temperature results

Test temperature (°C)		2	5	10	15
Mode of Movement	Acclimated	None	Walk	Walk & Run	Walk & Run
	Non-acclimated	None	Walk	Walk & Run	Walk & Run
Average Speed of Movement (cm/5 secs)	Acclimated	0	4.1	7.0	15.8
	Non-acclimated	0	3.5	7.0	16.0
Significance of difference - Wilcoxon Test		NS	NS	NS	NS

Temperature and time results for average speed of movement (cm/5s)

Test Temperature (°C)	Condition of beetles	Hours after start of Trial 1	2	3	4	5
2	Acclimated	0	0	0	0	0
	Non-acclimated	0	0	0	0	0
5	Acclimated	3	4	3.5	4	3.5
	Non-acclimated	3.5	2	3	3.5	4
Significance of difference - Friedman ANOVA		Acclimated = NS				
		Non-acclimated = NS				

where detection of prey took place were distinguished by the prefix "E". The categories were:

WO Touched prey but did not respond; Walk Over.

EWO Touched prey but walked over top of it while searching; Encounter Walk Over.

EL Touched prey but lostit by searching in wrong direction; Encounter Lost.

EW Touched prey but lost it because prey walked away; Encounter Walk.

EJ Touched prey but lost it because prey jumped away; Encounter Jump.

EF Touched prey but lost it because prey flew away; Encounter Fly.

ED Caught prey in jaws but then dropped it because either prey struggled or beetle mis-manipulated prey and prey escaped; Encounter Drop.

EC Caught prey and consumed it successfully; Encounter Capture.

T_h Handling time for prey.

These categories can be summarised briefly as:

PREY NOT CAPTURED -

because of "mistakes" by A. dorsale (WO, EWO, EL)

because prey actively escapes (EW, EJ, EF)

or

PREY CAPTURED -

prey lost (ED) or eaten (EC)

The proportions of encounters in each category are shown in Figures 6.15-6.17 for the three prey types. The Friedman 2-way analysis of variance (Siegel 1956) was used to show whether the proportions for any one category varied significantly with temperature for each prey type.

The results of Section 6.4 suggested that aphids were relatively easily caught by A. dorsale compared with other prey. The simple picture presented by Figure 6.15 confirms this. Only two categories changed significantly with temperature and these were by far the largest categories of encounters. As temperature increased A. dorsale

Fig. 6.15 The change in percentage of each encounter category with changing temperature for A. dorsale with APHIDS.

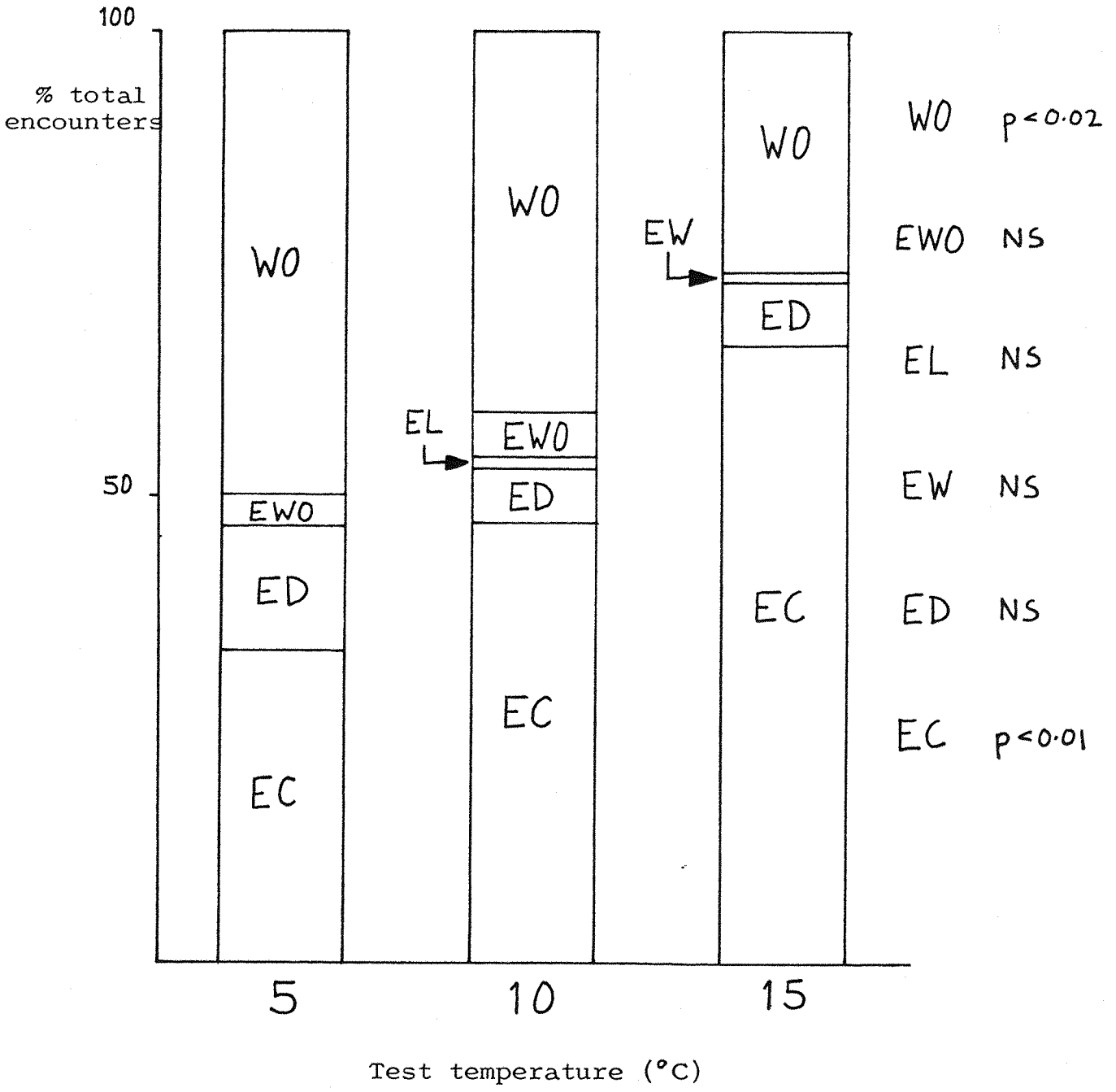


Fig. 6.16 The change in percentage of each encounter category with changing temperature for A. dorsale with COLLEMBOLA.

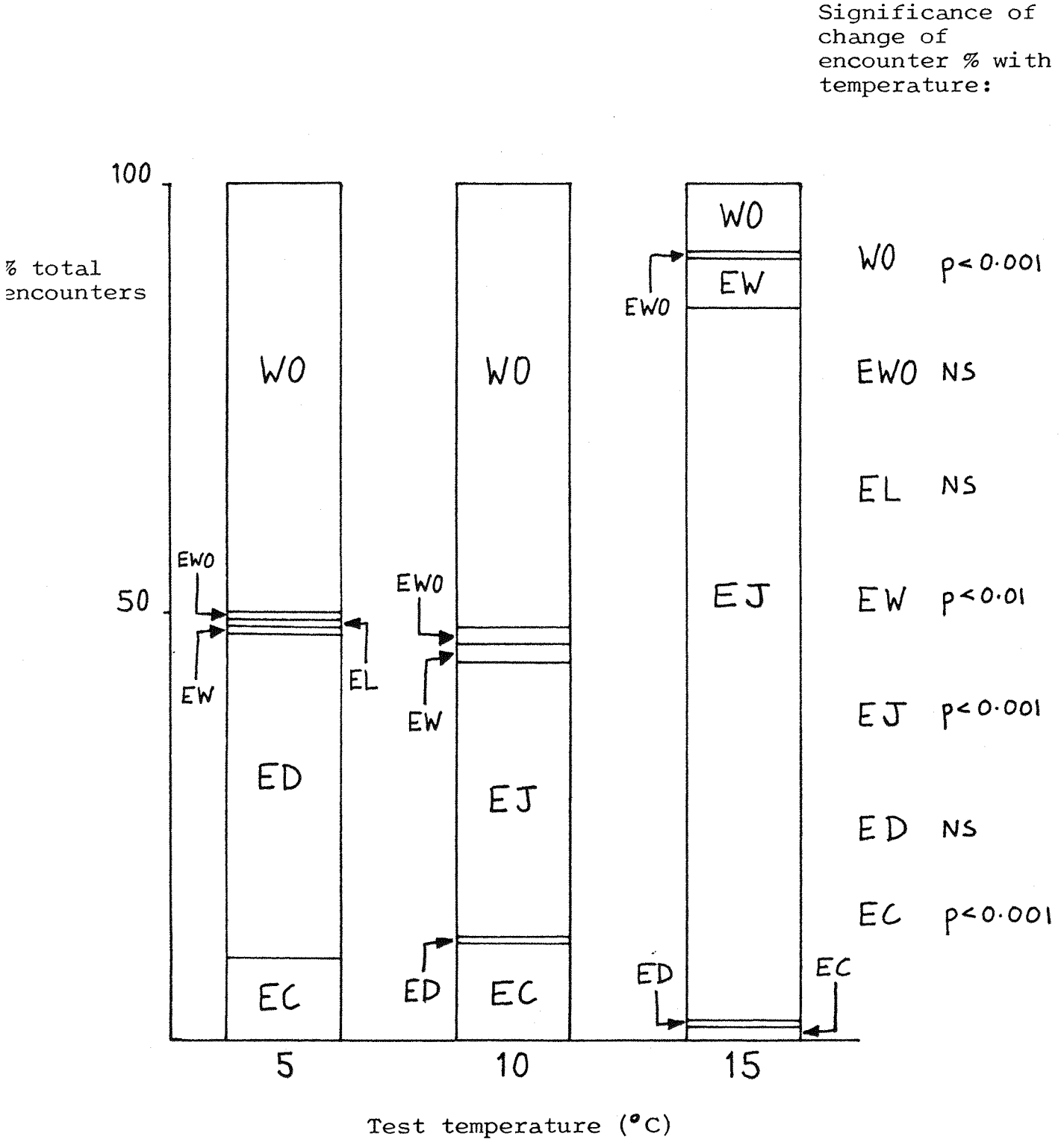
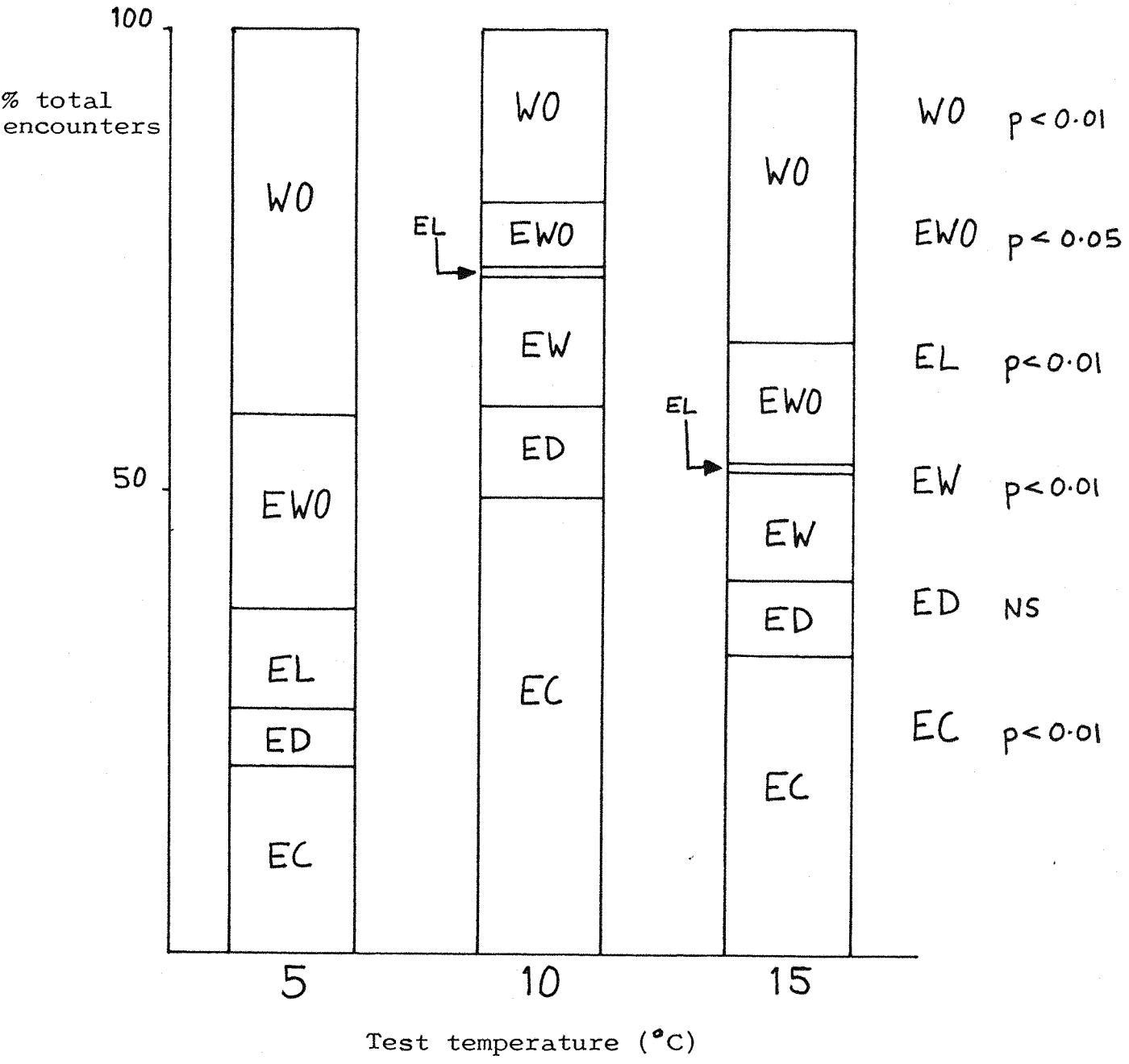


Fig. 6.17 The change in percentage of each encounter category with changing temperature for A. dorsale with NEMATOCERA.



detected more of the aphids it encountered (shown by the significant decrease in "Walk Overs") and there was a parallel (significant) increase in the number of aphids it successfully caught.

For Collembola, again there was a significant increase in the proportion detected by A. dorsale with increasing temperature (Fig. 6.16). As temperature increased however the proportion of Collembola captured decrease and this was due to the Collembola escaping more often (shown by the significant increase in the "Encounter Walk" and "Encounter Jump" categories).

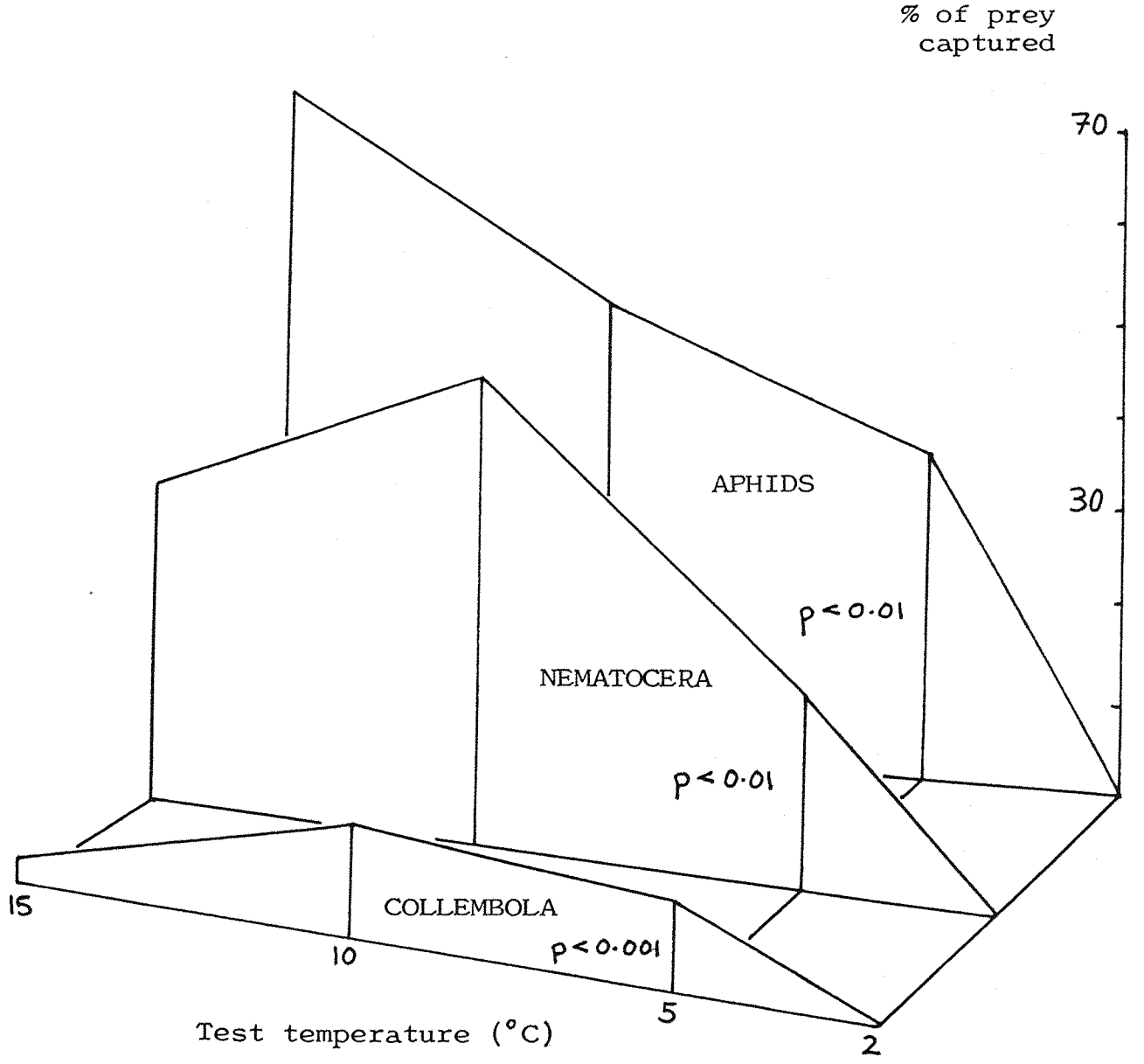
There was no uniformly-changing trend for Nematocera (Fig. 6.17); A. dorsale detected the highest proportion of Nematocera at 10°C with a corresponding maximum in captures at this temperature; the reasons for this peak are not clear. The three categories of mistakes by the beetle (WO, EWO, EL) decrease rapidly at 10°C (due probably to an increasing efficiency of the sensory and manipulatory apparatus of A. dorsale but inexplicably increase again at 15°C. The Nematocera seem to be more active at 10°C as there was a significant increase in "Encounter Walks". This may make it easier for A. dorsale to detect the flies, but if this is the case it should also happen at 15°C.

The interaction between A. dorsale and the prey is now analysed in more detail and a possible explanation given for the Nematocera trends.

Graphical representations of capture efficiency ("Encounter Captures"), handling times and numbers of prey eaten with changing temperature, for the three prey types, pinpoint the apparent anomalies in the data (Figs. 6.18-6.20). As A. dorsale is a poikilotherm, and if all the prey were assumed to be relatively immobile, it would be expected that as temperature increased capture efficiency and numbers eaten would increase and handling time would decrease. These expected trends are compared with the actual trends.

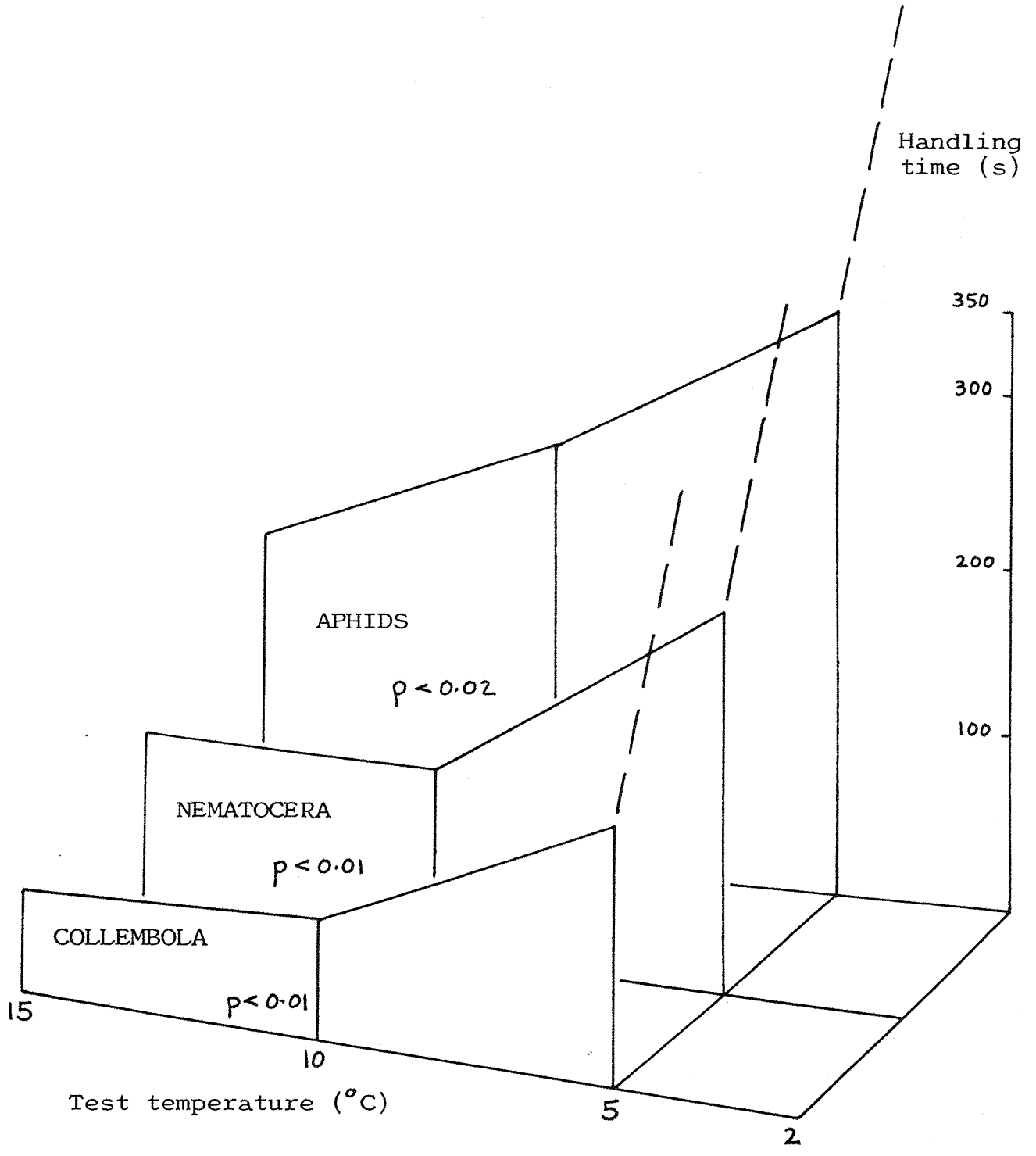
Capture efficiency (Fig. 6.18) should increase with temperature and this is true for aphids and for Collembola up to 10°C (above this the Collembola become sufficiently active to escape capture by jumping

Fig. 6.18 The change in capture efficiency with temperature for A. dorsale feeding on aphids, Collembola and Nematocera.



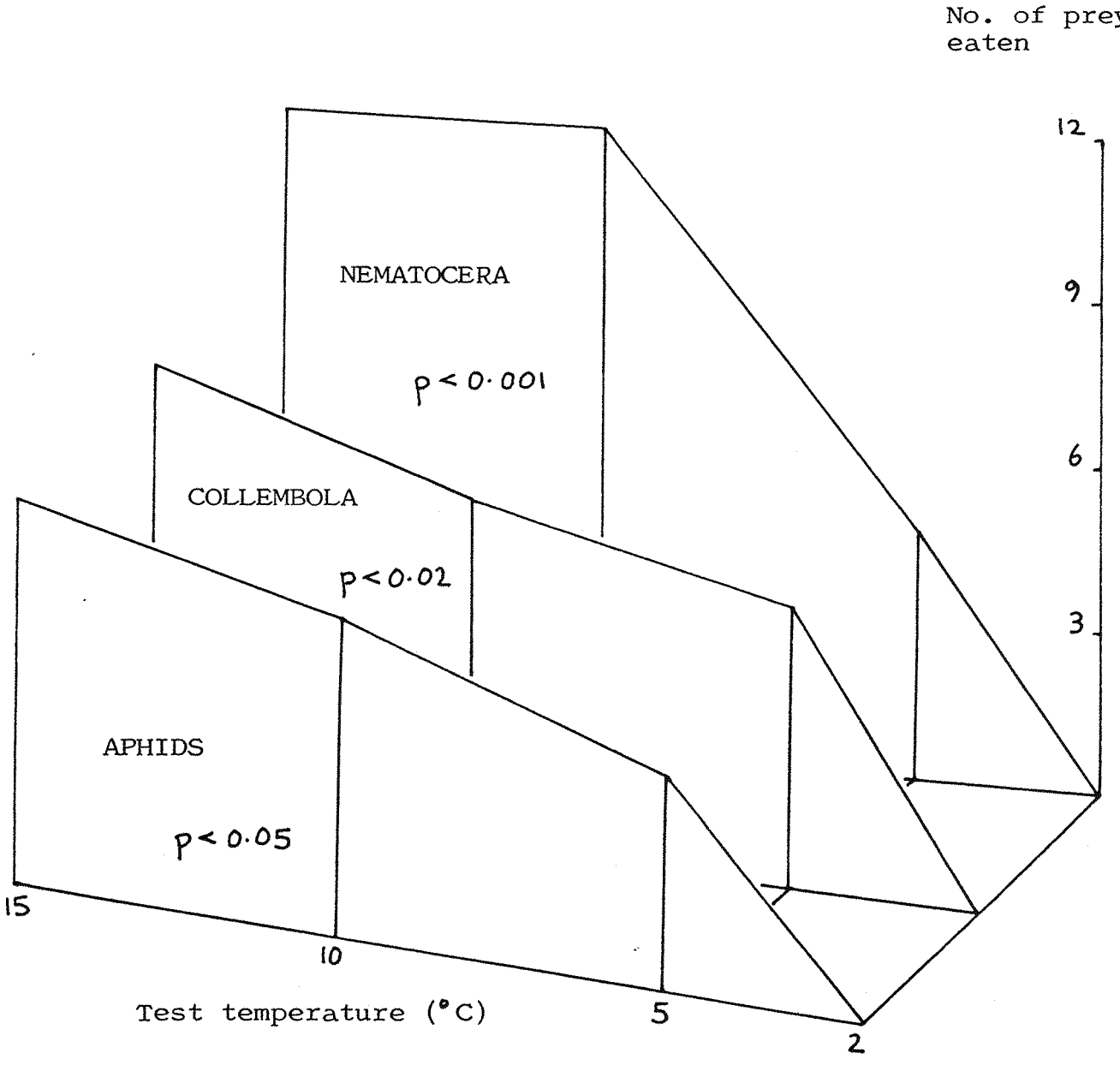
Probabilities are given for the significance of the difference between percentage captures at each test temperature for each prey type (Friedman 2-way ANOVA).

Fig. 6.19 The change in handling time with temperature for A. dorsale feeding on aphids, Collembola and Nematocera.



Probabilities are given for the significance of the difference between handling times at each test temperature for each prey type (Friedman 2-way ANOVA)

Fig. 6.20 The change in number of prey eaten with temperature for A. dorsale feeding on aphids, Collembola and Nematocera.



Probabilities are given for the significance of the difference between number of prey eaten at each test temperature for each prey type (Friedman 2-way ANOVA)

or walking away, Fig. 6.16). The decrease in capture efficiency at 15°C for Nematocera appears from Figure 6.17 to be due to an increase in "mistakes" made by A. dorsale. Why capture efficiency should first increase and then decrease is not clear.

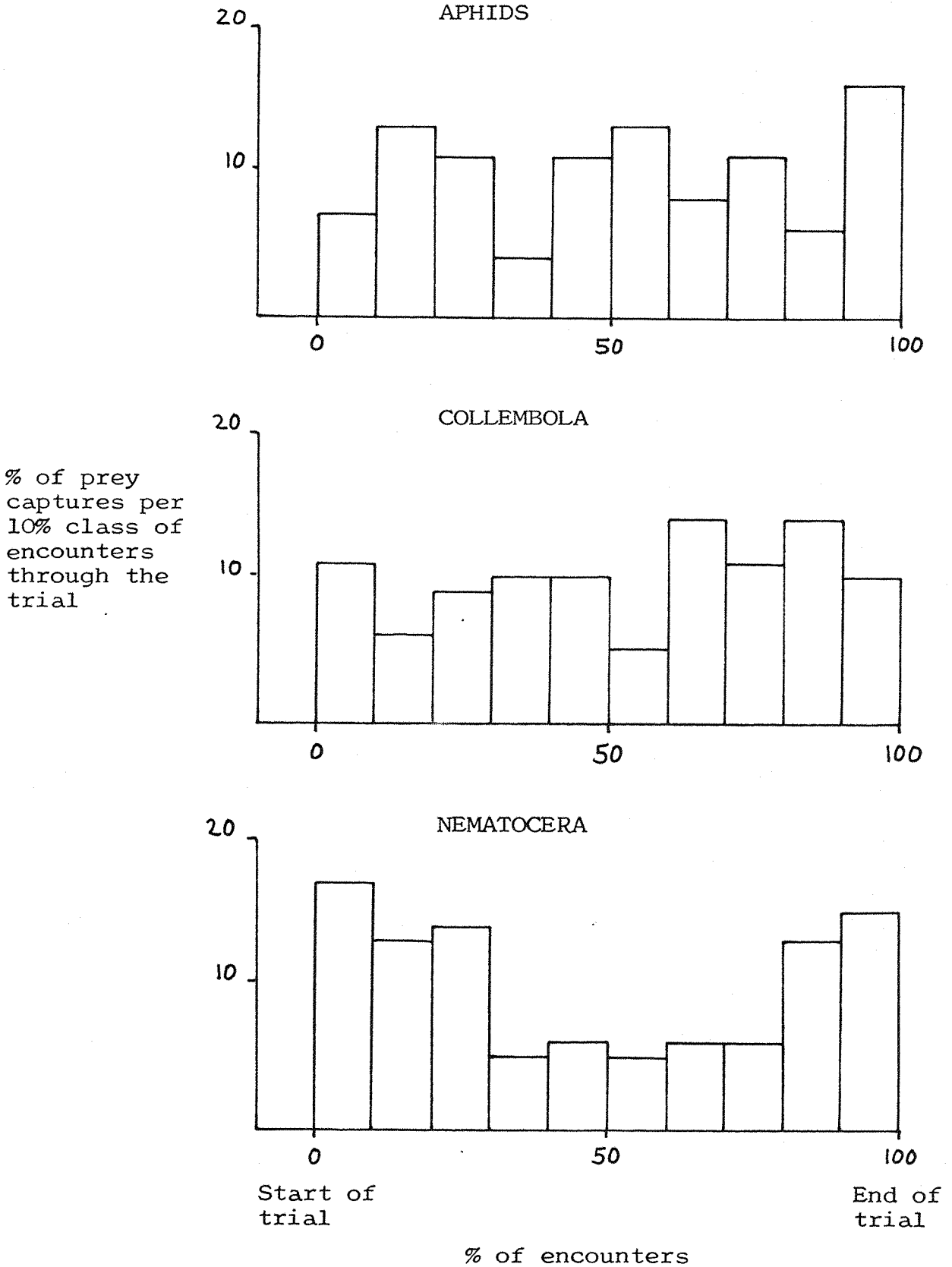
As predicted, handling time decreased with temperature (Fig. 6.19) for aphids, Collembola and Nematocera but appears to level off towards 15°C. This levelling off is probably due to limitations of A. dorsale rather than prey struggling more actively because the "Encounter Drop" category did not increase significantly with temperature for any of the prey types (Figs. 6.15-6.17).

Number of prey eaten increased with temperature as predicted for aphids and Collembola, but the number of Nematocera eaten levelled off between 10°C and 15°C (Fig. 6.20). The levelling off of numbers eaten must be linked with the decrease in capture efficiency for Nematocera.

Results suggest that A. dorsale starts to "ignore" Nematocera at temperatures above 10°C but there were no obvious differences in behaviour to account for this. One remaining possibility is that the combination of intermediate handling time but high capture efficiency for Nematocera led to high numbers being eaten and it may be that A. dorsale becomes satiated within the period of the trial at temperatures above 10°C. If this were the case then the proportion of encounters leading to captures should decline through the trial. If satiation were having no effect then there should be no clear trend. This appears to be the case for Nematocera (Fig. 6.21); there were no clear trends for aphids or Collembola but captures clearly declined for Nematocera, although they did increase again at the end of the trial. If this decline in captures represents satiation, then it clearly explains the levelling off in numbers of Nematocera eaten and the reduction in capture efficiency above 10°C. Once full, A. dorsale would leave further Nematocera it encountered producing an increase in the WO, EWO and EL classes (Fig. 6.17).

Corroboration of the satiation hypothesis comes from calculating the calorific content of the prey offered and using this to calculate

Fig. 6.21 The distribution of prey captures within the total encounters per trial at 15°C.



the calorie intake of prey at the different temperatures. This calorie intake is then compared with an expected maximum; the calorie intake over 24 h of A. dorsale when fed on a constant diet of aphids at different temperatures (Chapter 4.7).

Prey offered	Size (mm)	Dry Weight (mg)	Calorific Content
Aphids	1.4 - 1.7	0.31	1.84
Collembola	2 - 3	0.29	1.30
Nematocera	1 - 3	0.26	1.38

These data can be used to calculate the calorific intake of A. dorsale over the half-hour period of the trial. The intake simply equals the calorific content of the prey multiplied by the relevant number of prey eaten (Fig. 6.20).

	Calories ingested			
	Test Temperature (^{o}C)			
Prey offered	5	10	15	Average
Aphids	7.2	10.9	13.1	10.4
Collembola	6.6	8.2	10.4	8.4
Nematocera	6.4	15.9	15.3	12.5

The data from Section 4.7 showed that over 24 h A. dorsale could be expected to consume between 15 and 20 calories at temperatures above 10^{o}C and this represents a maximum with which to compare the ½ h intake results. Only when A. dorsale was feeding on Nematocera did it reach this level of calorie intake so only with Nematocera would satiation be expected to occur.

Despite the differences in interactions, capture efficiencies etc. between prey the average calorific intake of A. dorsale is very similar for all three types. This emphasizes the point made in earlier sections of this Chapter that A. dorsale is not distinguishing between prey types, it eats any prey in order to attain a constant daily intake of calories.

Often in the literature the number of prey attacked has been framed in terms of attack rates and handling times for invertebrate predators (Hassell 1978), and in terms of calorific content of prey and handling times for vertebrate predators (Krebs 1978). For A. dorsale the major factors controlling the numbers of each prey type attacked can be even further simplified to just one; capture efficiency. Assuming that the three main prey types (aphids, Collembola and Nematocera) were presented in a 1:1:1 ratio then it is possible to show how this ratio would be altered by the various factors such as capture efficiency:

Variable Acting on Original Ratio	Prey Types		
	Aphids	Collembola	Nematocera
Assumed original ratio	1 :	1 :	1
Average densities on the soil during the field season (see Chapter 7)	1.9 :	7.5 :	1
Capture efficiencies at 5°C	3.4 :	1 :	2
Capture efficiencies at 15°C	33 :	1 :	16.5
Handling times at 5°C	2.2 :	1 :	1.5
Handling times at 15°C	3.1 :	1 :	1.8
Calorific content of prey	1.42 :	1 :	1.1

At 5°C, capture efficiencies could not alter the presented ratio of prey by any more than the other variables but at 15°C their effect is an order of magnitude larger. As capture efficiencies seem to be so important in deciding the presented ratio, and hence (as A. dorsale forages randomly) in deciding the numbers of each prey type attacked, it should be possible to use them to correct actual field densities of the prey. If capture efficiencies are really the major factor then

after this correction the field densities of prey should correlate well with the proportions of prey in the A. dorsale gut contents (Chapter 7.3). This was done for the 1980 field data from the Damerham field site (Chapter 7.3) for the densities of prey on the soil surface with the corresponding gut contents of beetles from those sampling dates. Soil-surface prey densities were used because the work of Chapter 5.6 showed that A. dorsale rarely climbs.

The figures were converted as follows:

Hypothesis: A. dorsale takes prey in the ratio offered to it, but this ratio is altered by capture efficiencies that change with temperature. If the field densities of prey are adjusted to allow for changing capture efficiencies they should correlate with A. dorsale gut contents.

Gut data: The data are in the form of the proportion of beetles dissected containing a named prey type out of the total number of beetles dissected.

Soil density data: The densities of the three prey types were converted to proportions of prey available out of the total density of all three prey. These proportions were then corrected for the night temperature on the sample date by multiplying them by the relevant capture efficiency. To make the calculations simple the minimum night temperature was used to extract the capture efficiencies of each prey for the sample date from Figure 6.18 (ideally a form of day-degree calculation as in Gilbert et al. 1976 should be done).

The gut and soil data proportions were then arcsin transformed and conventional correlation analysis (Snedecor & Cochran 1967) used to examine the improvement in the fit of the data due to temperature correction of prey availability. The results of the analysis are summarised in Table 6.10.

Correcting for prey availability improves the correlation between prey density in the field and the presence of prey in the gut of

Table 6.10 The change in correlation between prey density in the field and proportion of prey appearing in the gut contents of A. dorsale

PREY TYPE	Untransformed prey density		Transformed prey density	
	Correlation Coefficient (r)	Significance of r	Correlation Coefficient	Significance of r
APHIDS	0.6153	NS	0.6630	$p < 0.05$
COLLEMBOLA	0.7653	$p < 0.05$	0.8260	$p < 0.025$
NEMATOCERA	0.061	NS	0.17	NS

A. dorsale. For aphids and Collembola the correlation was either made significant or appreciably improved. For Nematocera the correlation was improved but was still low. For about half the sample dates the correction for capture efficiency greatly improved the fit of the gut data to the field data; for the other half there was either no change or very little improvement. The possible reasons for this and a more detailed attempt to fit gut dissection data to field prey densities are considered in Chapter 7.3. Clearly, capture efficiencies improve the correlation between gut contents and field density of prey; for only two samples (with aphids) did the correction actually make the difference in proportion between these two variables larger. Not all the variation has been explained but this result is the field proof that capture efficiencies are important.

In summary, separately testing the interactions of the three main prey types with A. dorsale was justified because the beetle has been shown to act as a random forager. There were clear differences in the availability of aphids, Collembola and Nematocera to A. dorsale. These differences were produced by a combination of factors of which capture efficiency was the most important. Collembola for instance, although common in the wheat field, appeared unavailable to A. dorsale from the crude trials of Section 6.3. The reason for this was that the Collembola were usually able to escape from the beetle and would only form a significant part of the diet when they were at very high density. Aphids and Nematocera should be equally available. All the prey had a lower temperature threshold of activity than A. dorsale making them all unavailable at temperatures below $2^{o}C$. This correlates well with the $3.5^{o}C$ threshold found in the temperature vs voracity trials of Chapter 4.7.

The effect of temperature on capture efficiencies is likely to be a key factor influencing the availability of prey in the field. This was partially confirmed by using temperature/capture efficiency corrections to improve the correlation between field densities of prey and the frequency of occurrence of those prey in the gut contents of A. dorsale.

6.8 Discussion

Summary of experimental results

The experiments of this Chapter have been an attempt to show at what level A. dorsale can distinguish between the prey types available to it and if the beetle has any capacity for optimal foraging. Bomb calorimetry showed that for different prey types within any one size range there can be differences of 2 x to 5 x in calorific content. Other optimal foraging studies have shown that shore crabs (Elner & Hughes 1978) and great tits (Erichsen, Krebs & Houston 1980) were capable of foraging optimally when prey differed by this order of magnitude. Also, within their size range, aphids clearly had the highest calorific content. A. dorsale could be expected to forage optimally and may concentrate on aphids if calorific content were the major difference between prey types.

A wheat field contains a wide range both in size and type of potential prey; for studies on foraging it is important to know the limits of such a range of prey. For A. dorsale prey taken were between 1 and 6 mm long (as determined by the body length of prey). These limits being set at the lower end by the beetle failing to detect prey and at the upper end by the hairiness or strength of the prey cuticle preventing the beetle from damaging the prey. This range was effectively reduced to 1 to 3 mm for live prey because prey above 3 mm were sufficiently active to escape A. dorsale. Most of the prey in this size range were aphids, Collembola, Diptera or Thysanoptera, but an index of availability (based on maximum observed field densities x percentage of each prey type eaten by A. dorsale) showed that only the first three of these were likely to be important in the beetle's diet. Accordingly these were the prey used in later experiments.

Discrimination between prey can be very subtle (shore crabs seem able to compare apparently very similar mussles, Elner & Hughes 1978) so the first stage in determining the discriminatory ability of A. dorsale was to present it with prey that differed only in the efficiency with which the beetle caught them. This was achieved by giving A. dorsale a choice between two cereal aphid species, one of

which escaped more actively than the other, but which were otherwise eaten in identical numbers by A. dorsale. The beetle did not forage optimally and took prey in the ratio expected for a random forager.

Differences between prey offered were then extended to shape, size and calorific content by presenting A. dorsale with a choice between aphids and Collembola. In addition the beetles were fed exclusively on one or other of the two prey types prior to being presented with the choice. This "training" period was to assess whether A. dorsale would change either its perception of prey or its hunting method to improve its capture efficiency of the prey. Such a change would be revealed by the beetle strongly preferring the prey type it had been trained on when offered a mixture. No such preference was shown and A. dorsale ate aphids and Collembola in the proportions predicted for a random forager throughout the choice trials.

Bomb calorimetry had suggested that A. dorsale should show a preference for aphids; this was tested more fully by offering the beetles choices between aphids and a wide range of other wheat field prey. Although preferences were shown these were consistent only with the hypothesis that A. dorsale is a random forager; the beetle's finite daily appetite combined with the calorie differences between prey can produce an apparent preference for the larger prey which requires no element of choice by A. dorsale. No consistent preference for aphids was shown unless they were the larger (in calorific terms) of the two prey offered. Trials also showed that no consistent preference was shown for either of the two prey types presented unless they differed by at least 25% in calorific value. In effect this means that A. dorsale does not even recognise that it has eaten a larger prey item unless it is at least one quarter as big again as the prey previously eaten.

These results all showed that A. dorsale should behave like a random forager but left unexplained how the beetle seems to chase aphids in preference to other prey in the field. Many environmental factors may determine prey availability but temperature had already been shown to be important in determining the voracity of A. dorsale and this proved to be so for prey selection as well. The capture

efficiencies for the three most commonly available prey, aphids, Collembola and Diptera (Nematocera mainly), were not only very different but also changed substantially with temperature. This means aphids can be the most available prey even when Collembola or Diptera are at higher field densities and so make it seem that A. dorsale is actually showing a preference for aphids.

(i) A. dorsale and optimal foraging theories

Capture efficiencies proved to be more important than calorific differences between prey and this may be so for many invertebrate predators because they have to feed on prey often as large and as active as themselves. This is a strong contrast to the many vertebrate studies of optimal foraging where the prey were generally minute and defenceless against the predator. An attempt to show by modelling that invertebrates tended to random forage whereas vertebrates foraged optimally(Griffiths 1975) may have been more successful if this had been taken into account. Griffiths, because he had to make use of data collected by other workers, was forced to make the assumption that "Such factors as, for example, capture success ..... are assumed unimportant as availability factors".

The Chapter has shown that although A. dorsale apparently prefers aphids in the field, it does not do so by following optimal foraging principles. A mechanism based on differential prey capture efficiencies showed how A. dorsale could behave as a random forager but still apparently show a preference for aphids. But given that there were sizeable calorie differences between prey this does not explain WHY A. dorsale does not, or has not evolved, to forage optimally. A consideration of the type of animals so far shown to forage optimally and the information that they need about prey availability to do so shows why A. dorsale has not developed this potential.

Animals shown to forage optimally can be broadly divided into two classes:

Vertebrates feeding on different types and sizes of prey, e.g. bluegill sunfish (Werner & Hall 1974), pied wagtails (Davies 1977a),

redshank (Goss-Custard 1977) and great tits (Krebs, Erichsen, Webber & Charnov 1977).

Invertebrates feeding on different physical sizes or patch sizes of one prey type only, e.g. parasitoid wasps (Cook & Hubbard 1977), ladybirds and waterboatmen (Cook & Cockrell 1978), shore crabs (Elner & Hughes 1978), parasitoid wasps (Hubbard & Cook 1978), bumblebees (Pyke 1978) and parasitoid wasps (Waage 1979).

The essential difference seems to be that vertebrates are capable of producing a flexible response to a range of prey types; invertebrates however seem to require close adaptation to one prey type only in order to forage optimally (three of the above studies are on very host-specific parasitoids). Waage (1979) has shown that parasitoid wasps have a simple inflexible behaviour that is closely adapted to their prey and as a result closely approximates optimal foraging. Hughes & Elner (1979) have shown a similar result for the shore crab which while optimally foraging on its usual prey of mussels was unable to do so when encountering dogwhelks, even though the method of predation was essentially the same for both. This relative inflexibility of invertebrate behaviour has often been made use of in behavioural experiments (Hinde 1970) because it is little altered even in unnatural laboratory surroundings. The neurological limitations of the invertebrate body are the first reason for A. dorsale not having developed optimal foraging; an innate and hence inflexible response is just not sufficient to deal with the many different types and patch sizes of prey that a general predator will encounter (Cornell 1976). The tiger beetle (Cicindellidae) is in a similar situation and it has also been found not to show optimal foraging (Wilson 1978).

A consideration of how much sampling a predator must do in order to forage optimally shows more pragmatic reasons for A. dorsale not foraging optimally. Many of the animals quoted are in a position to do a large amount of sampling; both birds and parasites are highly mobile and both (birds by eating lots of small prey items and parasitoids by laying lots of eggs) have the capacity to sample several patches within a single searching period (see Bibby & Green 1980 for birds and

Hubbard & Cook 1978 for parasitoids).

Carabids have been shown to move large distances while searching (up to 50 m per night, Baars 1979) but this is probably not an adaptation to sampling because unlike birds, which have a good spatial memory (see Davies 1977b), or parasitoids, which can detect prey at a distance by odour cues (Sternlicht 1973), the beetles have no obvious way of finding or more importantly returning to prey patches.

Assuming that A. dorsale could actually discover and return to patches then there are still problems with the actual amount of sampling that the beetle can do in any one search period. It is instructive to compare the problem of A. dorsale deciding which prey type to take with that of the great tits of Krebs et al. (1978) deciding between two artifical patches with different reward rates.

What constitutes a sample?

In the case of the great tits they were required to hop a number of times on a perch to obtain a prey item so although an individual hop did not always produce a reward, the perch itself could be recognised as having a reward rate. For A. dorsale an encounter with a prey item will not represent a hop because, unlike the perches, unless the prey is actually caught it cannot be recognised. Elner & Hughes (1978) showed that shore crabs need 1 - 2 s to assess the value of mussles; Erichsen et al. (1980) showed that great tits needed up to 5 s to assess simple artificial prey so it seems unlikely that A. dorsale can recognise prey from the brief contact it will have with them when the prey escape from the encounter. In other words a sample for A. dorsale represents the catching and eating of at least part of a prey item.

How many samples are needed?

Krebs showed that the number of samples needed to assess the better of two patches depended on the size of the difference in reward rate between the two patches. If we consider aphids and Collembola as the two patches then their calorific rewards are 1.84 and 1.3 respectively. This difference corresponds to a 30:20 reward ratio in Krebs' experiment; a difference in reward rate of 10. Krebs showed (with a

simulation model used to solve gambling problems) that the great tits could not have done any better than the 40 samples they needed to recognise the better of the two patches. A. dorsale can be expected to eat about 10 prey items per day, i.e. it can make 10 samples per day. There are two consequences of this slow sampling rate; A. dorsale would take 4 days to tell the difference between a patch of aphids and a patch of Collembola by which time the patches are likely to have changed substantially in size and even location; the only study on memory in carabids to date (Plotkin 1979) has shown that the beetles can only retain information for a maximum period of about 3 h. In other words by the following day A. dorsale will have forgotten what patch it was sampling thus making sampling over several days an impossibility. Krebs' analysis showed that in this situation a predator can gain nothing from attempting to sample, the only strategy is to eat whatever is caught; to behave like a random forager.

Clearly, A. dorsale is constrained both by its own neurological limitations and by optimal sampling theory to forage randomly between prey types. Although A. dorsale does not choose aphids this does not mean that it is of no use in biological control. Section 6.7 showed that aphids are often the prey most readily available to A. dorsale with no element of choice necessary. In addition modelling studies have shown (Comins & Hassell 1979) that optimal foraging is not necessary per se for a predator to control/stabilise a prey population. Comins & Hassell found that there was no real difference between predators that optimally foraged and those that had a fixed aggregation strategy in terms of their effect on the prey population.

A. dorsale forages randomly for prey but this does not mean that it has no potential for biological control; this aspect will be examined further with some simple modelling in Chapter 9.

C H A P T E R 7

CHAPTER 7

THE SOUTH ALLENFORD FARM FIELDWORK

(See Chapter 2.7 for materials and methods)

7.1 Introduction

The field work at S. Allenford farm lasted from October 1978 to May 1981 with the majority of the work being carried out during 1979 and 1980. A brief calendar of events is given in Figure 7.1 to provide a frame of reference for this Chapter. The fieldwork can effectively be split into periods of collecting during winter months and the 1979 and 1980 summer field seasons. As little was known about the details of phenology and diet of A. dorsale the 1979 field season consisted of simple sampling to answer very basic questions about the field biology of the beetle. With the knowledge gained from 1979, the 1980 field work was designed to answer much more specific questions about beetle diet and prey availability. Attempts were also made to observe A. dorsale foraging at night in the wheat field. The 1981 fieldwork had the sole purpose of determining the time of emergence of A. dorsale into the field so that the detailed observational fieldwork at the Chilworth field site (Chapter 8) could be started on the correct date.

Fieldwork was used to answer questions in four main areas: methodology, phenology, foraging and potential for biological control. Most of the methodological questions were concerned with sampling of prey which is still crude and not easily related to actual prey availability in the field. As methodological questions occur throughout this Chapter they are dealt with as they arise. Broadly, the Chapter is divided into a section on the phenology of A. dorsale and a section on foraging. The implications of both these sections for the biological control potential of A. dorsale are reviewed in the final discussion of this Chapter.

Fig. 7.1 A calendar of events during the 1979 to 1981 fieldwork at S. Allenford farm, Damerham, Hampshire.

1978	OCTOBER - DECEMBER	Collection of A. dorsale adults from hedgerow overwintering sites for use in laboratory experiments. Surface searches of adjoining fields for adults overwintering.
1979	JANUARY - FEBRUARY	As above, but in addition a site with large aggregations of A. dorsale was chosen for the summer fieldwork.
	MARCH - MAY	Pitfall trapping at selected field site (Bottom Down) to establish beginning of activity of beetles and emergence into the field. End of May pitfalls moved to other side of field to avoid I.C.I. pesticide trials.
	JUNE - AUGUST	Pitfall trapping/D-vac to sample A. dorsale and prey in the field.
	SEPTEMBER - DECEMBER	Pitfall trapping to establish end of activity/return to hedgerow overwintering sites and collection from there of adults for laboratory work.
1980	JANUARY - mid MAY	Pitfall trapping to establish beginning of activity of beetles, collection of adults and selection of a new field site (Watersfield) unaffected by spraying trials.
	mid MAY - JULY	Pitfall trapping (weekly and overnight), overnight sampling of prey by D-vac, plant clipping and soil samples. Attempted observation of A. dorsale at night, naturally and in an enclosure, in the field.
	mid JULY - DECEMBER	Pitfall trapping to establish time of return of adults to hedgerow overwintering sites and cessation of activity.
1981	JANUARY - MAY	Pitfall trapping to assess time of emergence of beetles as a guide to when to start the fieldwork proper at the Chilworth site (Chapter 8). Collection of adults for laboratory and Chilworth fieldwork.

7.2 The phenology of A. dorsale

(i) Distribution and movement between the field and field boundaries

In the Introduction to this thesis the known data on the phenology of A. dorsale were summarised. The two most important conclusions were: A. dorsale migrates from field boundaries into fields in the spring returning to the boundaries in the autumn and it belongs to the "spring breeder" class of carabids (Thiele 1977). The former is important in the context of the widespread destruction of hedges that has occurred on farms (Moore, Hooper & Davis 1967) and because migration enables A. dorsale to escape mortalities caused by agricultural practices such as ploughing, rolling or burning of fields. The latter is important in terms of biological control because spring breeding carabids are active as adults in the spring and early summer but these then die and are replaced by larvae in late summer. The precise timings and details of changes in the A. dorsale population had not been recorded in relation to the timing of other events in the wheat field.

Two methods were used to assess the distribution and movement of A. dorsale between boundary and field through the year. The first, searching by quadrat, has the advantage that it gives a measure of density but has the disadvantage that it is too time-consuming to do on an extensive scale (see Southwood(1978) for a review of sampling costs). The second, pitfall trapping, is much less time-consuming allowing sampling of beetles over wide areas but gives an estimate that combines size and activity of the population which may not be related in any simple way to the density of beetles (Briggs 1961; Mitchell 1963; Greenslade 1964). A combination of these two methods was used to assess the distribution of beetle populations in selected fields at S.Allenford farm.

(a) Distribution between field and field boundaries

As A. dorsale was known to aggregate in field boundaries (Pollard 1968; Thiele 1977) over the winter, collections were made of the adults at this time for use in laboratory experiments. During collecting periods records were made of the fields that contained the most boundary aggregations so that pitfall traps could be set in a field likely to

have a high population of beetles the following summer. Collecting trips showed that aggregations of A. dorsale could be found in almost any field boundary from a simple grass bank with a fence to a wooded shelter belt. Aggregations were most often discovered under patially-buried large stones or other debris. Although not quantified it was noticeable that in some boundaries (often those at the lower end of fields) no aggregations were found while in others they were common, although similar searching efforts were made in both areas.

During the 1979/1980 winter collecting, quadrat counts were made of A. dorsale numbers in a section of hedge and adjoining field in Watersfield (Chapter 2; Fig. 2.15) which was known from previous collecting to contain aggregations of the beetle (in the field boundaries). The quadrat was 0.25 m^2 and searches were made within it by turning over all large stones/surface debris and disturbing the top few centimetres of soil. This searching gave an estimate of about 150 A. dorsale for the 25 m length of boundary (= 12 m^2) sampled and no A. dorsale for the 25 m^2 of field sampled. This gives a boundary density of 12.5 beetles per m^2 and a field density of 0 beetles per m^2. These values are very close to those found by N.W. Sotherton (pers. comm.) when he soil-sampled a wide variety of boundaries and fields on S. Allenford farm (boundary densities ranged from 10-20 per m^2, according to type, and field densities were all 0).

The quadrat counts support the hypothesis that all A. dorsale adults appearing in a field during the summer have migrated from the adjacent field boundaries. Thus it should be possible to calculate an expected field density of beetles by knowing the size of the A. dorsale population overwintering in the boundaries (i.e. average beetle density in boundaries x area of boundaries) and dividing this by the area of the field. The size of the overwintering population is easily calculated if the boundary is a narrow hedge or grass bank because the beetles are distributed throughout the width of the boundary. If however the boundary is a shelter belt or the edge of a wood, the area is less obvious because it is not known how far into these boundaries A. dorsale penetrates. Results from Thiele (1977) imply that penetration is no more than 3 m into such boundaries; Sotherton

makes a distinction between woodland and 12 m-wide wooded shelter belts, and shows that individuals were found in the latter but not the former. As Watersfield has largely wooded boundaries, calculations of a density of A. dorsale were made on the basis of both the aforementioned 3 m wide, and 12 m wide, suggestions of the width of the beetle's overwintering site (the section of hedge boundary was measured as 2 m wide).

The dimensions of Watersfield are shown in Figure 7.2; the field has an area of 138,387 m^2 and an overwintering site area of 4601 m^2 if beetles penetrate 3 m into the woodland boundaries and 17,426 m^2 if they penetrate 12 m into woodland boundaries. Using the beetle density established in this study (12.5 per m^2) the boundary area with 3 m penetration into woodland should contain

$$4,601 \times 12.5 = 57512.5 \text{ beetles}$$

while the boundary area with 12 m penetration into woodland should contain

$$17,426 \times 12.5 = 217,825 \text{ beetles.}$$

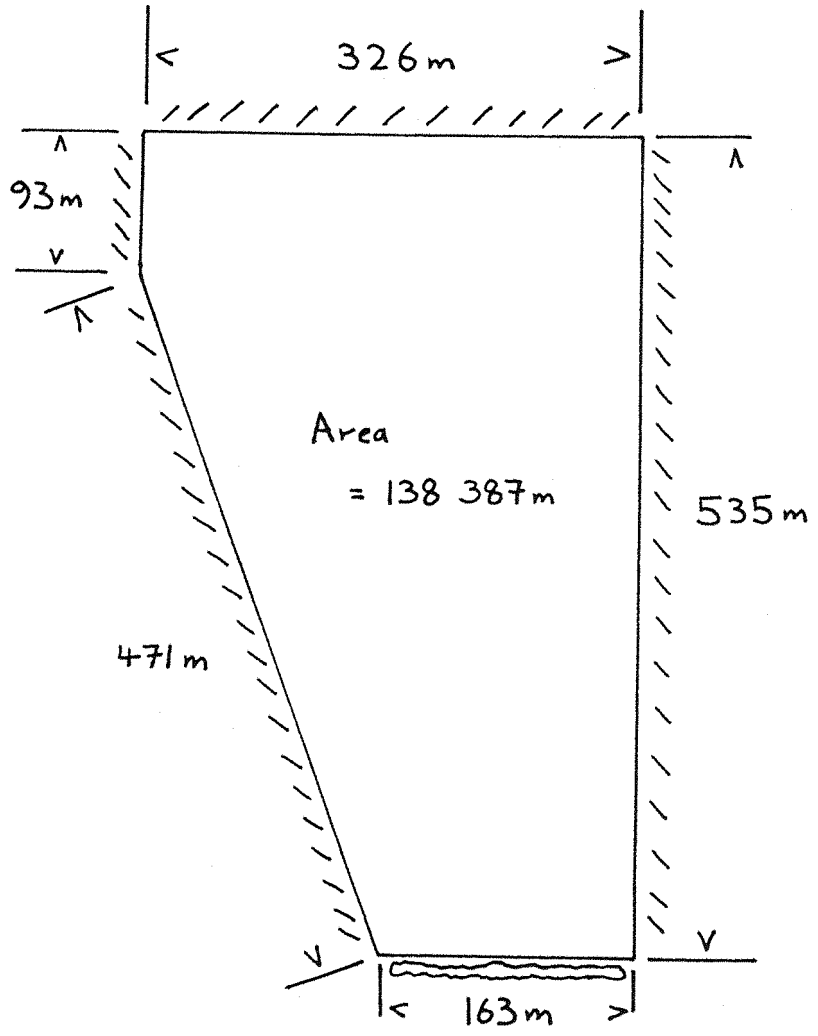
If these numbers of beetles were spread evenly over the field they would give densities of

$$57512.5/138,387 = 0.416 \text{ per } m^2$$
(for 3 m-wide boundaries)

and
$$217,825/138,387 = 1.574 \text{ per } m^2$$
(for 12 m-wide boundaries)

Clearly the density of A. dorsale in the field is always likely to be low compared with that in the field boundaries. This will be even more so in situations (unlike Watersfield) where field boundaries come between two field of equal "attraction" to A. dorsale so that the boundary population is spread over twice the field area.

Fig. 7.2 The area and boundary type of the Watersfield field site.



= hedge boundary (2m wide)

= wooded boundary (taken as 3m or 12m wide - see text)

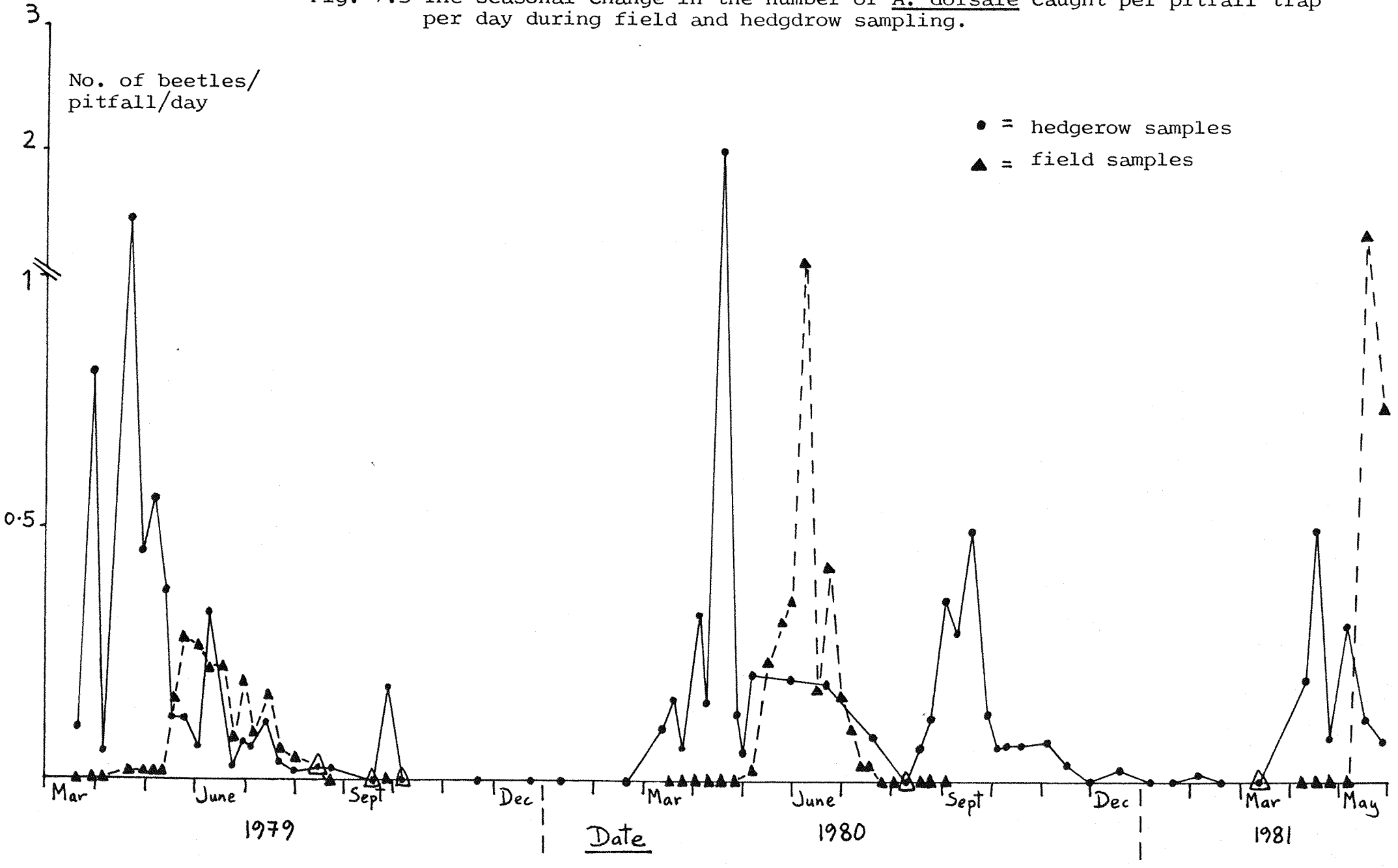
The low expected field density has two important implications. The quadrat samples gave a density of 0 beetles per m^2 in the field; this may have been simply because A. dorsale numbers were the same in hedge and field and hence field densities were very low (the expected catch from the area sampled would be only about 12 under this hypothesis). Observation of A. dorsale in the field at night is likely to be difficult if the beetle is at a density of 1 per 2 m^2.

(b) Seasonal activity and movement between field and field boundaries

Mark-recapture studies (Pollard 1968; Sotherton pers. comm.) have shown that A. dorsale adults caught in hedgerows in spring do move out into the field in summer, thus corroborating the winter quadrat data. Pitfall trap data also confirm this picture of seasonal migration to and from field boundaries. Traps were run from early 1979 to mid 1981 at S. Allenford farm, this period being split into March-October 1979 at the Bottom Down site and November 1979-May 1981 at the Watersfield site (Chapter 2; Fig. 2.13, map of field sites). As these sites are only about 800 m apart in the same land depression and have a similar history of cropping, it was assumed that the populations sampled would have similar phenologies so information is presented continuously from 1979 to 1981.

Pitfall trap catches revealed a consistent seasonal pattern of activity from year to year (Fig. 7.3). A. dorsale was active in field boundaries from mid March until September/October while field activity was restricted to the period mid May to mid July. Within these periods there were identifiable peaks of activity which when combined with data on the reproductive state of the population (see next Section for reproductive changes in the population) present a coherent picture of phenological events in the beetle population. (In 1979 peaks were less well defined after April and this reflects the fact that pitfall traps had to be moved across the Bottom Down site to avoid pesticide spraying trials). Yearly activity can be summarised as: adults showed no activity over the winter but rapidly became active in field boundaries in April. Activity in the boundaries decreased in May and this was accompanied by an onset and rapid increase of field activity (reaching

Fig. 7.3 The seasonal change in the number of A. dorsale caught per pitfall trap per day during field and hedgdrow sampling.



a peak in late May/early June). Activity in both field and boundaries then progressively decreased to nearly zero by mid June/August; this was followed by a second smaller peak of activity in the boundaries in late August/September.

These trends in activity support the hypothesis that A. dorsale migrates out from field boundaries in May and returns to them in August/September. Further analysis of pitfall catches shows how A. dorsale spreads out into the crop (Fig. 7.4). There were no beetles in the crop until mid May when they were caught in numbers 20 m into the crop. By early June beetles had spread 40 or 50 m into the crop and by the end of July catches had decreased to zero again. Figure 7.4 emphasises how limited the period of activity in the field is. In 1981 an extra row of pitfalls was placed at 5 m from the boundary in Watersfield. These showed that A. dorsale begins to move into the field in late April/early May but is not caught further out until mid May (Fig. 7.5). Identical patterns of movement were shown by A. dorsale in other fields on the S. Allenford farm in 1981 and 1982 (N.W. Sotherton, pers. comm.).

A survey of the literature on the time of emergence of the genus Agonum into crops shows it to be the same (i.e. May) across middle Europe (Dawson 1965; Pollard 1968; Neudecker 1974; Pauer 1975; Jones 1979; Kreckwitz 1980; Brown pers. comm.). The date of emergence for the three years monitored in this study was always mid May; identical dates were recorded for other fields on S. Allenford farm (N.W. Sotherton pers. comm.) and for Bridgets' Experimental Husbandary Farm (M.A.F.F.), near Winchester, (K.D. Bryan pers. comm.) in 1982. The factors controlling date of emergence were not investigated in this study but Figure 7.6 shows that of the main weather factors only the change in daylength gave a regular pattern from year to year around the time of emergence. (The shaded areas above the three-year mean for each weather statistic in Figure 7.6 are only to aid visual comparisons between years). Daylength could be the controlling factor for date of emergence and this agrees with the results and conclusions of other studies (see references quoted earlier) which show a generally similar time of emergence across middle Europe.

Fig. 7.4 The seasonal change in the distribution of A. dorsale over a winter wheat field as measured by pitfall catches.

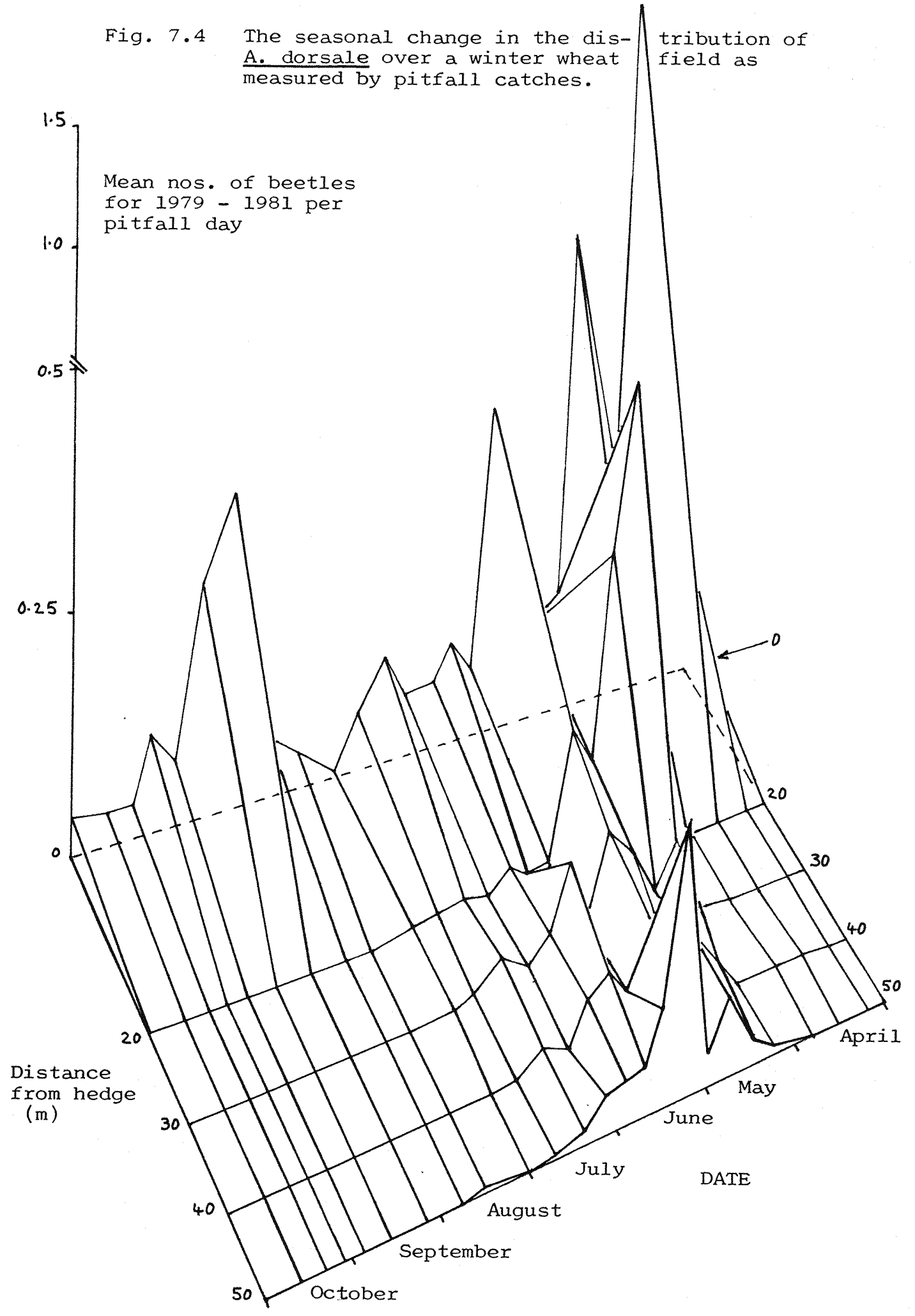


Fig. 7.5 The change in distribution of A. dorsale near a hedge boundary in the early part of the 1981 field season.

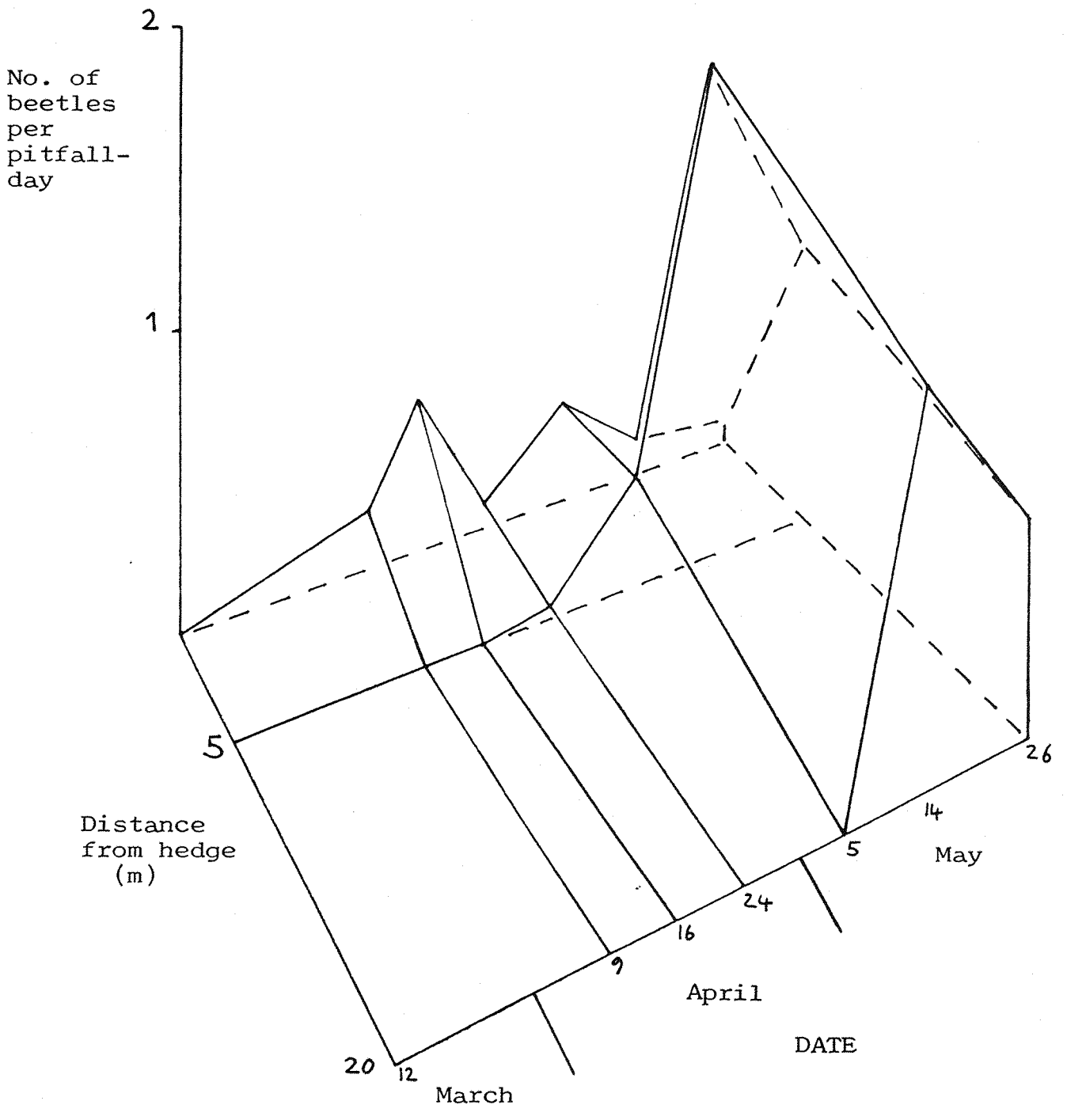
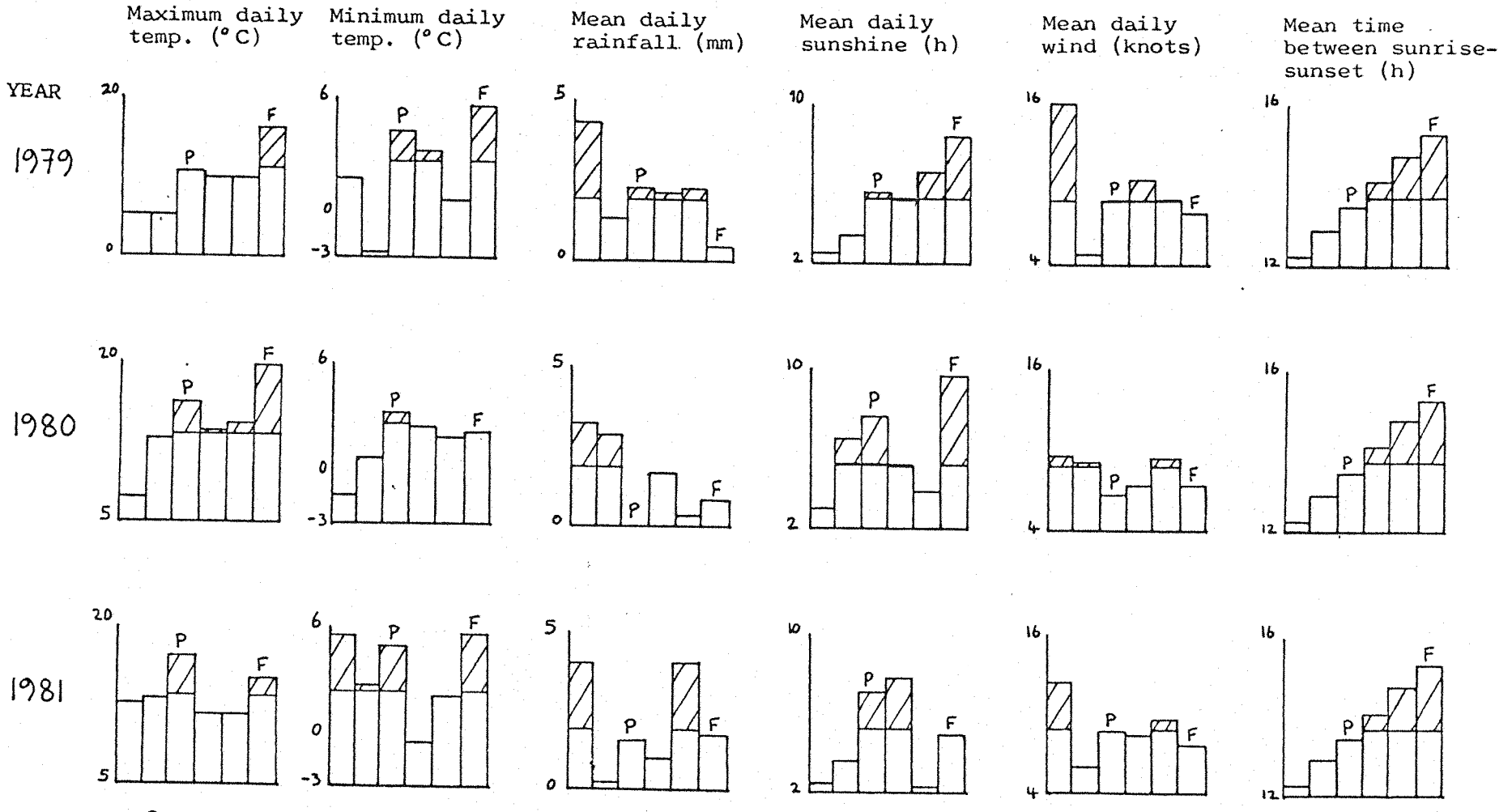


Fig. 7.6 The difference between years for 6 weather statistics at the time when A. dorsale shows activity in hedges followed by movement out into the field.



P = Peak activity in hedge
F = Time of emergence into field

The 6 bars represent the dates: Late March, Early, Mid and Late April, Early and Mid May.

▨ = Data above mean value for 1979-1981 (for each weather statistic)

(ii) Reproductive changes in the population

(a) Male and female reproductive states

Dissection of adults caught at the field sites showed that the stage of reproductive development of both sexes changes markedly through the year. Reproductive development could be divided into a number of clearly recognisable "states" for both sexes:

Males

1 - immature

Internal organs of abdomen traslucent/white in colour. Fat bodies occupy more of the abdomen than do the reproductive organs.

2 - mature

Internal organs of abdomen white/yellow in colour. Few fat bodies, instead reproductive organs greatly increased in size to occupy most of abdominal cavity, causing abdomen to appear swollen.

3 - spent

Internal organs of abdomen dark yellow/brown in colour, ragged in texture. No or few fat bodies with great reduction in size of reproductive organs, abdomen largely empty.

Females

1 - immature

Internal abdominal organs translucent/white in colour. Abdomen mostly occupied by fat bodies, ovaries small - no eggs developing.

2 - early egg

Internal abdominal organs white/yellow in colour. Ovaries yellow and containing developing eggs (orange). No eggs fully developed (fully developed eggs were identifiable by the presence of a dark orange/brown chorion).

3 - mid egg

Internal abdominal organs white/yellow in colour, few fat bodies in abdomen. Ovaries yellow in colour and containing a mixture of developing and fully-developed eggs, but most eggs still developing.

4 - late egg

Internal abdominal organs yellow in colour; few fat bodies in abdomen. Almost all eggs fully developed, forming a solid mass of ovaries/eggs and making the abdomen very swollen in appearance.

5 - spent

Internal abdominal organs dark yellow/brown in colour, all fat bodies gone, tissues ragged in texture. No or very few eggs left, abdomen almost empty.

In addition, females that had already laid one batch of eggs, usually in the previous field season (Jones 1978), could be distinguished by the presence of dark structures in the ovaries known as corpora lutea. These and the main reproductive organs of male and female A. dorsale are shown in Figure 7.7

Female A. dorsale, like most other female Coleoptera, have spermatheca (Fig. 7.7) in which sperm received from perhaps a single mating are stored until required for fertilising eggs. Thus by dissecting females taken periodically from the field the time of mating can be established by noting the date from which the females contained sperms in their spermatheca.

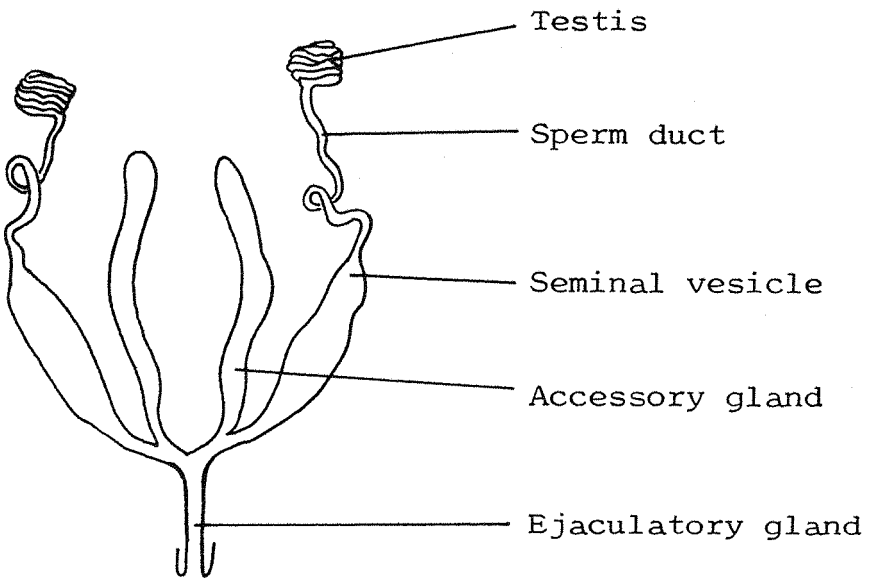
Clearly both sexes have large reserves of fat at the beginning of the reproductive cycle, these are then replaced with the developing reproductive organs. Once reproduction has been completed the reproductive organs disappear too.

(b) The seasonal change in reproductive maturity

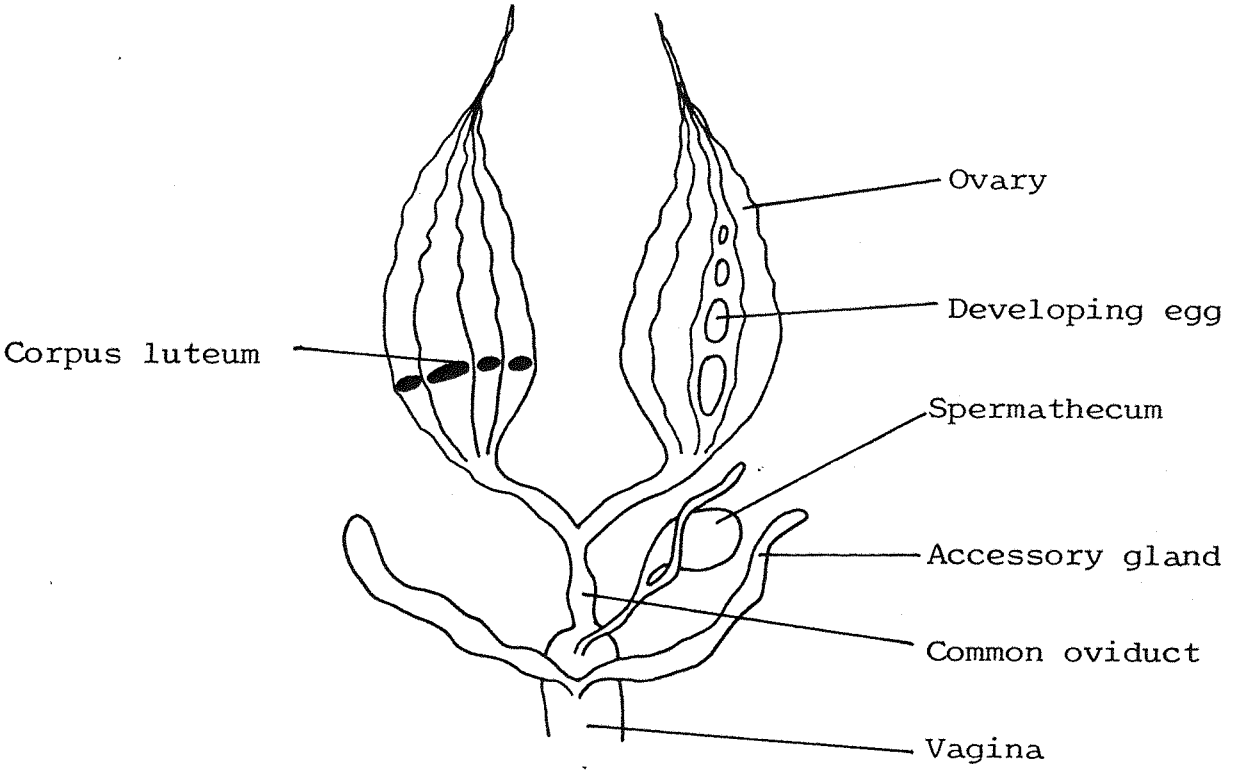
The individuals taken from the field during collecting or pit-falling were dissected and scored for reproductive state. An average reproductive state was calculated for both sexes on each sample date

Fig. 7.7 The male and female reproductive organs of A. dorsale.

MALE:



FEMALE:



by dividing the sum of the reproductive state scores by the number of beetles dissected:

If three males were dissected and one was state 1 and two were state 2, this would give an average state of

$$\frac{1 + 2 + 2}{3} = 1.7$$

The average number of fully-developed eggs per female (counting only those containing fully-developed eggs) was also calculated for each sample date.

The seasonal changes in average reproductive state for both males and females in the field boundary and the field occurred in synchrony with seasonal changes in activity (Fig. 7.8). Individuals of both sexes were reproductively immature throughout the winter months; development started in early to mid May with the population containing mature and spent individuals by June. The population was still composed of mature individuals through July but by the end of August the population contained mostly immature individuals. At this time a large proportion of individuals were callow, i.e. freshly emerged from pupae.

The overall picture is one of the beetle population going through a rapid reproductive cycle within the months May-July and for the rest of the year being composed of immature adults.

It is generally recognised (Gilbert et al. 1976) that poikilotherms do not have a time-scale measured in calendar days but in an integration of temperature and days : day degrees. If the time axis in Figure 7.8 is adjusted to day degrees then a truer idea of the rate of change in reproductive state of the population is obtained (Fig. 7.9). A threshold temperature of 2.9°C was set in calculating the day degrees for each calendar month. Below this temperature A. dorsale is inactive (Chapter 6.7) and has a voracity of zero (Chapter 4.7) so it was assumed that reproductive development would not occur either. Adjustment for day degrees shows that the reproductive cycle, rather than being completed in just under one third of a year, actually occupies half of the A. dorsale "physiological" year. This conversion also shows clearly

Fig. 7.8 The seasonal change in the reproductive maturity of A. dorsale populations sampled from wheat fields and adjacent hedgerows.

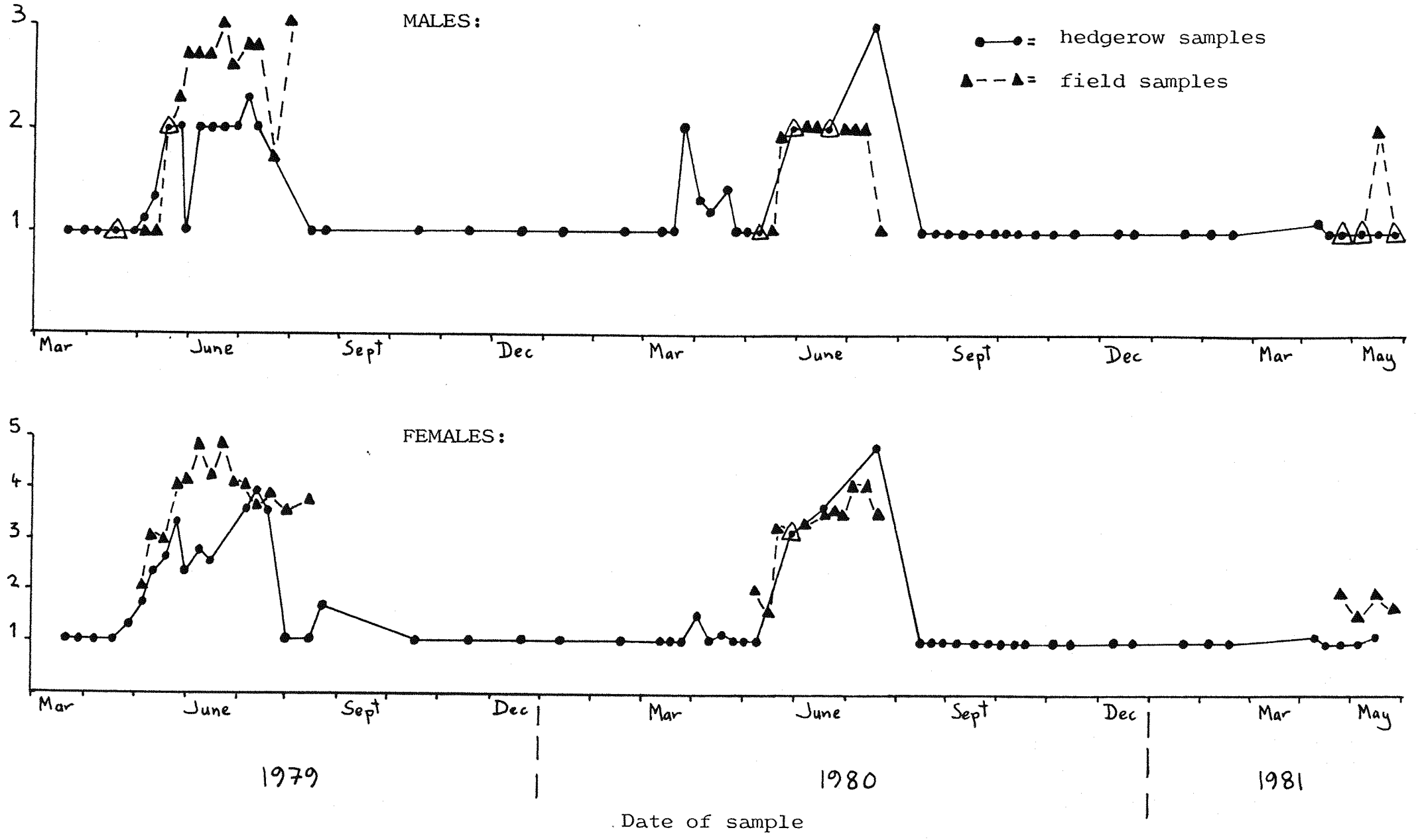
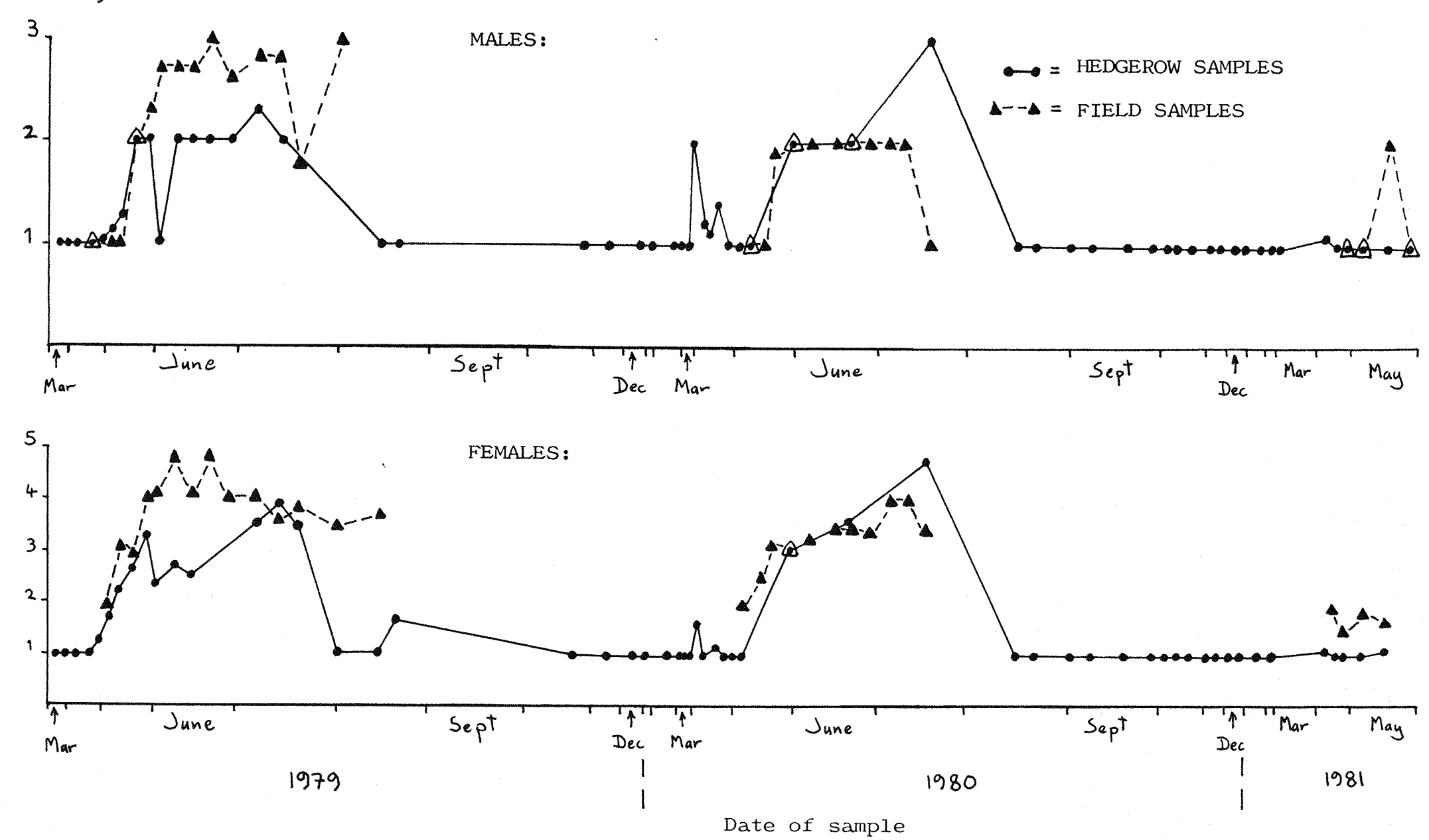


Fig. 7.9 The seasonal change in the reproductive condition of A. dorsale sampled from wheat fields and adjacent hedgerows (on a day degree scale).



that May-October are the "longest" months of the year and so need to be sampled at shorter intervals (in calendar days) than other months to provide a full picture of events in the A. dorsale population; (this was not done for the 1979 August-October period).

Egg numbers were closely linked to reproductive state and hence mirrored the seasonal reproductive changes, with peak numbers per female in June/July (Fig. 7.10). There was no obvious reason for the large peak in numbers in July 1979. There were four sets of egg data (field 1979, boundary 1979, field 1980 and boundary 1980) and comparisons were made between the numbers of eggs per individual for each reproductive state between these four data sets. Analysis of variance (Snedecor & Cochran 1967) was used to determine whether there was any difference between the data sets for each reproductive state. If there was an overall difference, a least significant difference (L.S.D.) range test (Steel & Torrie 1980) was used to show where the differences lay between the data sets. The mean values and results of the significance tests are shown in Figure 7.11. The analysis showed that there was a difference between the four sample dates for reproductive state 3 only where the 1979 boundary females contained significantly fewer eggs. Referal to Figure 7.8 shows that female boundary beetles were less reproductively mature than the 1979 field or 1980 females; there was no obvious reason for this. This consistency of egg numbers from year to year or site to site has two important implications; reproductive development in female A. dorsale may be very rigid, i.e. once the cycle has started the females produce a fairly constant number of eggs, and/or the qualitative divisions of the cycle into five reproductive states were also sufficiently quantitative to produce this consistent egg number.

Dissection of females in the 1981 field samples included examination under a high power microscope of the spermatheca (Fig. 7.7) for the presence of sperm. The proportion of females containing sperm increased in both hedge and field from April to May (Fig. 7.12); unfortunately the beginning of mating could not be pinpointed as even females dissected in early April contained sperm. Unless a large proportion of females do not mate (which seems unlikely when so many produce eggs) then mating must occur in the boundaries and the field at least over the period of April/May.

Fig. 7.10 The seasonal change in average number of fully-developed eggs per female in hedgerow and field samples.

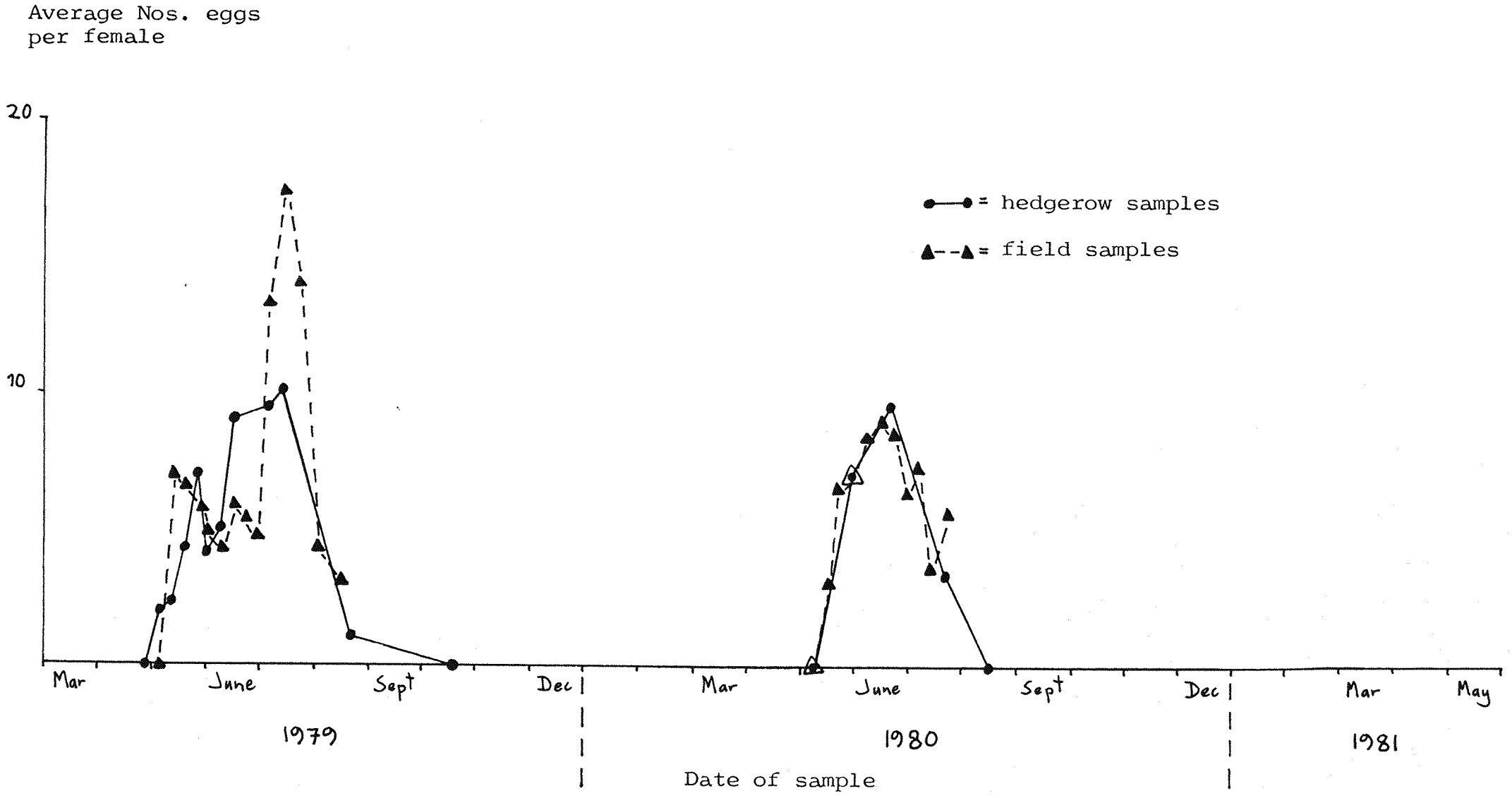
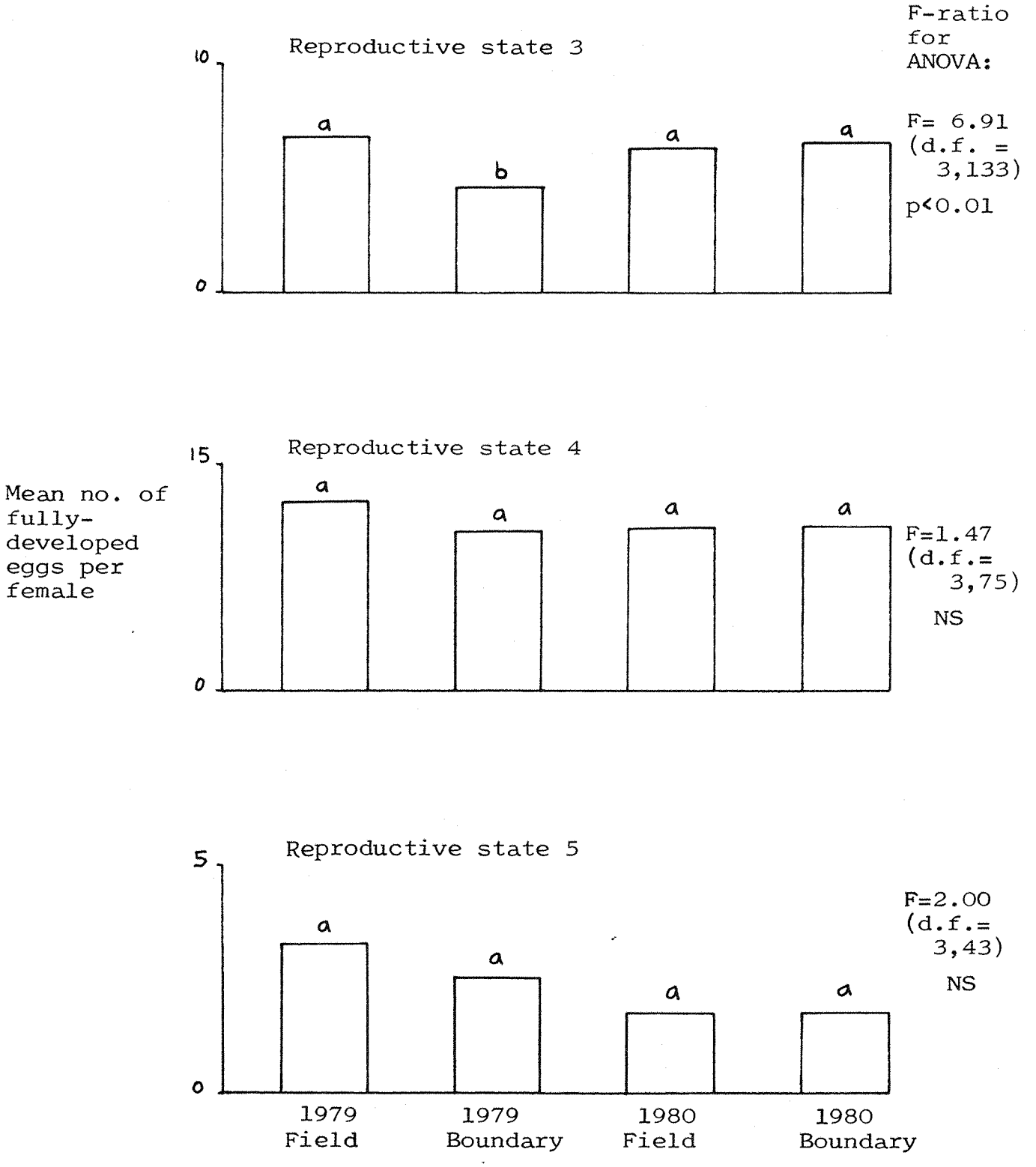
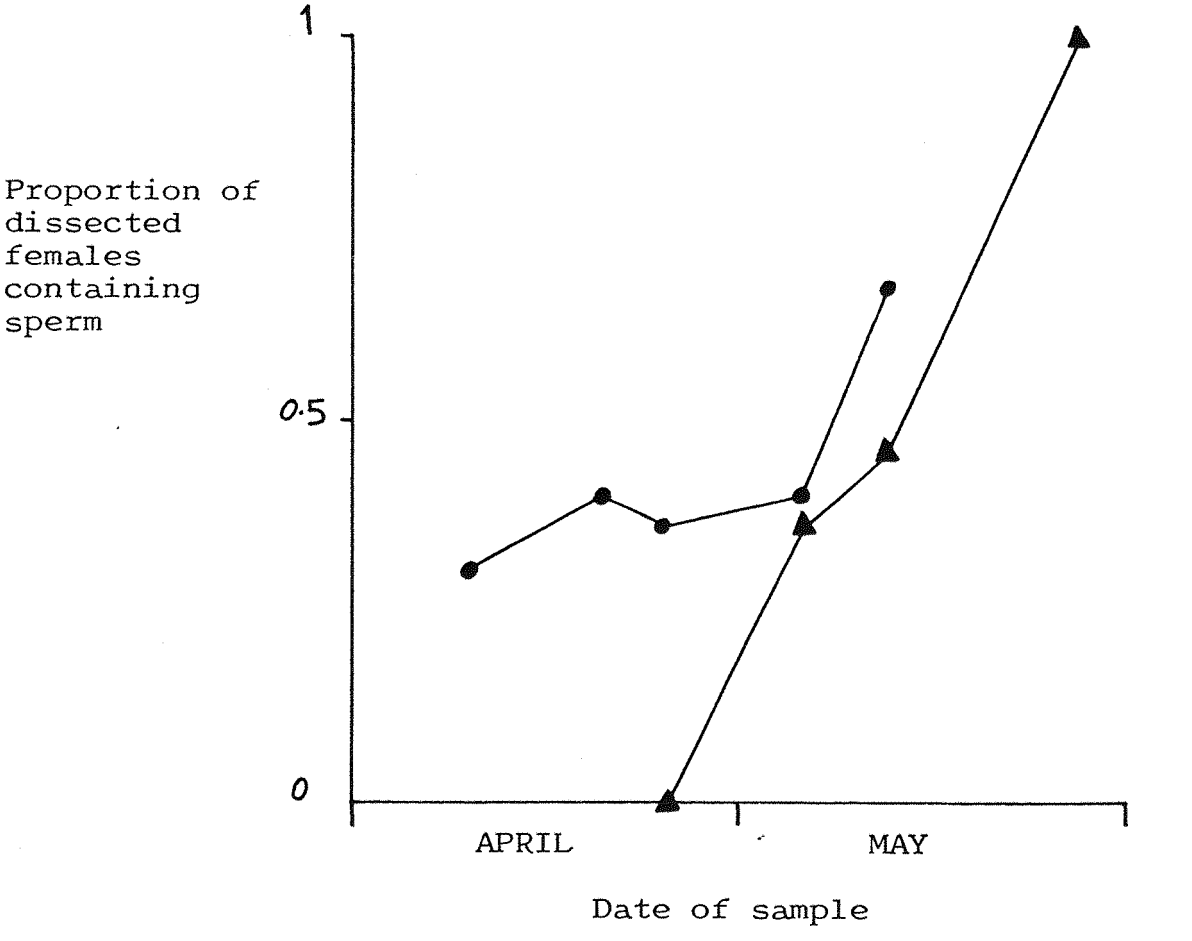


Fig. 7.11 The mean numbers of fully developed eggs per female for each reproductive state in populations sampled in 1979 & 1980 in the field and adjacent boundary.



(Columns with the same letter are not significantly different at the p=0.05 significance level)

Fig. 7.12 The proportion of females that had mated (contained sperm) during the 1981 Damerham field season.



Data on the sex ratio of boundary and field populations from 1979 to 1981 were divided into the discrete generations as revealed by the pitfall trapping and dissection showing reproductive states. There were substantial changes in the sex ratio from year to year (Fig. 7.13), but within years the trends were the same between boundary and field samples. The binomial test (Siegel 1956) was used to test whether the number of times the percentage of males was recorded at over (or under) 50 was significantly different from the expected 1:1 ratio. Hedge samples were never significantly different from the expected ratio, but in the field samples there were more males than expected in 1979 ($p < 0.02$) and in 1980 less males than expected ($p < 0.003$) while in 1981 there was no significant difference. When the same test was applied to the field and boundary sample sex ratios over all three years there was no significant difference.

(c) Changes in feeding activity

Both hedge and field samples of A. dorsale from 1979 to 1981 were dissected and the proportion of individuals with either obvious liquid remains or solid fragments of prey in the gut recorded. This was used as an index of when the population was feeding during the year (Fig. 7.14). The seasonal changes in the proportion of individuals feeding coincided with the changes in activity and reproductive state. Individuals began to feed in the boundary in March reaching a peak in May/June and ceased feeding in November/December. Almost all individuals sampled in the field contained prey on all sampling dates suggesting that by the time A. dorsale moves into the field it is fully active both reproductively and in terms of feeding rate.

7.3 Prey distribution and foraging by A. dorsale in the wheat field

(i) Introduction

The previous Chapters (5 & 6) have provided the hypothesis that A. dorsale has no special adaptation for finding cereal aphids and that even though cereal aphids give the highest calorie intake per unit handling time, the beetle does no more than forage randomly when offered the choice between these and other prey. There was feedback

Fig. 7.13 The seasonal change in the % of males in the field and hedgerow samples of A. dorsale populations.

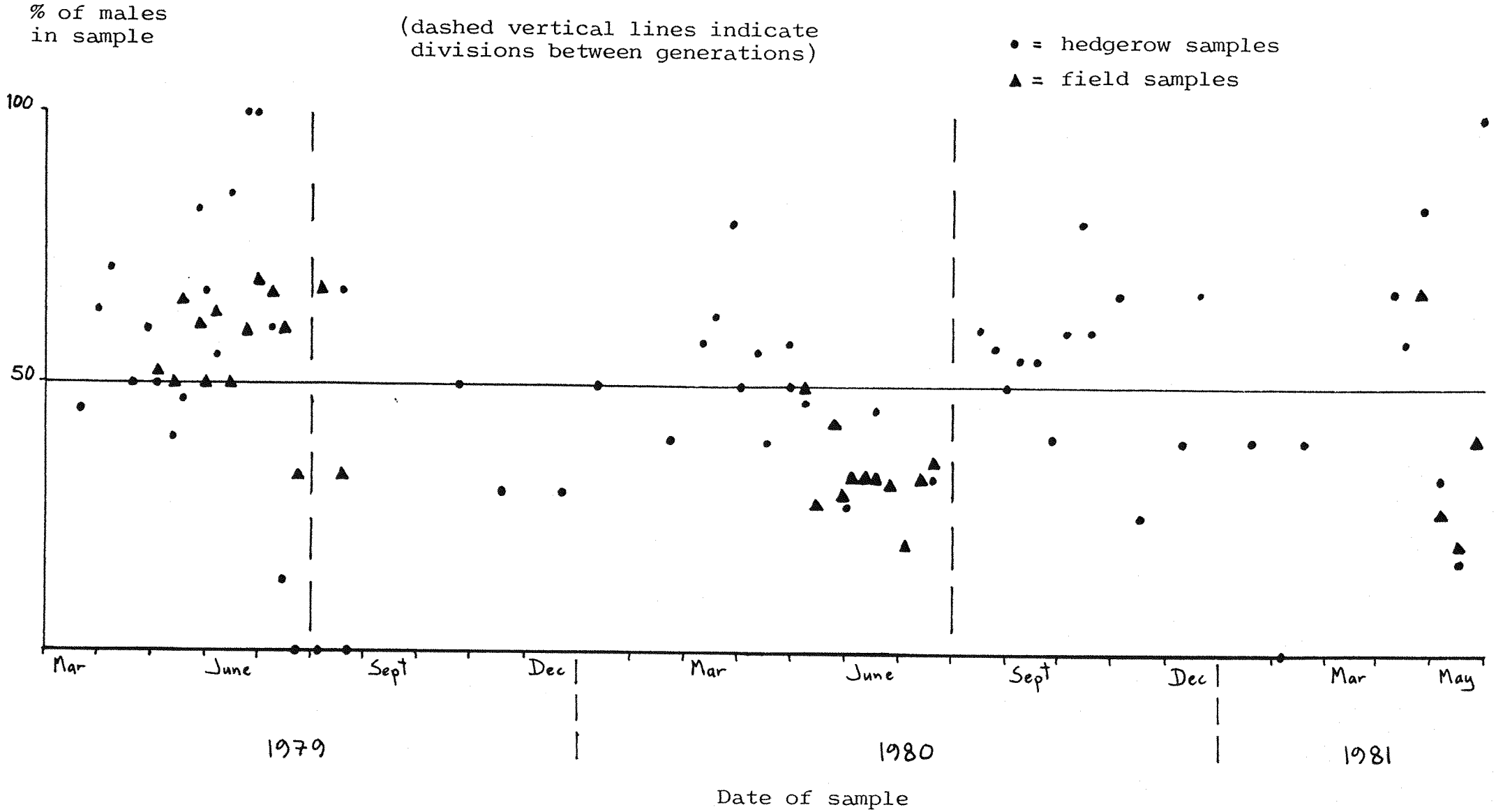
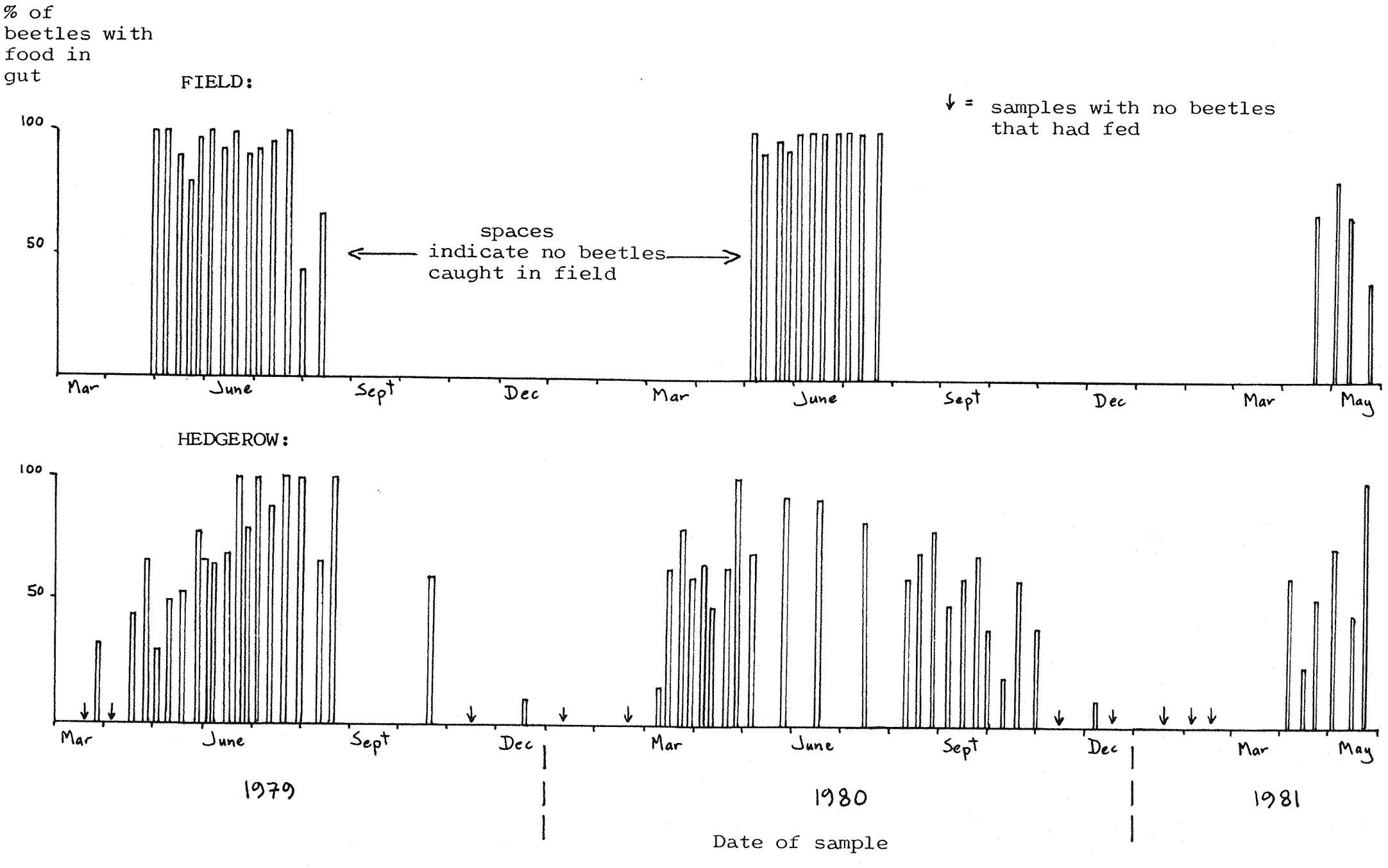


Fig. 7.14 The seasonal change in feeding activity of A. dorsale sampled from wheat fields and adjacent hedgerows.



between field and laboratory work without which the experiments of previous Chapters could not have been designed. Even so the predictions of these Chapters have now to be tested against field data and in addition the field data provide information on prey distribution which shows why A. dorsale should be a "random" rather than an "optimal" forager.

Essentially the method by which A. dorsale forages can be reduced to a correlation between prey appearing in the gut contents of the beetle and prey available in the field. A predator that concentrated on aphids (either because it was specialised to do so or because it was optimally foraging) should respond to the density of aphids not the proportion that aphids form of all prey available (see Introduction, Chapter 6, for detailed discussion). In contrast a "random" predator, i.e. a predator that takes prey in the ratio that they are presented to it, should "respond" to the proportions of prey available to it. Hence in the former, the proportion of aphids in the gut of A. dorsale should correlate best with the density of aphids in the field while in the latter the best correlation should be between proportion of aphids in the gut and the proportion aphids form of all available prey.

The findings of the previous Chapter (6.7) show that such simple correlations may be erroneous or insignificant because prey availability is changed markedly by temperature. These findings will be used to adjust field estimates of prey density or proportion available to show their effect on the basic correlation between prey in the gut of A. dorsale and prey in the field.

(ii) Identification of prey in field samples and gut contents

(a) Identification of prey sampled direct from the field.

Prey sampled by D-vac, plant clippings or soil scrapings were identified by use of the standard keys in Chinery (1973) and Lewis & Taylor (1967). Identification was never beyond the family level except for the Aphididae where individuals were taken to species using the Prior (1975) key. In some cases identification was not taken below super-family or order because prey remains in the gut were insufficient.

(b) Identification of prey remains in the gut.

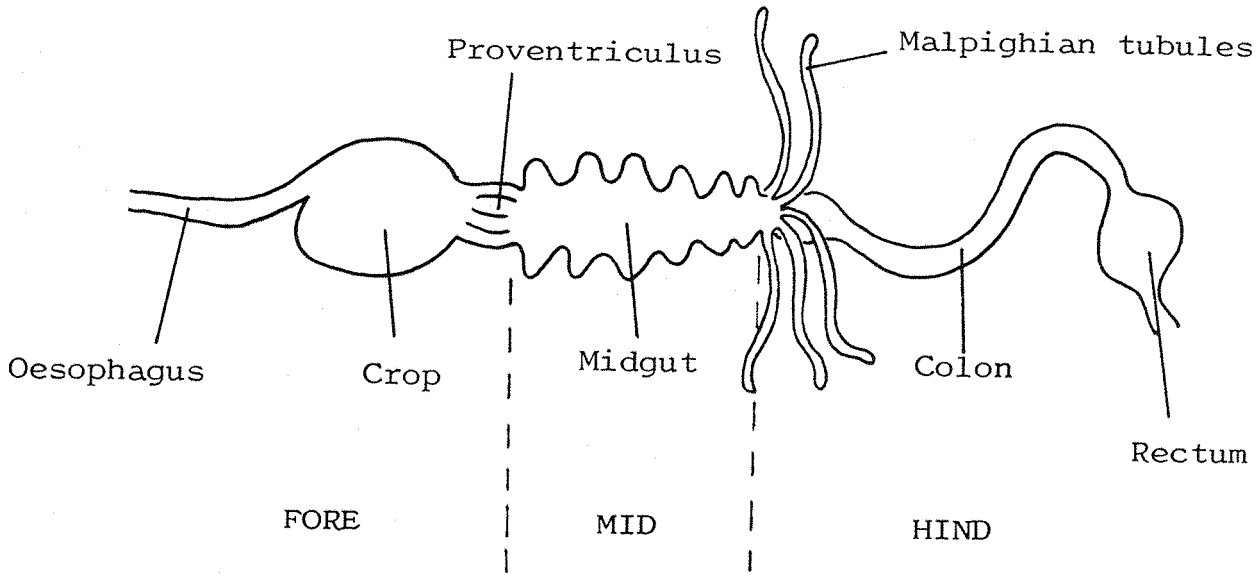
Identification of prey fragments in the gut of A. dorsale was generally not below family and usually to order only. This was for the pragmatic reason that visual identification of prey below this taxonomic level was only possible in a minority of beetles dissected because too few fragments remained for certain identification. There is also an important procedural point; gut dissection was laborious (in the order of 10-30 mins/beetle) if it was attempted to identify prey below order/family; the sacrifice in time is only worthwhile if A. dorsale is distinguishing between prey at less than an order or family level. This may be so for a preferred prey but is unlikely for prey generally consumed. This mixture of pragmatism and procedure has also been extensively applied to other gut dissection studies on the Carabidae (Davies 1953; Smit 1957; Skuhravy 1959; Dawson 1965; Penney 1966; Cornic 1973; Luff 1974; Sunderland 1975; and for a review, Thiele 1977). A summary of the diagnostic features used to identify the common prey types is presented in Figure 7.15.

The results of earlier feeding trials (Chapter 6.3) showed that A. dorsale often drops wings, legs and antennae of the prey it is consuming. As these are some of the main diagnostic structures, gut dissection is unlikely to be accurate below order level. Although some prey seemed to have a characteristic colour in the gut, e.g. Collembola often appeared purple/blue, this was not relied on after the discovery that aphids changed from green to orange during their passage through the gut (Chapter 4.6).

(c) Electrophoresis, an alternative method of gut content analysis.

Electrophoresis of predator gut contents across polyacrylamide gel slabs has been used successfully to identify prey that predators have consumed even up to 50 h before (Murray & Solomon 1978). A pilot study was made of the method. It relies on identifying prey enzymes in the predator gut and has several potential advantages over visual identification of prey remains. The time taken to process single beetles by each method is shown in Figure 7.16; these are average times recorded while processing beetles. Visual identification takes over

Fig. 7.15 The main structures of the A. dorsale gut and the diagnostic features of prey fragments found in the gut.



PREY ITEM	DIAGNOSTIC FEATURES
Acari	legs, chelicerae
Aphididae	tarsal claws, siphunculi, rostrum
Araneae	many large coarse hairs, chelicerae
Coleoptera-larvae	tarsi, sclerotized mouth parts
Coleoptera-adults	thick dark cuticle, mouth parts
Collembola	claws, head, antennae
Diptera (not Nematocera)	light brown cuticle, many fine hairs, tarsal claws, eye fragments, wings
Oligochaeta-Lumbricidae	chaetae
Fungal spores	tiny size/shape
Parasitic hymenoptera	antennae, reduced wing veination, metallic sheen to cuticle, few hairs
Nematocera	delicate cuticle/legs, threadlike antennae
Thysanoptera	strap-like wings, antennae, legs

Fig. 7.16 A comparison of the process of identification of prey in A. dorsale gut contents by gut dissection/visual identification or an electrophoresis technique.

Visual Identification		Electrophoresis	
Cut open beetle	1	Cut open beetle	1
Note reproductive state	1	Note reproductive state	1
Remove gut	2	Remove gut	2
Place on microscope slide, tease apart fragments, refer to reference collection	15	Macerate gut in butter	1
		Place on gel (24 h + 4 h staining)	1
		Record bands on gel	2
Total time/beetle (min)	19		8

	Possible gut contents				
Identification method	Empty gut	Minute traces of prey	Liquid remains only	Few solid fragments	Many solid fragments
Visual	X	X	X	X	✓
Electrophoresis	✓	✓	✓	✓	✓

X = no positive identification (of prey or empty gut)

✓ = positive identification (of prey or empty gut)

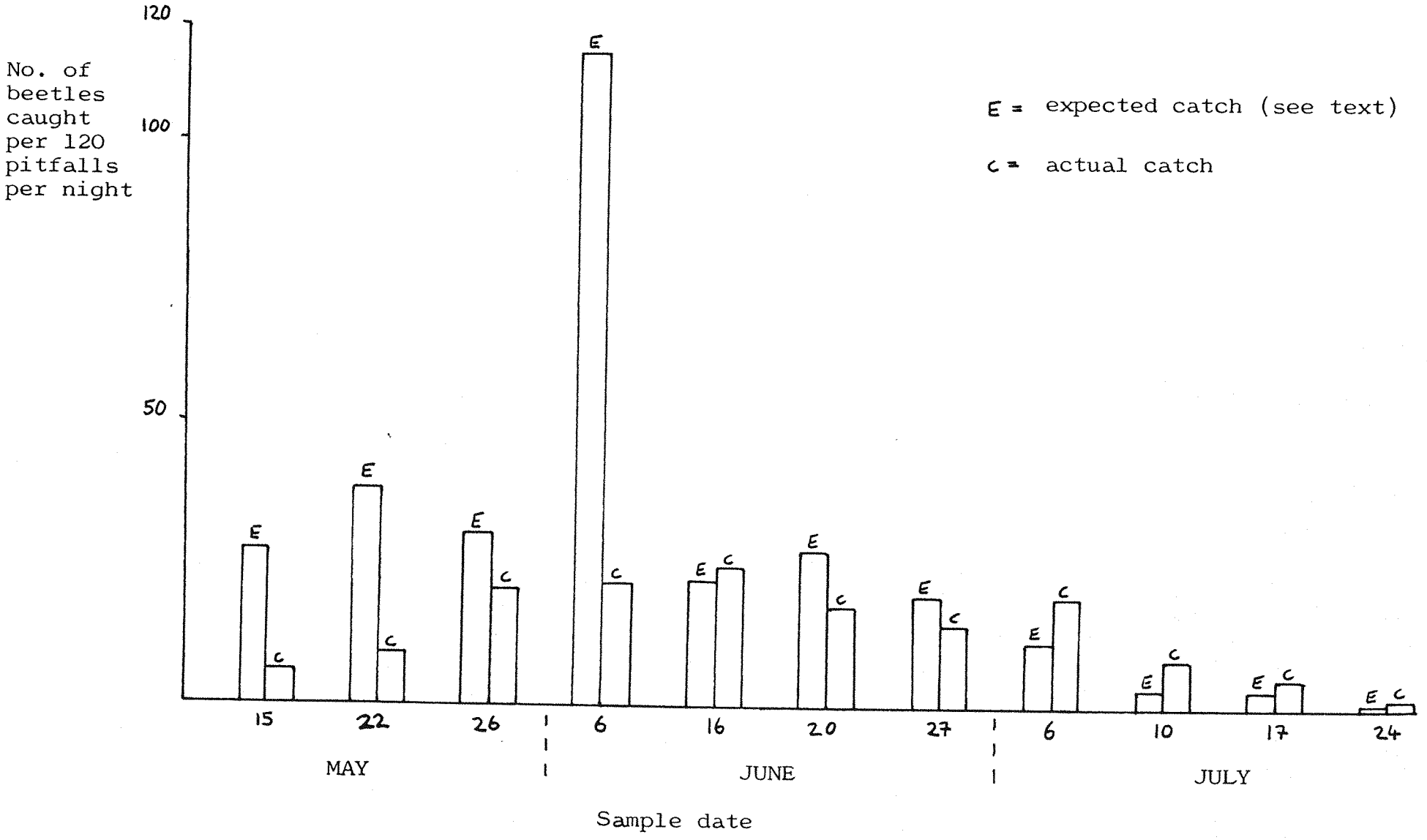
twice as long as the electrophoretic technique (note that although there is a 24 h gap for gels to be run, this does not preclude the preparation of the next set of gut macerations which can be run the moment the previous batch have finished), in an eight hour working day the difference would be between 25 as opposed to 60 beetles processed. More importantly, the amount of information obtained from visual identification is likely to be less than that obtained by electrophoresis.

The major problem with electrophoresis is that the dissected beetles must have their (and the prey's) enzymes intact; beetles must be caught live hence precluding the use of preservatives in pitfall traps and making it necessary to empty traps daily. This means that weekly pitfall sampling of individuals must be by collecting trapped individuals either daily from a small number of water-filled pitfalls or on one day per week from a large number of water-filled pitfalls to collect an adequate sample. In this study the latter approach was adopted and is made even more labour intensive because many Carabidae are attracted to the common pitfall trap preservatives (Luff 1968). Thus the water-filled traps actually catch less Carabidae than preservative-filled ones; this is shown for A. dorsale in Figure 7.17. The expected catches are calculated by dividing the previous week's preservative-pitfall catches by seven and multiplying by six to give an equivalent catch per 120 pitfall nights.

Gels were run with guts from starved laboratory A. dorsale, cereal aphids (S. avenae), Collembola (Entomobryoidea) and Nematocera (Mycetophiliade and Cecidomyidae) to show the banding patterns of the beetle and the most common prey types free from the interactions that may occur when the prey is in the beetle gut. A. dorsale guts containing either aphids, Collembola or Nematocera (prepared in the laboratory) were also run to show whether the banding patterns remained constant.

The distance travelled by esterase proteins was taken as the distance from the end of the gel (to which the samples were applied) to the leading edge of the dark band produced by staining the esterases

Fig. 7.17 The difference between the number of A. dorsale caught overnight in dry pitfalls and the predicted numbers from the previous weeks catch in pitfalls containing preservative (1980 field season).



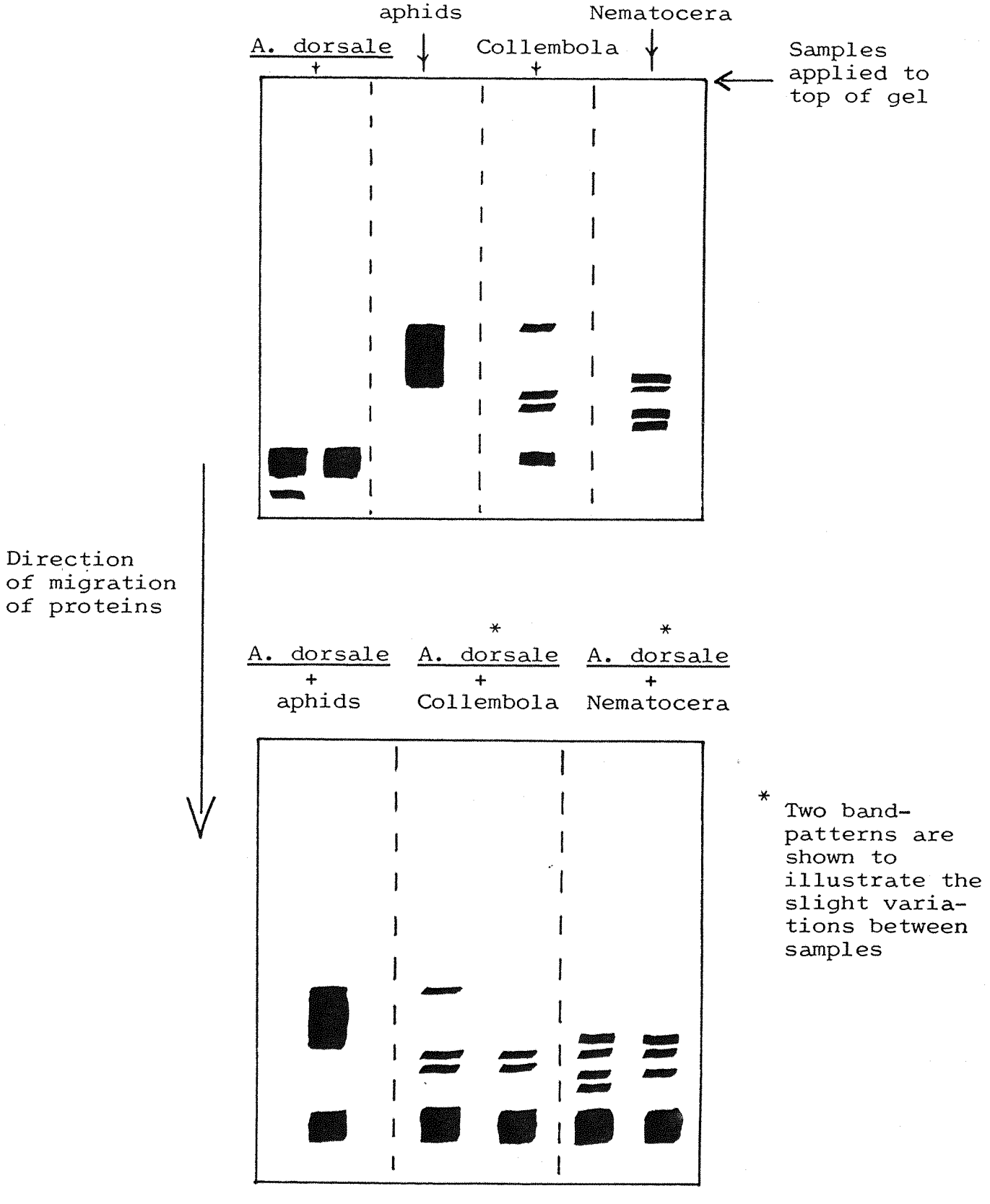
black. These distances never varied by more than 1 or 2 mm, making them robust indicators of various esterase types. The characteristic bands for A. dorsale and aphids, Collembola and Nematocera are shown on the upper gel in Figure 7.18. For A. dorsale there were two types of individual, signified by the presence or absence of the lower/smaller band. This less frequent band had no obvious correlation with sex of the beetle. Aphids (S. avenae) had a very distinctive dark band but both Collembola and Nematocera were less clearly identifiable. This was even more so when the A. dorsale with prey in the gut were analysed. Aphids remained clearly identifiable but Collembola and Nematocera lost some of their distinctive bands (see lower gel diagram, Fig. 7.18) which made them hard to separate. There was little overlap with the banding pattern of A. dorsale, an important criterion if this method is to be effective.

Samples of live A. dorsale were taken from the Watersfield site during May and June 1980; further analysis of the information obtained from them by electrophoresis for the different prey types is presented later in the Section on the correlation between prey available and prey appearing in the A. dorsale diet. It was possible to recognise aphid, Collembola and Nematocera banding patterns from field samples of A. dorsale gut contents.

Information content should be higher in samples analysed by electrophoresis (Fig. 7.16), this proved to be the case (Table 7.1). For the visual samples many prey were unidentified simply because there was insufficient cuticle in the gut. Unidentified prey in the electrophoresis samples still leave clear banding patterns; once these patterns have been identified by further prey sampling/electrophoresis then previous gels can be referred back to and unknown bands identified.

Through electrophoresis there is the potential to reduce the percentage of unidentified and/or empty (and hence potentially unidentified) guts to four (see Table 7.1). With visual dissection the percentage of empty and hence potentially unidentified guts is much higher; 25 for field samples and about 70 for hedge samples (see Fig. 7.14). The percentage is higher for hedge samples because A. dorsale

Fig. 7.18 Banding patterns on polyacrylamide gels stained for esterases after 24 h electrophoresis of starved A. dorsale, prey and A. dorsale with prey in their gut.



(Gels and banding patterns drawn to scale)

Table 7.1 Information content of electrophoretic analysis of *A. dorsale* gut contents compared with visual analysis

		% gut contents		
Technique	Sample Dates	Unidentified	Empty[1]	Identified
Electrophoresis	May/June 1980	25	4	71
Visual*	May/June 1980	13	10	77
Visual (field)	1979, 80, 81	11	14	76
Visual (hedge)	1979, 80, 81	16	52	32

* These samples were taken on the same nights as those analysed by electrophoresis.

[1] In the electrophoretic analysis prey bands were never obtained without the characteristic *A. dorsale* bands, so if only *A. dorsale* bands showed then it was recorded as an empty gut.

populations almost certainly do not feed while overwintering in hedge boundaries. Electrophoretic analysis could show conclusively whether individuals in the hedges contained no food.

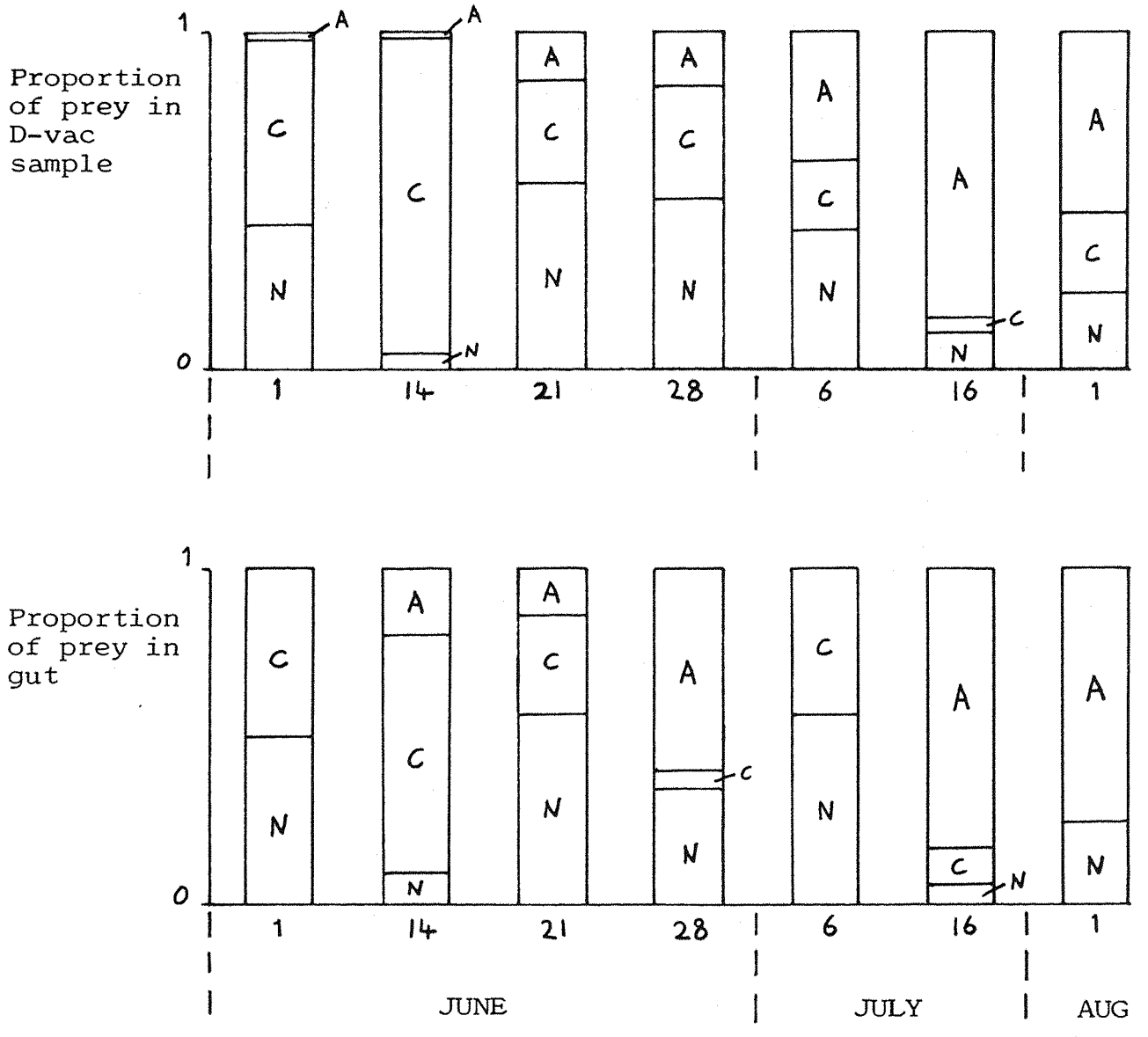
(iii) The 1979 S. Allenford farm fieldwork

Both pitfall trapping and D-vac sampling were interrupted during late May by spraying trials so that matched samples of prey and A. dorsale could only be taken in June and July. In addition D-vac samples were taken during the day which can give a false impression of the prey available to a nocturnal predator such as A. dorsale. Samples during the 1980 season (see next Section) taken during the light and dark hours of the same day showed that the proportion and density of prey can change markedly. In consequence the 1979 results are presented briefly and analysed only superficially.

Three prey types dominated (c. 75%) the gut contents of A. dorsale sampled in 1979; aphids, Collembola and Nematocera. These three prey types were also among the most numerous of the prey sampled by D-vac. The change in proportion in the gut of A. dorsale and in the proportion of these prey available is shown in Figure 7.19. Following the argument put forward in the Introduction that correlation between proportions of prey in gut and prey available signifies a random predator while correlation between density of prey and proportion in the gut means a specific predator, correlations were made for the three prey types (Fig. 7.19). The prey density never correlated significantly with proportion (arcsin transformed) of prey in the gut; A. dorsale did not seem to respond directly to the numbers of prey including aphids (a log conversion was also tried as this relationship need not be linear). When proportions were correlated these were not significant for aphids and Collembola but highly significant for Nematocera. This result is difficult to interpret because if A. dorsale was behaving as a random predator, then the proportions correlation should be significant for all three prey types.

Although the correlative evidence was inconclusive this field work did show that A. dorsale was finding aphids at very low densities

Fig. 7.19 The change in the major prey items in D-vac samples and gut dissections through the 1979 field season.



(A= Aphids, C= Collembola, N= Nematocera)

Variables correlated		d.f.	r, significance level		
D-vac vs. gut contents			Aphids	Collembola	Nematocera
Density	Proportion	1,5	0.55,NS	0.55,NS	0.11,NS
Logs (Density	Proportion)	1,5	0.42,NS	0.33,NS	0.14,NS
Proportion	Proportion	1,5	0.61,NS	0.68,NS	0.89, $p < 0.01$

in the field; this was nottrue for Collembola or Nematocera. For the mid-June sample, aphids were estimated to be at a density of about 3 per m^2 (about 1 per 200 stems) yet 20% of A. dorsale contained aphid remains on dissection. By the end of June aphid density had risen to 50 per m^2 (about 1 per 12 stems) and 60% of the beetles contained aphids on dissection. A. dorsale is nocturnally active and the fact that the D-vac samples were taken during the day may however have influenced these results.

In summary: there were no conclusive correlations between prey density, or proportional prey abundance, and the appearance of prey in the diet of A. dorsale. There was evidence that aphids could form a substantial part of the A. dorsale diet and that the beetle was finding and eating aphids even though they were at very low densities in the field.

(iv) The 1980 S. Allenford farm fieldwork

The sampling program in the summer of 1980 was much more intense than in 1979 and investigated several aspects of sampling methodology as well as prey availability and foraging by A. dorsale.

Microclimate and climate data

A. dorsale is nocturnally active, so sampling during the 1980 field season was done at night, measurements were also taken of the temperature and humidity profiles in the crop at this time. Microclimate measurements were taken between 01.00 and 02.00 h during the period of prey sampling. Humidity was always about 100% throughout the crop even when daily rainfall was low and this was obvious from an examination of the wheat which became covered with droplets of moisture during the night. As night humidity/water droplets in a crop result from a combination of dewfall and distillation from the ground (Jones 1976) it is not surprising that these quantities bear no relationship to rainfall. Temperatures were 1-2^{o}C higher at ground level in the crop than the air temperature at this time of night, but references show that unlike humidity this temperature gradient reverses as the ground cools during the night, (Rosenberg 1974; Jones 1976).

The net result is that average air temperatures approximate very closely to average ground temperatures for the night. It was sufficient then to take single air temperature and humidity readings as these were effectively the same as those in the crop.

In any fieldwork the local climate can strongly influence results; it was not possible to have a full range of meteorological instruments at S. Allenford farm so data from Hurn meteorological station (N.G.R. SU 115980) was used instead. This station is 20 km south of the farm site. To show that climate at Hurn was related to that at S. Allenford farm, temperatures (the most potentially variable climate factor, Jones (1976)) at the two places between 01.00 and 02.00 were correlated. Temperatures were predictably higher and varied less at Hurn (which is 8 km from the sea) but the correlation between the two was significant ($r = 0.693$; $d.f. = 6$) showing that Hurn provides a good relative measure of climate at the farm site.

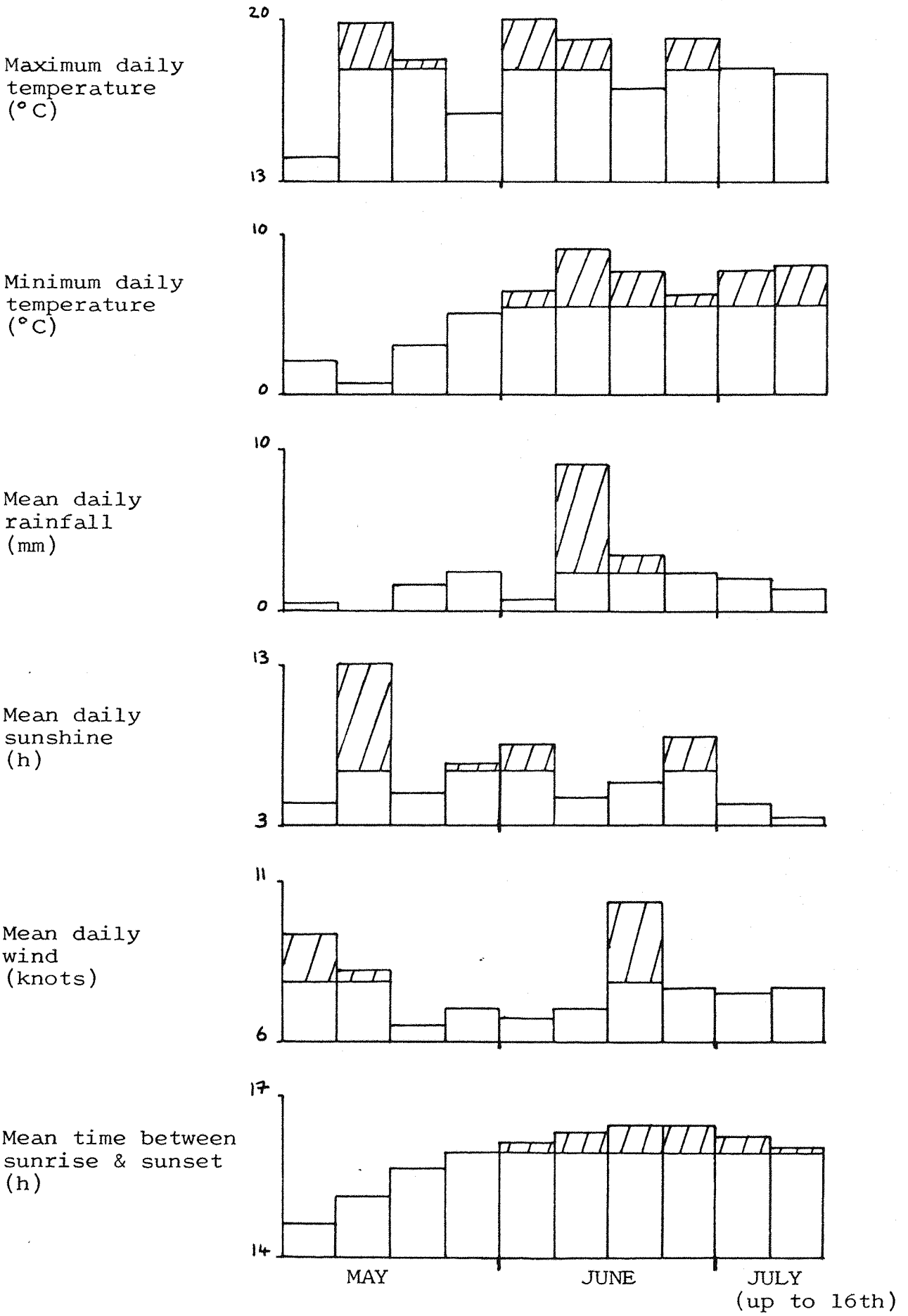
The change in principal climate factors during the 1980 field season is shown in Figure 7.20; all these data except for mean time between sunrise and sunset (extracted from Collingbourne 1976) were taken from Hurn meteorological readings. Obviously some of these factors varied in an unpredictable manner (maximum daily temperature, rainfall, sunshine, wind) while others changed more regularly (minimum daily temperature, hours between sunrise and sunset). Sudden changes in weather may have most effect on prey availability while more gradual changes (e.g. temperature) may have most effect on the seasonal voracity of A. dorsale. Changes in the climate will be referred to in later Sections to help explain sudden changes in prey and assess overall seasonal control potential of A. dorsale.

(v) Sampling of available prey

(a) Day vs. night sampling.

A. dorsale is nocturnally active and this was confirmed at the Watersfield site in 1980 by running pitfalls separately during the hours of light or dark for the early June sample date. Pitfalls open during the day caught one A. dorsale; pitfalls open overnight caught 21 A. dorsale, the number of pitfalls used being 120 in both cases.

Fig. 7.20 The change in 6 weather statistics during the 1980 period of field activity of A. dorsale.



▨ = data above mean of all data for May - July 16th

Sampling of prey should also be nocturnal as prey availabilities and abundances are likely to change with the diel activity cycles of the wheat-field fauna. To assess how great the changes in fauna were, prey sampling was undertaken at midday and midnight for the early June sample date. The proportions of the six most abundant prey available changed considerably for all three sample methods (Fig. 7.21) e.g. for D-vac samples, aphids changed from 34% of the catch to 73% from day to night and so on (see next Section for a discussion of the methods). Note that in Figure 7.21 the bar charts showing prey proportions are split up into the separate prey types for clarity only. Although the three sampling methods collected different prey types with different efficiencies, all caught more prey during the day than at night; this was particularly so with the D-vac. A single exception to this was the Thysanoptera; when sampled by plant clippings a higher number were caught at night than during the day.

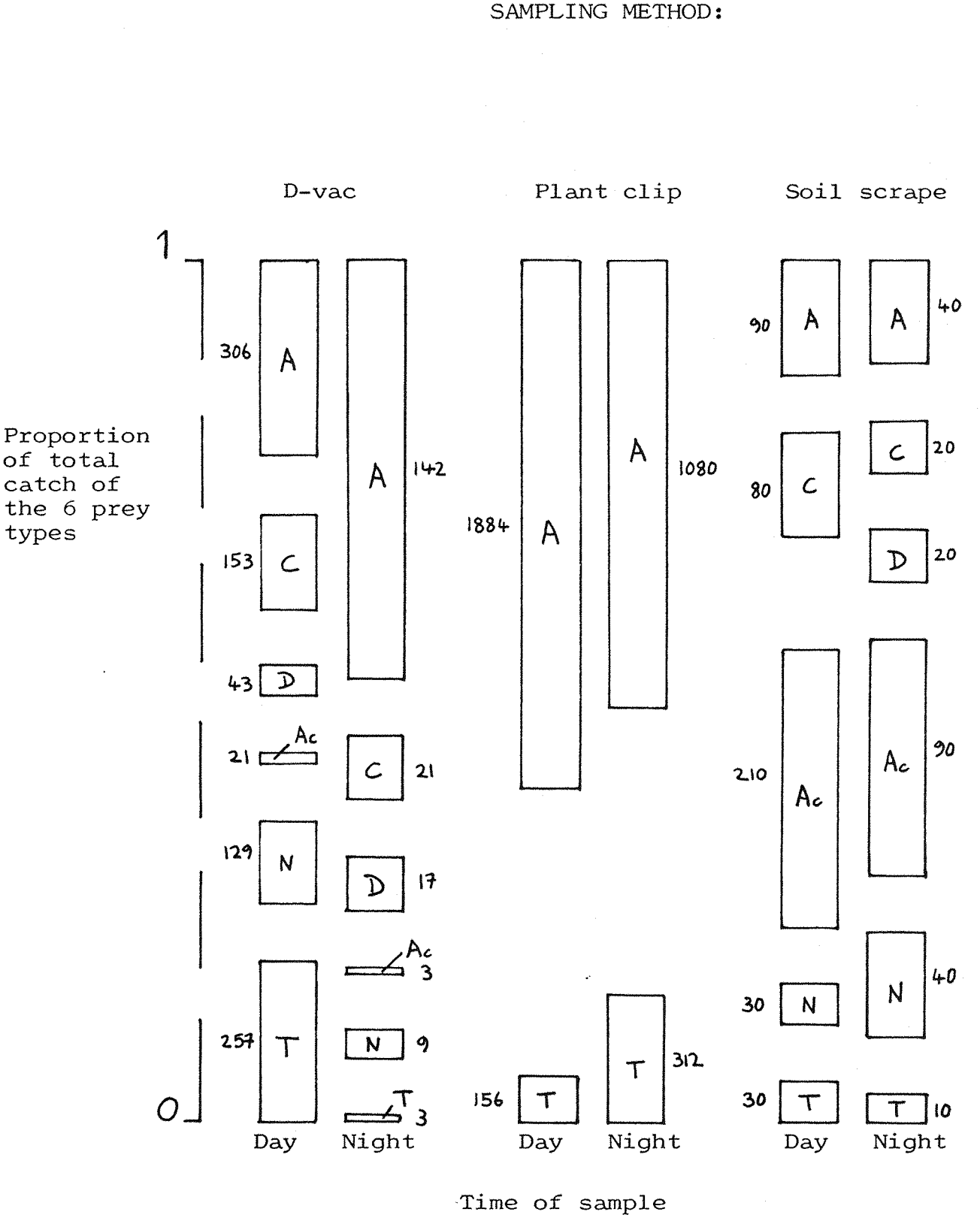
Differences in numbers of prey caught between night and day are likely to be a combination of changes in the efficiency of the sampling methods and changes in the activity of the prey. The D-vac is known to be less efficient when used to sample damp vegetation (Southwood 1978; Hand pers. comm.). Changes in activity will also influence catches and the Thysanoptera are a good example; plant clippings showed that there were more Thysanoptera on plants at night than in the day but the D-vac caught more Thysanoptera during the day than at night. The probable explanation is that during the day Thysanoptera may be flying from plant to plant and hence will be sampled by the D-vac but not by plant clips. At night they are on the plants and are not sampled efficiently by the D-vac in the damp conditions but are caught by the plant clippings.

As a result of these differences between the day and night samples all prey sampling was at night.

(b) The difference between prey sampling methods

Three methods were used to sample prey at night; the D-vac to sample all prey, plant clipping to sample prey on the wheat and soil scrapes to sample prey on the ground. Six prey types were most abundant

Fig. 7.21 The proportional differences in prey caught between day and night sampling in early June.



A=aphids, C=Collembola, D=Diptera, Ac=Acari, N=Nematocera, T=Thysanoptera.

(Numbers are no. prey per m^2)

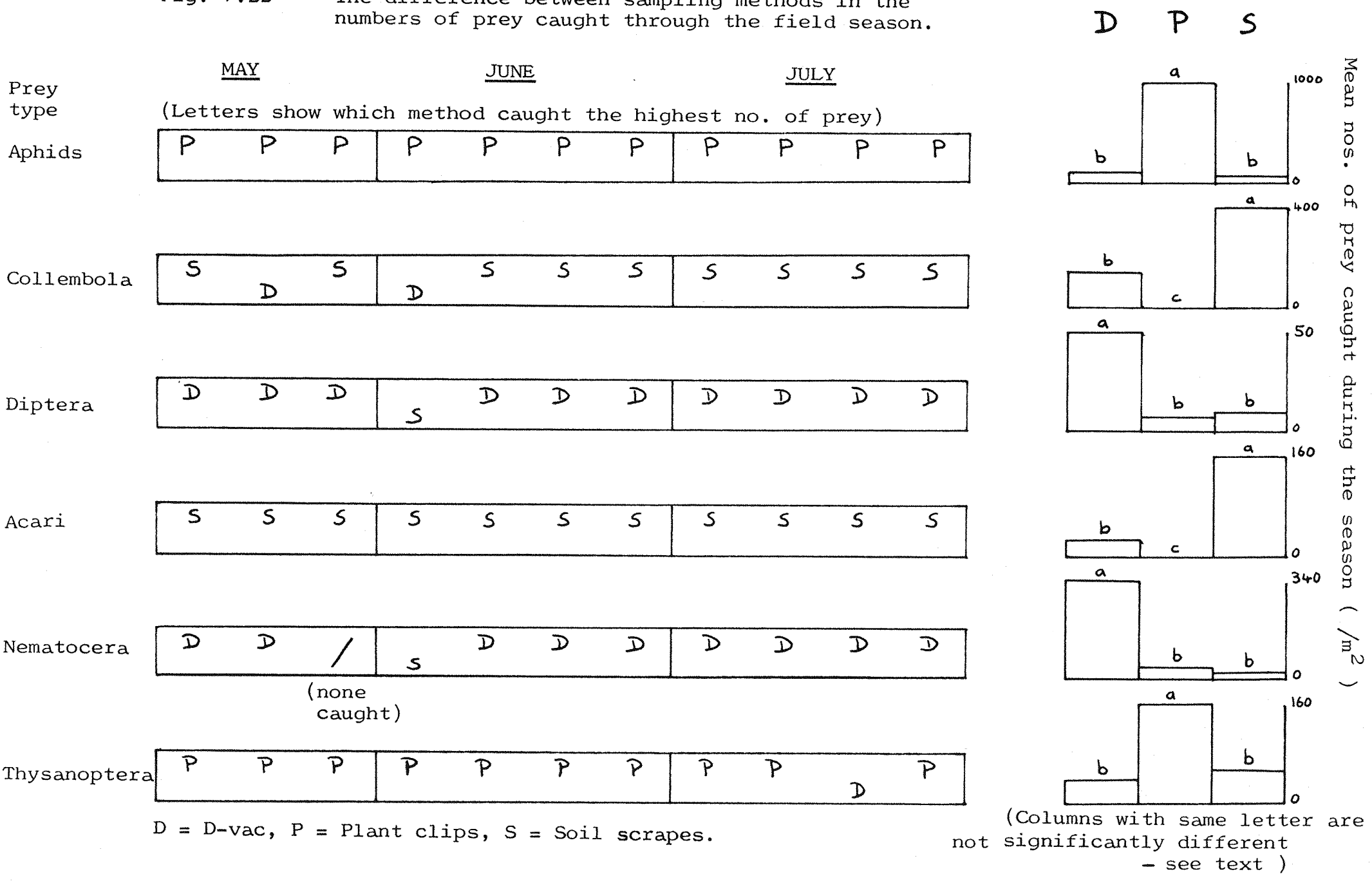
in the samples and these were used to show the difference between the methods in the efficiency with which they sampled prey. The six prey types can be split into three broad categories; air-born prey (Diptera and Nematocera), plant-living prey (aphids and Thysanoptera) and soil-living prey (Acari and Collembola). As expected these groups were sampled most efficiently by the technique most suited to these categories; D-vac, plant clipping and soil scraping respectively (Fig. 7.22). Each method consistently sampled more of its two prey types over the season, and this was shown to be significant by statistical analysis (Fig. 7.22). For each prey type the numbers caught over the field season by each sample were compared using the Friedman 2-way ANOVA (Siegel 1956). If this analysis showed a significant difference then the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to show which method was significantly different from which (see Chapter 5.6 for a full discussion of this statistical technique). The letters on the bar charts in Figure 7.22 show which methods differed significantly from which.

It is not possible to sample all prey adequately using any one method; more importantly each method tends to sample best a particular type of prey (flying, plant-living etc.). Laboratory results (Chapter 5.5) suggest that A. dorsale spends most of its time on the ground so soil scraping may sample the prey most available to the beetle. In the final Section the proportions of prey in the gut of A. dorsale will be correlated with the prey (proportion and density) shown to be available by each sampling method. The method giving the best correlation with gut contents for all prey types will be taken as the one sampling prey most available to A. dorsale.

Sampling methods are prone to errors at two stages; errors occurring in the use of the method to collect the prey and errors occurring in sorting the prey back in the laboratory.

D-vac: Field errors; the D-vac is known to have a reduced efficiency for damp vegetation (Southwood 1978); comparison of aphid numbers caught by plant clipping showed that the D-vac was sampling a maximum of 9% of aphids available and 16% for Thysanoptera. As the

Fig. 7.22 The difference between sampling methods in the numbers of prey caught through the field season.



wheat crop was always damp at night (see climate section) the relative change in numbers of each prey type should be unaffected by this error.

Laboratory errors: sorting of prey was done under a binocular microscope and errors in identification were thought to be minimal as prey were classified only to the order or family level.

Plant clips: Field errors; the main source of error was likely to be prey moving or falling off the plants while they were being cut and placed in a polythene bag. Many Diptera may have escaped at this stage but aphids were thought to have been sampled efficiently because so few fell off in the polythene bags used to transport the wheat back to the laboratory and because the method was so much more efficient than the D-vac. Trials with the method during the day showed that it was possible to clip the wheat and place it in a bag without dislodging aphids. It is not known whether few Diptera were caught because they are flying at night, remain on the ground or are lost due to disturbance during sampling.

Laboratory errors: again, sorting in the laboratory was thought to be almost free from error; samples were placed in the deep freeze to kill prey and identification was only to order or family level.

Soil scrapes: Field errors; soil scrapes were taken to a depth of a few centimetres because A. dorsale is not known to burrow and because 80% of arthropod fauna are within this depth of soil (Edwards & Fletcher 1971). The method is similar to plant clipping in that Diptera may have escaped from the sample but less active prey should have been caught effectively.

Laboratory errors: Salt flotation (Edwards & Fletcher 1971; Southwood 1978) was used to extract arthopods from the soil and an efficiency of 80-90% was achieved for aphids (assessed by adding known numbers of aphids to sterilised soil of the same volume and consistency as the soil scrapes and measuring the recovery rate). It was assumed that the percentage extraction would be similar for other arthropods (see also Edwards & Fletcher 1971). Identification was again by binocular microscope and errors should have been minimal for this.

Errors in sampling and the differences between sampling methods will be discussed further in relation to prey availability in the final Section. But as the D-vac samples prey from both ground and plant its overall efficiency (as a percentage of the method sampling the most prey) can be assessed by comparing it with the combined plant clip and soil scrape catches of the six most common prey types:

Prey	D-vac	Plant and soil
Aphids	9	100
Collembola	36	100
Diptera (other than Nematocera)	100	35
Mites	17	100
Nematocera	100	20
Thysanoptera	16	100

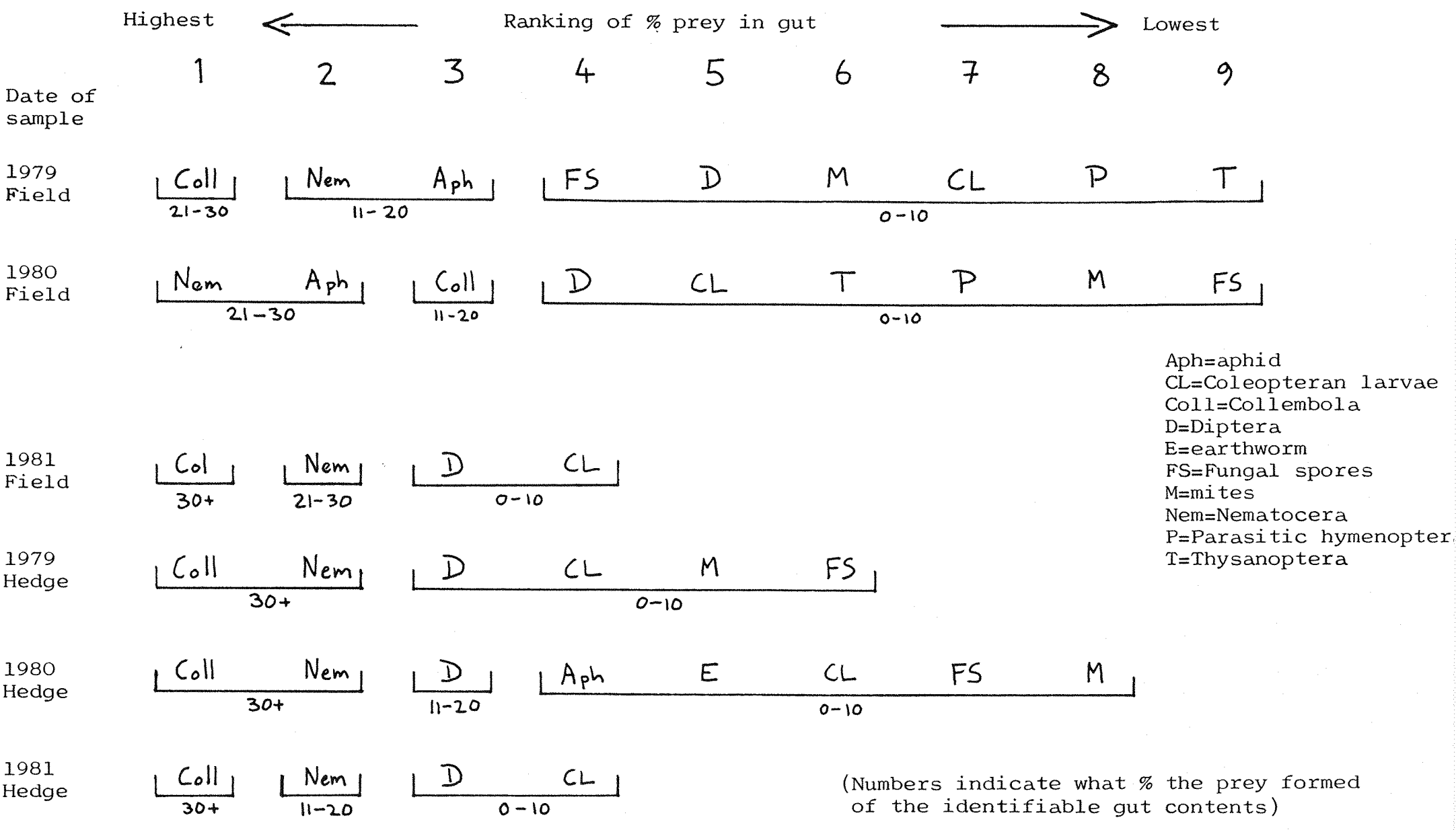
Clearly the plant and soil scrapes sample the prey more effectively than the D-vac on average but they miss the flies; this does not matter if the flies are active at night and hence unavailable to A. dorsale but is important if this is a function of sampling technique only.

(vi) Assessment of A. dorsale diet

(a) Predominant prey types in the diet of A. dorsale

Gut dissection showed that A. dorsale was truly polyphagous, taking a wide range of prey types. Some prey types were more common in the diet than others. There are obvious advantages in terms of sample size when correlating prey availability with prey presence in using these common prey types. Dissection of field- and boundary-sample A. dorsale showed that three prey types were consistently

Fig. 7.23 The difference between years in the ranking of the percentages of prey types in the gut of A. dorsale.



dominant in the diet; aphids, Collembola and Nematocera (Fig. 7.23). The 1979 and 1980 field data are separated from the other data in Figure 7.23 because no prey samples were taken in the boundaries or the 1981 field season. This means that the presence or absence of prey in the diet for these four samples could be due to selection by the beetle or to the presence or absence of prey in these habitats. Cereal aphids for instance are not likely to be present in the field boundaries in significant numbers nor were they likely to be present in the field in 1981 because samples were only taken to the beginning of May when cereal aphids are at very low abundances. Where prey samples were taken (1979 & 1980 Field) the three most predominant prey items were also present in the field in large numbers.

Despite the lack of supportive prey samples, aphids, Collembola and Nematocera consistently dominated the gut contents of A. dorsale from year to year. Only these three prey types are used in the following analysis of the relationship between the proportions of prey appearing in the beetles' gut and prey availability.

(b) Difference in diet between sexes

An analysis of all three years' gut dissection data was made with comparisons between males and females being made separately for each generation of A. dorsale sampled. The samples for the three years were divided into the periods shown in Figure 7.13. The hedge samples for instance were divided into the periods March-July 1979, August 1979 - July 1980 and August 1980 - May 1981 for analysis.

The analysis was in two parts for each sample period; an initial scan was made of the data to see if the sexes differed in the dates on which they started to feed (i.e. when the number of beetles with empty guts decreased) or consume aphids, Collembola or Nematocera; this was followed by a Wilcoxon matched-pairs signed-ranks test (Siegel 1956) to show differences between the sexes for each of these four diet variables. Each pair in the Wilcoxon test consisted of the frequency of males and females containing either aphids, Collembola, Nematocera or nothing for one sample date. The frequencies were corrected to allow for the difference in numbers of males and females dissected on each sample date. The results of this analysis are summarised in Table 7.2.

Table 7.2 The difference between the sexes in diet for boundary and field samples of A. dorsale from 1979 to 1981

	Gut Item			
DATE OF SAMPLE	Empty	Aphid	Collembola	Nematocera
Boundary samples				
March-July 1979	NS	/	NS	NS
August 1979-July 1980	NS	/	NS	NS
August 1980-May 1981	$p < 0.05$ (♂ > ♀)	/	NS	NS
Field samples				
May-July 1979	$p < 0.05$ (♂ > ♀)	NS	NS	NS
May-July 1980	/	NS	NS	NS
May 1981	/	/	/	/

/ = too few sample dates for analysis to be possible.

(♂ > ♀) = more males had empty guts than females.

The initial inspection showed no differences in the timing of the occurrence of aphids, Collembola, Nematocera or zero in the gut between sexes. The Wilcoxon tests showed that there were no differences between sexes for aphids, Collembola or Nematocera but there were significant differences for the frequency of empty guts. In the boundary samples for August 1980 - May 1981 females showed a smaller frequency of empty guts than males and this was also true for the field samples of May - July 1979. It is not possible to interpret this result biologically as the difference was not consistent from year to year.

In a few cases it was also possible to compare differences in diet between reproductive states (see Section 7.2) for either sex. The same technique as above was used except that the pairs were made up from frequencies of prey items in the gut for two reproductive states of either male or female A. dorsale. Small sample sizes meant only three comparisons could be made:

Males, Field 1979	No significant difference between states 2 & 3 (mature & spent) for the frequency of Nematocera in the diet.
Females, Field 1980	No significant difference between states 3 & 4 (mid & late egg) for the frequency of aphids or Nematocera in the diet.

As there were no consistent differences between males and females or between reproductive states within sexes all gut content data were combined in later analysis. This confirmed the laboratory feeding trial results that showed there was little difference between sexes in consumption (Chapter 4.8) or prey choice (Chapter 6.5).

(c) Sampling of A. dorsale for gut analysis

Sampling of prey was overnight whereas most samples of A. dorsale were pitfalls run over a week. This discrepancy may result in the average gut contents of the beetle being different from the prey available. To test this three types of sample were taken during the 1980 field season:

Pitfall samples taken over the 7 days leading up to the prey sample; visual analysis of gut contents.

Pitfall samples taken over the same night as the prey sample; visual analysis of gut contents.

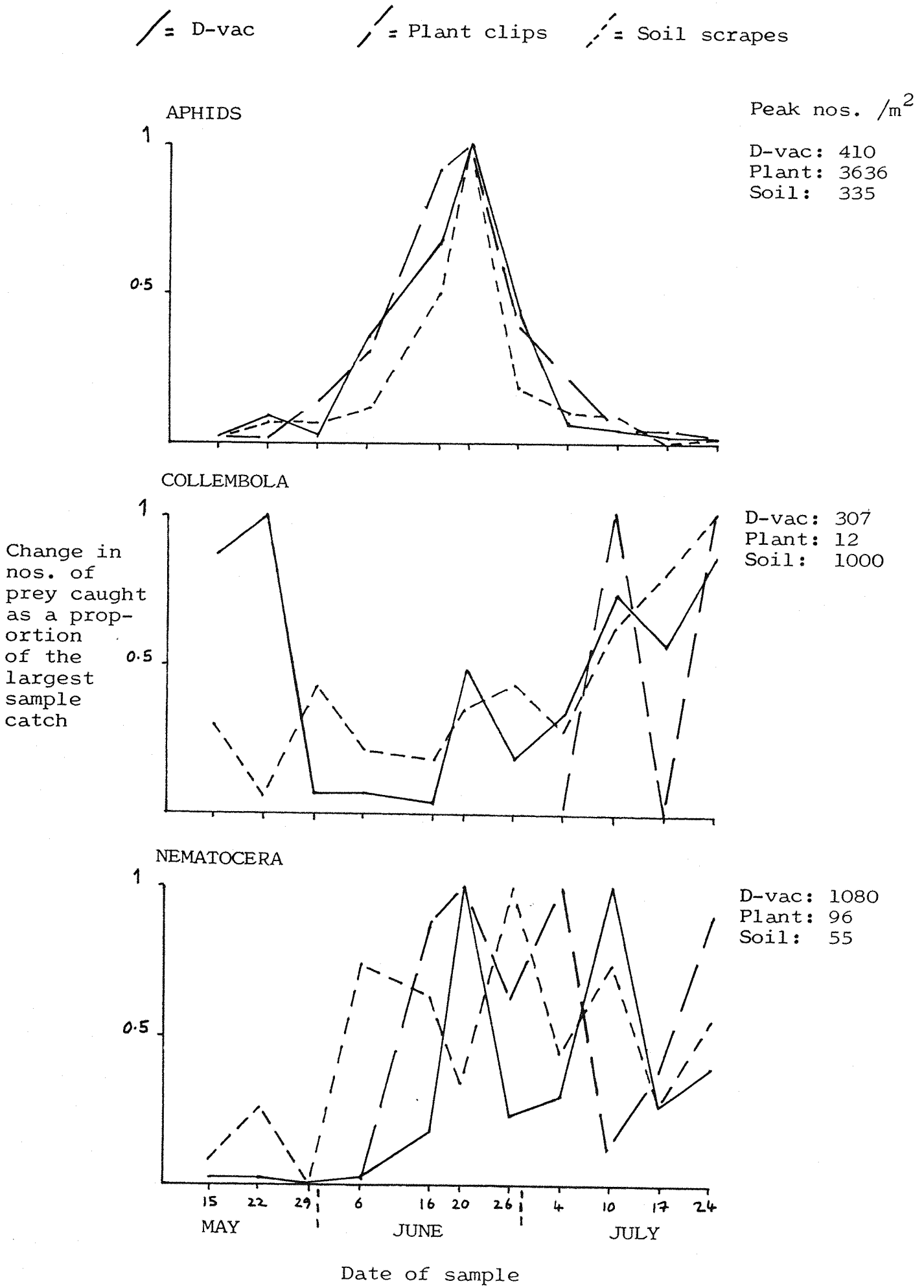
Pitfall samples taken over the same night as the prey sample; electrophoretic analysis of gut contents.

Prey abundances can change markedly in 7 days (Fig. 7.24) so that the gut contents of beetles sampled over 7 days may bear little resemblance to the prey abundances shown by a sample at the end of this period. Comparisons between the 7 day and the 1 day pitfall samples should show whether this is true. Alternatively prey availability may fluctuate rapidly from day to day (e.g. Diptera have flight temperature thresholds) in response to climatic conditions so that an average picture of prey taken by A. dorsale over several days may correlate more closely with the prey sample than the gut contents of the beetle when sampled on just one night. Again comparisons between the 1- and 7-day pitfall samples will show whether this is true.

The three main prey types may pass through the gut at different rates or may leave different amounts of identifiable cuticle which may result in the gut contents not correlating with prey abundances. Electrophoresis will detect prey enzymes, so overcoming the problem of there being insufficient or differing amounts of visually identifiable cuticle for different prey. A comparison between the 1-day pitfall catches that were analysed by visual dissection and those analysed by electrophoresis will show if this is an important factor.

Ideally A. dorsale could be observed foraging naturally in the wheat field and a record made of the prey types that it consumed overnight. The number of each prey type eaten could then be correlated directly with assessments of prey availability thus avoiding problems inherent in gut analysis techniques. In addition this technique would reveal the most important factors controlling how successful A. dorsale is in catching each prey type in the field. This could be compared with the results of the laboratory study on the effect of temperature on successful capture of prey (Chapter 6.7).

Fig. 7.24 The proportional change in prey numbers through the season as shown by the three sampling methods.



An attempt was made to observe A. dorsale at night at the Watersfield site using a hand held torch equipped with a red filter. Two methods of search were used; walking along tractor wheelings inspecting the ground on either side for individuals or placing a 1 m^2 quadrat on the ground and observing it for 15 min. Neither method resulted in the observation of any A. dorsale although both were carried out on nights when pitfall catches were good (Fig. 7.17). Furthermore Pterostichus melanarius, a large (15-20 mm length) black nocturnal (Thiele 1977; Luff 1978) carabid, which was caught in far larger numbers (up to 20 x) in pitfalls than A. dorsale, was only rarely seen. This would suggest that if even large, very active carabids were difficult to see, then observing the smaller (6-8 mm body length) A. dorsale is never likely to be possible.

All three types of pitfall/gut data are used in the following correlative comparison between prey found in the gut contents of A. dorsale and prey sampled from the field.

(vii) The correlation between prey in the diet of A. dorsale and prey available

(a) Correlations between prey sampling methods

If the three sampling methods (D-vac, plant clipping and soil scraping) showed the same relative changes in prey numbers from week to week, there would be little point in correlating them all with prey in the gut contents of A. dorsale. However as they sample different parts of the wheat field habitat in different ways they are unlikely to correlate exactly. The change in the numbers of prey sampled by each method is shown in Figure 7.24 (N.B. the numbers are given as a proportion of the highest catch for that method so that all three methods can be compared on the same scale), only the three prey types most commonly eaten by A. dorsale are shown. Changes in the numbers of aphids were very similar whichever sampling method was used; this was not so for Collembola or Nematocera. Correlation (Snedecor & Cochran 1967) between pairs of sampling methods showed that all three methods correlated significantly ($p < 0.001$, d.f. = 1,9) for sampling aphids but there were no significant correlations for Collembola or Nematocera. (For each prey type there were three possible correlations

between sampling methods; D-vac vs. plant clippings, D-vac vs. soil scrapings and plant clippings vs. soil scrapings. The probability level for a significant correlation should thus be reduced to 0.05/3 = 0.017).

In addition if these three prey types are represented as the proportion they represent of their combined total at each sample date, it is clear that the proportions of prey change differently between methods (Fig. 7.25). As the D-vac samples both ground and plant, the comparison is between D-vac and the combined plant clipping and soil scraping samples to show how the prey changes in a complete section of wheat from ground to plant.

It is not possible to show whether the sample methods did not correlate because of differences in the efficiency with which they sampled prey or whether the differences reflect genuine differences in prey availability. For instance, the methods may have correlated when used to sample aphids either because aphids are evenly distributed in the crop or because aphids, being relatively sedentary, did not escape when sampled by plant clipping or soil scraping. Sampling error causes must be kept in mind in the following correlation of gut contents with prey samples.

(b) Correlations between the three methods of gut content sampling and analysis

Three methods were used to assess the gut contents of A. dorsale (Fig. 7.26) (again only the three most common prey types are referred to) and comparisons between them were to show whether overnight sampling of A. dorsale improved the fit between gut contents and prey samples compared to week-long sampling and whether electrophoresis improved the fit compared to visual gut dissection. As with the prey sampling methods there would be little point in comparing the three methods if they correlated well with each other.

The Spearman Rank Correlation Coefficient (Siegel 1956) was used for the correlations because of the small sample sizes (Fig. 7.26). The proportions of each prey type shown by the different methods were correlated in pairs (7-day dissection vs. 1-day dissection, 7-day

Fig. 7.25 The difference in the proportions of the three main prey types of A. dorsale between D-vac and Plant/Soil samples.

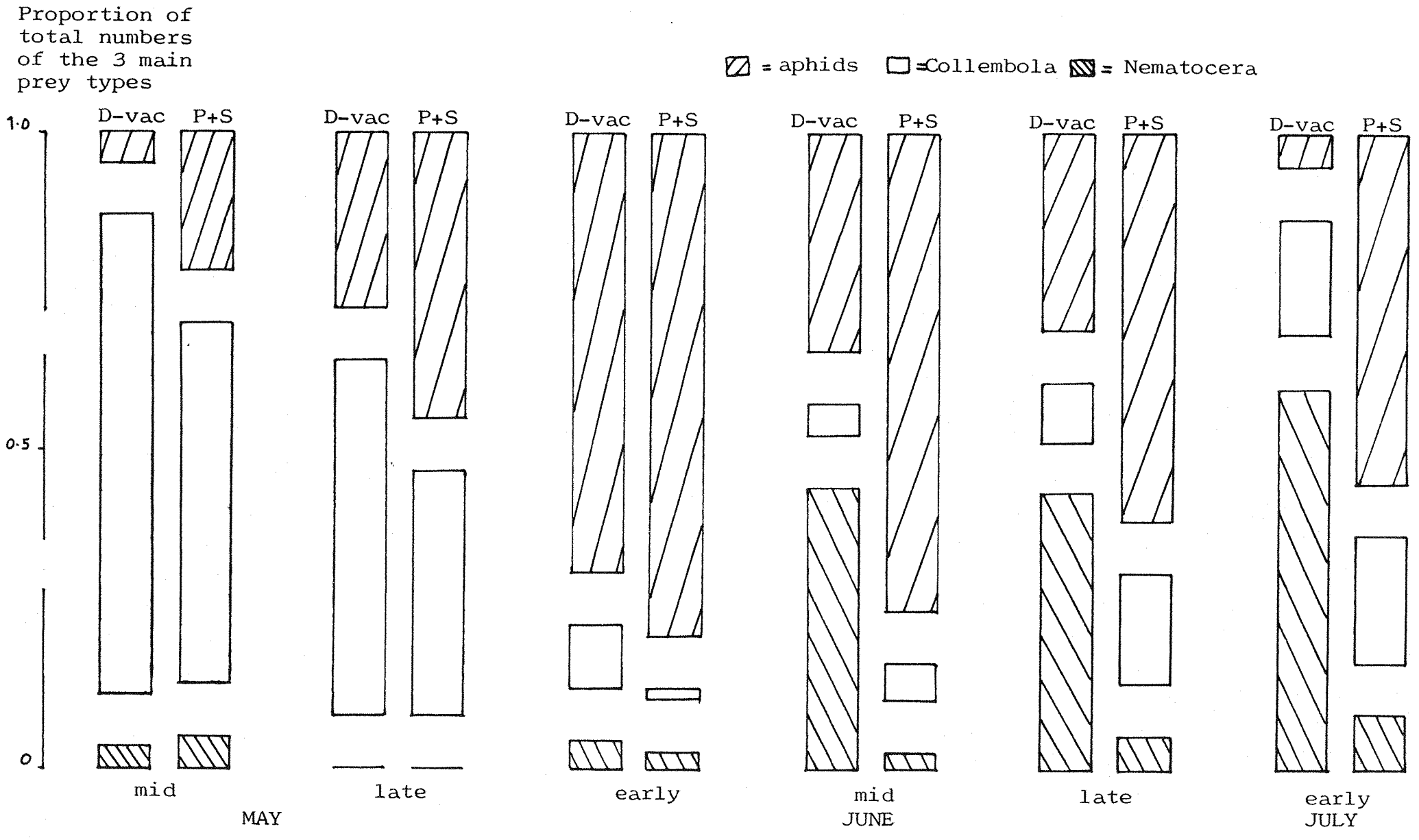
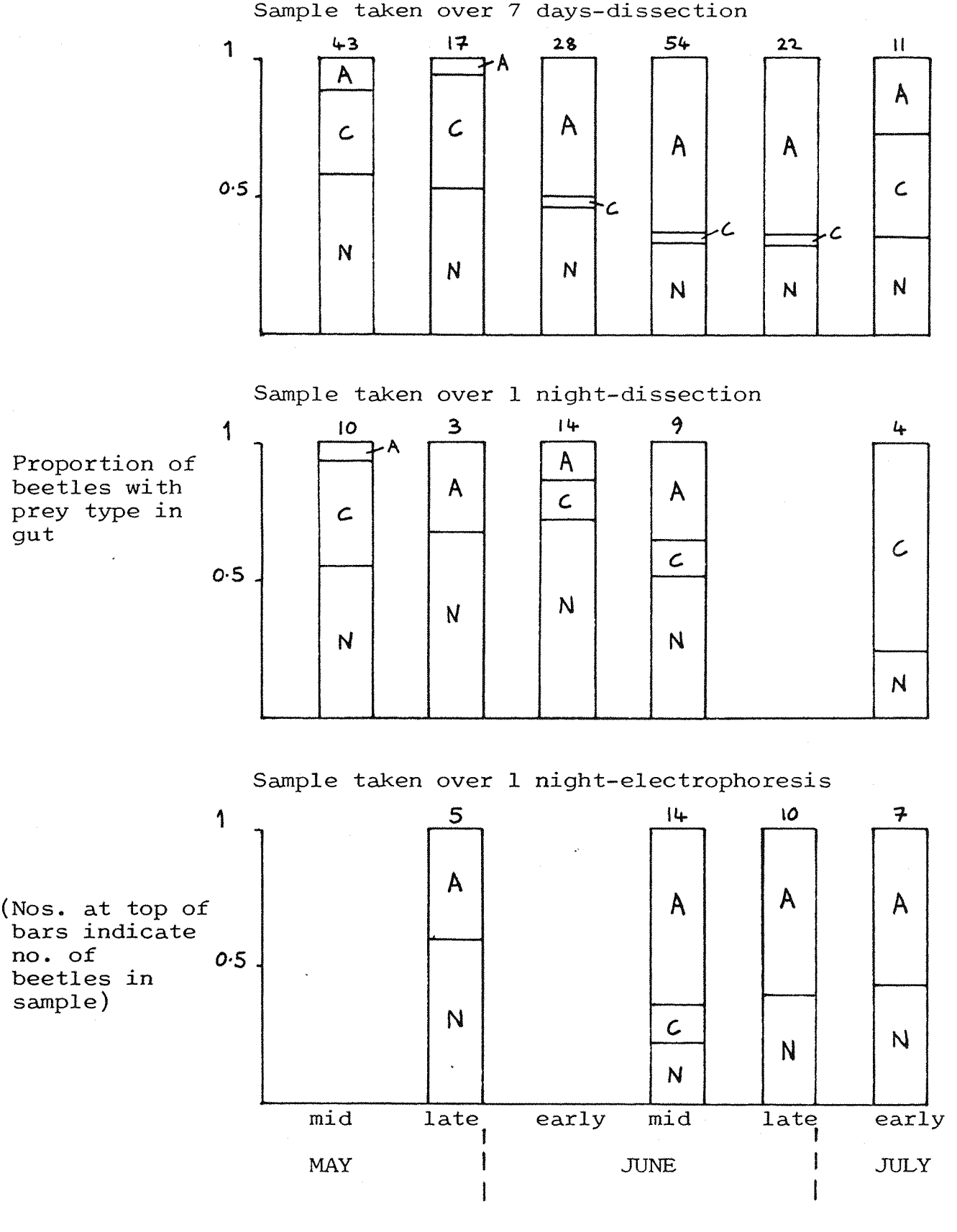


Fig. 7.26 The change in the proportion of prey found in the gut contents of A. dorsale over the 1980 field season and the difference between three methods of sampling the gut contents.

A=aphids, C=Collembola, N=Nematocera.



dissection vs. 1-day electrophoresis and 1-day dissection vs. 1-day electrophoresis). As with the prey sampling methods the probability level for a significant correlation was lowered to 0.05/3 = 0.017. There were no significant correlations between the three gut analysis methods for any of the three prey types. Again there are two possible reasons for the lack of correlation; sampling error (due to small numbers of beetles for some sample dates) or genuine differences between 1- and 7-day sampling and visual or electrophoretic analysis. Figure 7.26 shows that both are probably involved in this instance; visual comparisons between the prey proportions for dates where samples were larger (at least 10 beetles dissected containing the three prey types) show that in some cases they are similar, in others not. Both sampling errors and genuine differences must be kept in mind when interpreting the gut content : prey availability correlations. For instance, at first sight it makes sense if prey are sampled overnight to sample A. dorsale (i.e. gut contents) over the same night. It is possible however that A. dorsale responds to the day-to-day changes in the climate more quickly than the prey so that sampling the beetle over just one night may give an atypical picture of the prey it has been taking over that week.

(c) Correlating gut content data with prey availability

The preceding laboratory studies of Chapters 5 and 6 would suggest A. dorsale should take aphids, Collembola and Nematocera on the ground and in the ratio presented to it, i.e. no element of preference. The work in Chapter 6.7 showed that in combination with the densities of the prey the success rate (temperature dependent) with which A. dorsale caught the prey types was the most important factor controlling the ratio of prey presented to the beetle. In other words for any one prey type the proportion of the prey in the gut contents should correlate with the "capture rate" corrected proportion of that prey found on the ground in the field. But as correlations are never proof of a causative link between two or more variables, it would explain little simply to show that these proportions correlated significantly. Comparisons between correlation coefficients when these same variables are used, but transformed according to different foraging models, can at least show which of the models best fits the data. This technique is used

here to pursue a sequence of correlations which are aimed at showing whether A. dorsale is foraging in a random manner (takes prey as they are offered) or is preferring aphids.

Although some of the data (e.g. gut contents) could not be shown to be parametric, a computerised parametric correlation program was used for speed of calculation because of the large number of correlations required. As the parametric correlation is more rigorous than the non-parametric Spearman rank correlation (Siegel 1956) this does not result in significant correlations being identified where the non-parametric method would show no relationship.

As there were a large number of cross-comparisons in producing the correlation coefficients, attaching a significance level to the coefficients becomes meaningless; the more comparisons, the more likely it is by chance that some will be significant. A partial solution to this problem is to specify that for a particular sampling method (of gut and prey) the correlation must be significant for all three prey types before any significance is read into the result. Accordingly the 5% level of significance was applied to individual correlations but all three prey type correlations had to be significant before the gut data were considered to match the field data (hence no actual r-values are given in the following data tables).

Correlation coefficients were used to answer three main questions:

Which of the three gut analysis methods correlates best with prey availability?

Which of the three prey sampling methods correlates best with the gut content data?

Do the correlations fit the model of a predator specialising on aphids or the model of a random predator best?

Within each of these questions there is the additional question of whether the correlation (or lack of it) is due to sampling errors (too small a sample, prey escaping etc.) or to genuine differences between sample methods, prey availability or foraging method.

The first step was to ask a slightly more simple question; are changes in the field densities of any of the three main prey types reflected by changes in the relative proportions of each prey type in the gut contents? In other words, is A. dorsale responding directly to the density of any one of the three prey types by eating it more often? As this relationship could be linear or curved the correlations were made using normal and log scale axes. Where proportional data were used an arcsine transformation (Snedecor & Cochran 1967) was used to "normalize" the data.

These correlations are summarised in Table 7.3 and were not significant in almost all cases. Neither of the one day sampling methods gave any significant correlations; there were no significant correlations with the soil-scraping prey sampling method. The only significant correlations were with aphids when sampled by D-vac or plant samples and these correlated with the 7-day gut samples. Referral back to Figures 7.24-26 shows that this is as expected because in the prey samples aphids increase both numerically and proportionately and this is mirrored by a similar increase in their proportion in the gut contents.

The relationship between aphids sampled in the field and appearing in the gut was expected to be a simple one because aphids are reasonably sedentary and their population increased and then declined smoothly through the season. Clearly the relationship is not so simple for Collembola and Nematocera and the more active behaviour and larger fluctuations in population make them more difficult to sample. It is not clear why there was no significant correlation between aphids sampled by soil-scraping and aphids in the gut contents.

(d) The two correlation models

Aphid preference model

In this model it is assumed that A. dorsale chooses aphids but feeds randomly off Collembola and Nematocera. This means that the frequency with which aphids appear in the gut contents should be directly related (linearly or curvilinearly) to the density of aphids in the field. For Collembola or Nematocera however, it is the proportion

Table 7.3 The correlation between the proportion in the gut of the three prey types, measured by three different methods and field densities of three prey types, measured by three different sampling methods.

Prey sampling method			Method of gut analysis: 7 - day dissection (df = 1,6)	1 - day dissection (df = 1,5)	1 - day electrophoresis (df = 1,3)
D-vac					
		Aphid	$p < 0.05$	NS	NS
	Normal	Coll	NS	NS	NS
		Nem	NS	NS	NS
		Aphid	$p < 0.01$	NS	NS
	log	Coll	NS	NS	NS
		Nem	NS	NS	NS
Plant					
		Aphid	$p < 0.05$	NS	NS
	Normal	Coll	NS	NS	NS
		Nem	NS	NS	NS
		Aphid	$p < 0.05$	NS	NS
	log	Coll	NS	NS	NS
		Nem	NS	NS	NS
Soil					
		Aphid	NS	NS	NS
	Normal	Coll	NS	NS	NS
		Nem	NS	NS	NS
		Aphid	NS	NS	NS
	log	Coll	NS	NS	NS
		Nem	NS	NS	NS

which either forms of the total frequency with which Collembola and Nematocera appear in the gut that is related (linearly) to the proportion which either forms of their (Collembola and Nematocera) total field density. Note that for aphids the relationship may be linear or curvilinear because A. dorsale is represented as making a choice to eat aphids and if this involved a switching mechanism the relationship would be curved whereas a more simple response to aphid density could be linear. For the other two prey items the response can only be linear; A. dorsale eats prey as it comes across them, there is no searching-out or choice of prey.

For the data to fit this model then, the following correlations would have to be significant for any one combination of prey and gut content sampling methods:

1.	Aphid density	vs.	frequency of aphids in gut contents
	(normal or logged data)		
2.	Proportion of remaining prey that are Collembola	vs.	Proportion of remaining prey in gut that are Collembola
3.	Proportion of remaining prey that are Nematocera	vs.	Proportion of remaining prey in gut that are Nematocera

No preference model

In this model it is assumed that A. dorsale takes all three prey types "randomly"; this means that there should be correlations between the same quantities for all three prey as there were for just Collembola and Nematocera in the above model:

1.	Proportion of prey that are aphids	vs.	Proportion of prey in the gut that are aphids
2.	Proportion of prey that are Collembola	vs.	Proportion of prey in the gut that are Collembola

3.	Proportion of prey that are Nematocera	vs.	Proportion of prey in the gut that are Nematocera

The treatment of data for correlation under the constraints of these two models is summarised in Figure 7.27. An additional constraint is that the correlations have to be positive; as a prey type increases in the field (in numbers or proportion) then its presence in the gut contents of A. dorsale increases (in frequency or proportion). (In fact all significant correlations were positive but clearly a significant negative correlation would not fit either model).

The first set of correlations involved only the steps shown in Figure 7.27; in the second set of correlations the initial field densities of each prey type were corrected for successful capture rates established in the laboratory experiments of Chapter 6.7. This needed only the additional step of multiplying each field density by the relevant proportion of prey that would be captured successfully. These proportions were taken from Figure 6.18 (Chapter 6.7) and for simplicity the temperature measurements made between 01.00 and 02.00 hours on the night of the sample were taken as the average temperature for the whole night.

The correlations for the uncorrected data are summarised in Table 7.4 and those for the corrected data in Table 7.5. For the reasons discussed at the beginning of this correlation section, the actual r-values are not given, only significance at the $p = 0.05$ level or below is indicated. The three correlations required for each model are boxed-in in Table 7.4 and 7.5 to indicate that comparisons should be made between these boxes and not between individual correlations.

(e) Uncorrected correlations (Table 7.4)

There were no significant correlations between any of the prey sampling methods and the 1-day electrophoresis gut samples. This may be because of the low number of gut contents that made up the latter samples (Fig. 7.26). The 1-day and 7-day dissection gut samples gave

Fig. 7.27 The transformation of data for the aphid-preference and the no preference correlative models.

For data from <u>each</u> sample date:

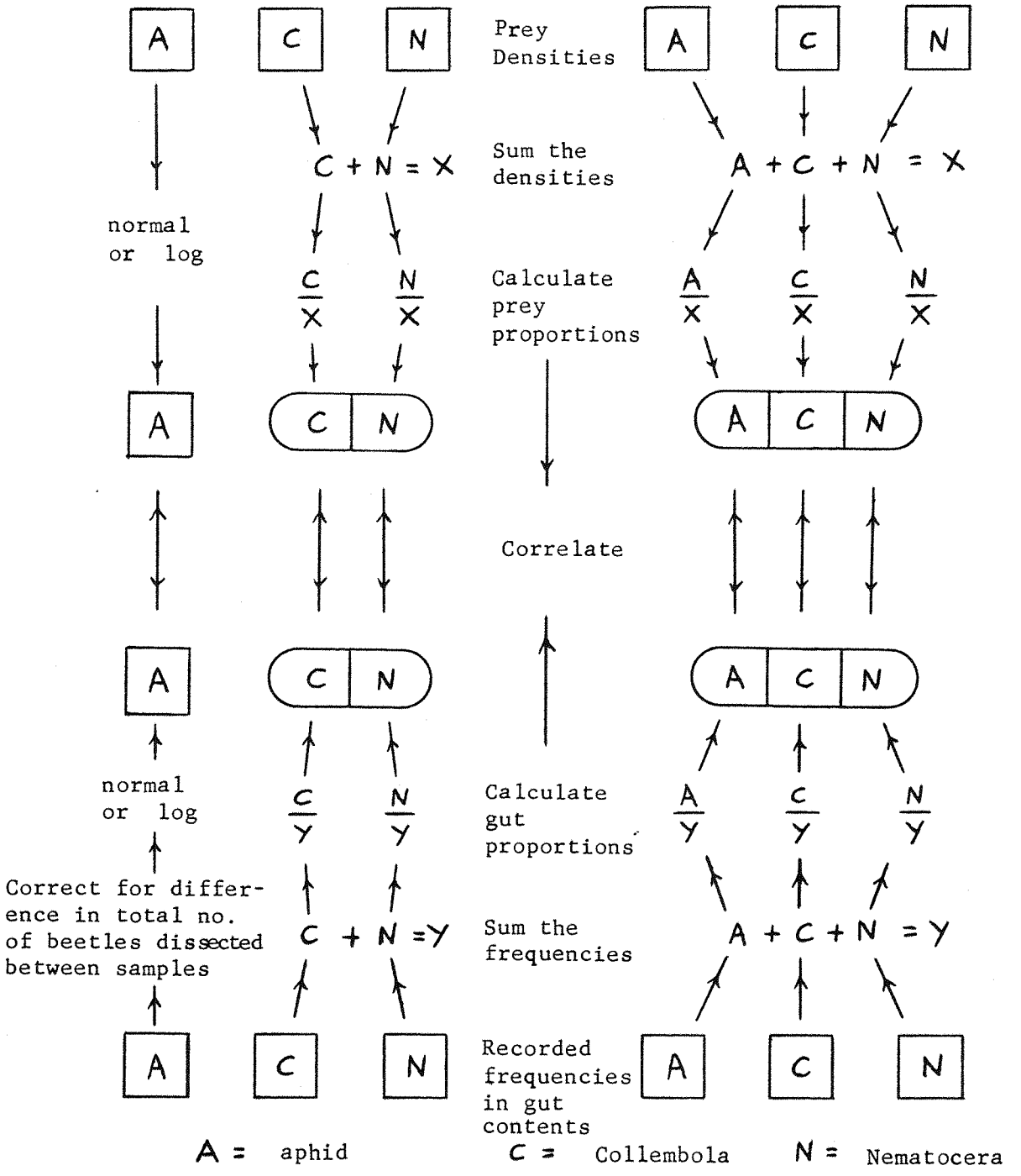


Table 7.4 The significance of correlations between prey field densities and prey in the gut contents of A. dorsale for the aphid preference and the no preference models.

Prey sample method	Model	Prey	Method of gut analysis: 7 - day dissection (d.f. = 1,6)	1 - day dissection (d.f. = 1,5)	1 - day electrophoresis (d.f. = 1,3)
D-vac	Aphid-p	Aphid	p< 0.02, p< 0.01	p< 0.05, NS	NS, NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	NS	NS	NS
		Coll	p 0.05	NS	NS
		Nem	NS	NS	NS
Plant clipping	Aphid-p	Aphid	p< 0.01, p< 0.05	p< 0.05, NS	NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	NS	NS	NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
Soil scraping	Aphid-p	Aphid	NS, p< 0.05	p< 0.05, NS	NS, NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	NS	NS	NS
		Coll	p< 0.05	NS	NS
		Nem	NS	NS	NS

N.B. Where two probabilities are given, i.e. p< 0.05, p< 0.01 the first is for a correlation with the normal axes, the second for a correlation with logged axes.

Table 7.5 The significance of correlations between prey field densities corrected for prey capture rate and prey in the gut contents of A. dorsale, for the Aphid-preference and No-preference models.

Prey sample method	Model	Prey	Method of gut analysis: 7 - day dissection (d.f. = 1,6)	1 - day dissection (d.f. = 1,5)	1 - day electrophoresis (d.f. = 1,3)
D-vac	Aphid-p	Aphid	p < 0.01, p < 0.01	p < 0.05, NS	NS, NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	NS	NS	NS
		Coll	p < 0.05	NS	NS
		Nem	NS	NS	NS
Plant clipping	Aphid-p	Aphid	p < 0.01, p < 0.01	p < 0.05, NS	NS, NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	NS	NS	NS
		Coll	NS	NS	NS
		Nem	NS	p < 0.05	NS
Soil scraping	Aphid-p	Aphid	NS, p < 0.01	p < 0.05, NS	NS, NS
		Coll	NS	NS	NS
		Nem	NS	NS	NS
	No - p	Aphid	p < 0.05	NS	NS
		Coll	p < 0.02	NS	NS
		Nem	NS	NS	NS

N.B. Where two probabilities are given, i.e. p < 0.01, p < 0.05 the first is for a correlation with normal axes, the second for a correlation with logged axes.

significant correlations for aphids using the aphid-preference model. The 7-day dissection gut samples also correlated significantly for Collembola with the no preference model. These correlations applied more or less to all the sampling methods.

Using the criterion that all three correlations must be significant in any one box to establish a good fit to the model, the data did not fit the aphid-preference or the no preference model. Aphids probably show so many significant correlations because of the smooth changes in their population (Fig. 7.24) and the good correlation between the three prey-sampling methods for aphids (see prey-sampling section). The 1-day electrophoresis gut samples gave no significant correlations probably because of the small number of sample dates (Fig. 7.26).

(f) Corrected correlations (Table 7.5)

Once again there were no significant correlations with the 1-day electrophoresis gut samples and this supports the hypothesis that this is due to a low number of sample dates (Fig. 7.26). The 1-day and 7-day dissection gut samples again gave significant correlations for aphids using the aphid-preference model. There were some additional significant correlations with aphids, Collembola and Nematocera using the no preference model with both 1-day and 7-day dissection gut samples. The distribution of these correlations between sampling methods was different from the uncorrected data correlations but still included all three sampling methods.

Using the criteria that all three correlations must be significant in any one box to show a good fit to the model then the data did not fit the aphid-preference or the no-preference model. The prediction from the laboratory data was that A. dorsale was a random ground predator and that prey availability was most influenced by the varying rate of successful captures of the prey with temperature. Thus the fit between model and data should have been best for the no-preference model with prey sampled by soil scraping and whichever gut sampling method was of a large enough sample size to reflect what A. dorsale had been eating. This box is double-ringed in Table 7.5 and is the only case where there was a significant correlation for more than one of the prey types. Ideally all three would need to be significant but

there may be good biological reasons as to why the correlation for Nematocera was not significant.

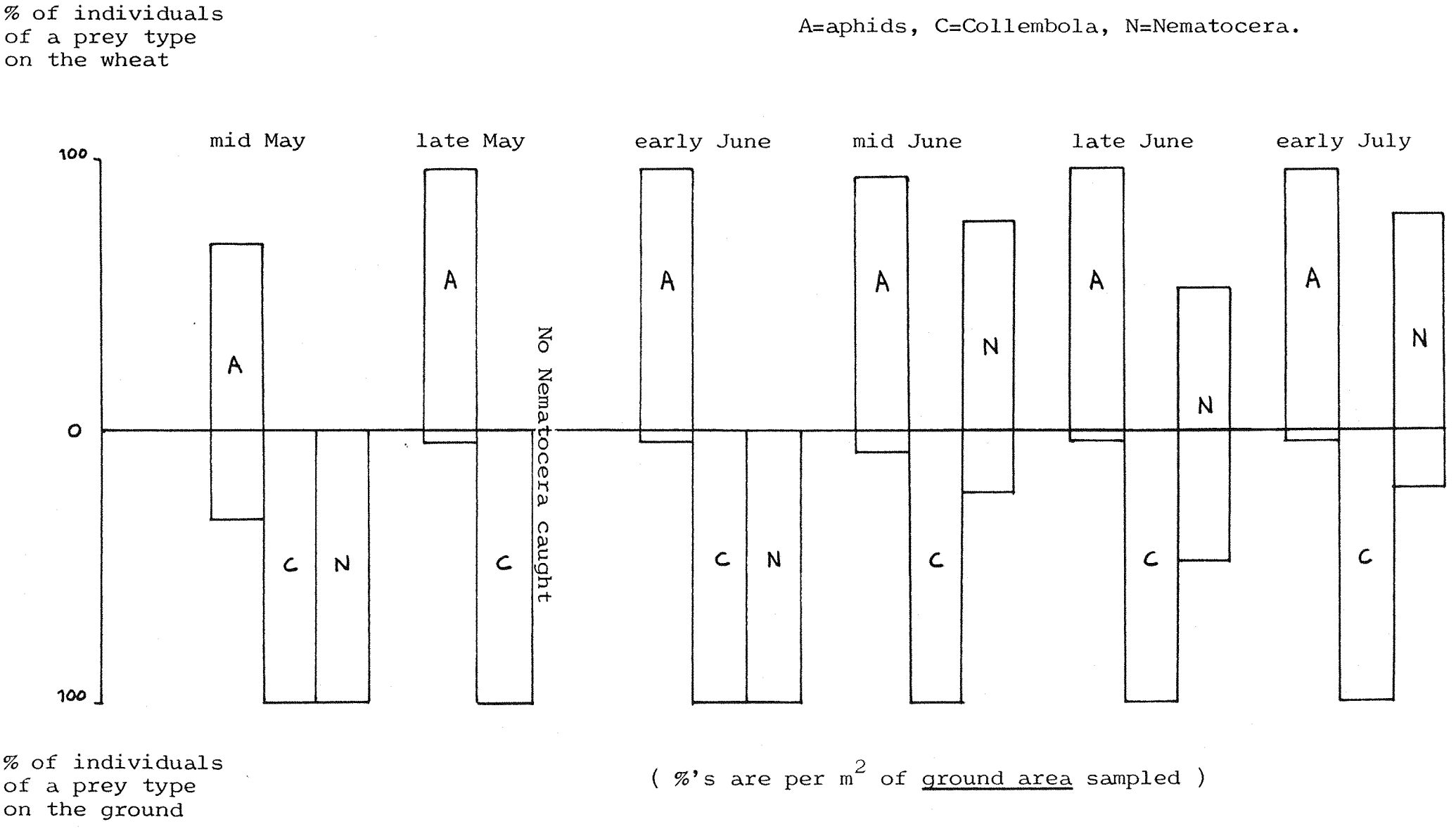
The plant clippings and soil scrapings were taken to show the distribution of aphids between plant and ground in a way that D-vac sampling cannot. Both are likely to undersample certain prey types in the same waym e.g. Diptera could escape by flight equally well during the taking of both these samples. The samples should then provide a realistic assessment of the relative changes in distribution between plant and ground from week to week of the three main prey types. These data are summarised in Figure 7.28, the position of the columns about the central zero line showing how the distribution changes with time. Clearly aphids and Collembola remain constant in their distribution of mostly on the plant and all on the ground respectively. Nematocera however change markedly between early and mid June from a distribution on the ground to one mainly on the plants. Referral back to Figures 7.24 and 25 shows that this is the period when the D-vac suddenly caught more Nematocera and the climate data (Fig. 7.20) show that this was also when minimum night temperatures rose substantially (by 2-4^{o}C). These facts combined imply that Nematocera were more active after early June because of warmer temperatures and were thus caught in greater numbers in the D-vac and on the wheat plants. If this is so then the Nematocera capture rates measured in the laboratory may not apply to the field situation. This would mean that the correction applied in Table 7.5 would not produce a good fit between the proportion of Nematocera available and their proportion in the gut contents.

It is possible that the laboratory-measured capture rates would be correct for the early part of the season when night temperatures were lower and so in the range of the laboratory experiments. This could be tested by repeating the correlation for Nematocera but using data up to (and including) early June only. This was not really possible because there were too few sample dates (four only) to produce such a correlation and when this was tried no significant correlations were obtained.

(viii)Foraging in the wheat field

Laboratory results showed that A. dorsale was a general predator

Fig. 7.28 The change in the distribution of the 3 main prey of A. dorsale between the wheat and the ground through the field season.



(Chapters 5 and 6) and the preceding field results seem to confirm this. The use of the "successful capture rate" correction on the prey available account for most of the variation between prey availability and appearance of prey in the gut contents of A. dorsale. The corrected samples also showed how aphids could be at low density in the field and still form a substantial proportion of the gut contents. In the 22 May (1980) prey sample for instance, aphids were at a density of about $30/m^2$ as measured by D-vac but actually formed about 40% of the prey available on the ground.

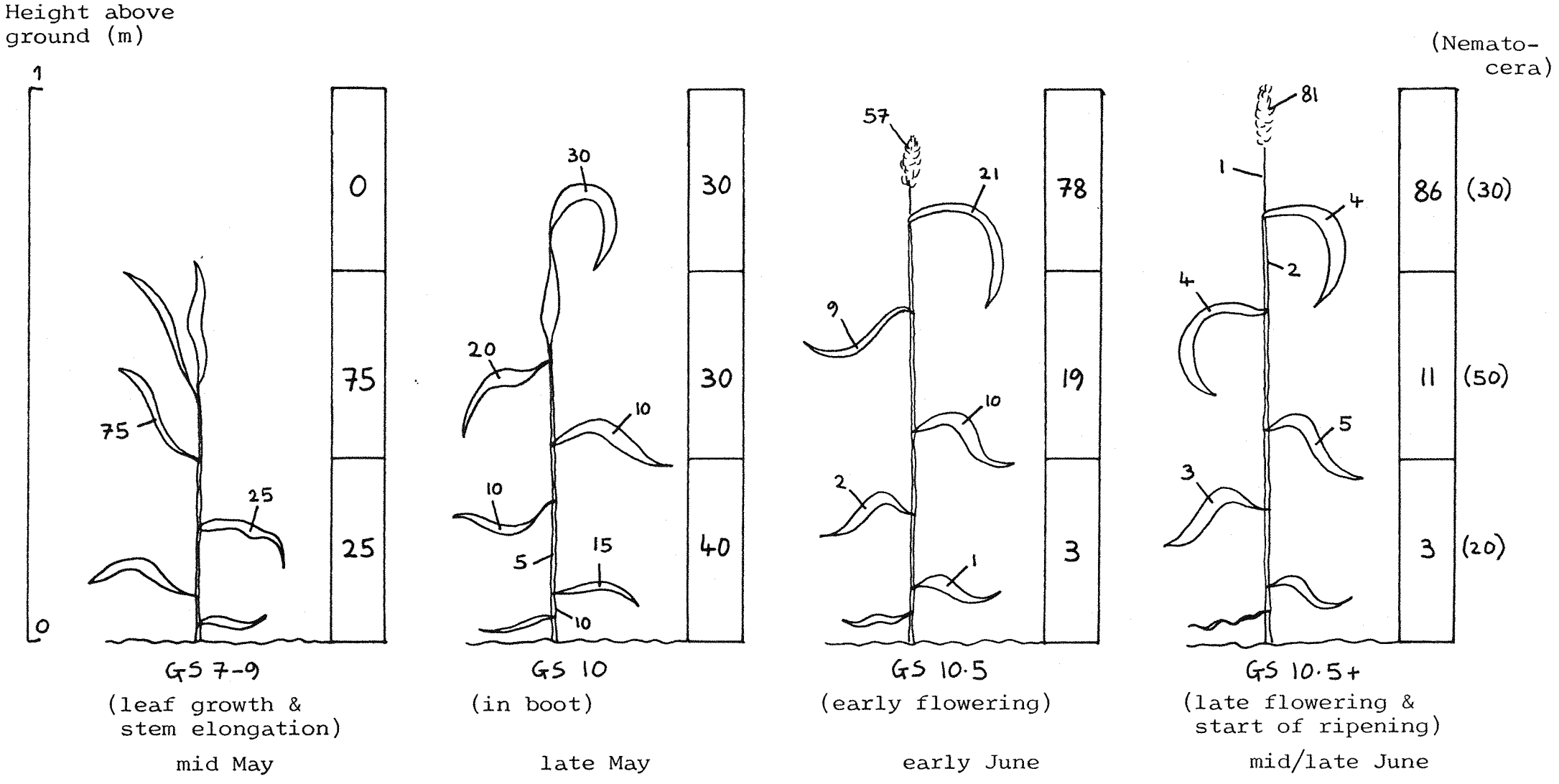
Aphids were the prey most easily caught by A. dorsale and the plant and soil samples seem to show that they represent a ready supply of prey but are mainly confined to the wheat plants (Fig. 7.28). It seems surprising then that the beetle does not utilise this food resource. Both laboratory and field data have so far indicated that A. dorsale forages almost exclusively on the ground.

In Chapter 6 it was shown that it was very unlikely that an invertebrate such as A. dorsale would have the capacity to forage optimally. Invertebrates such as parasitoids do have this capacity but only because they were very specific, and hence well adapted, to one prey type or species only. It would not be possible for A. dorsale to specialise in this way on cereal aphids because of their highly transitory and sporadic presence in cereals. Without this specialisation A. dorsale is presented with the double problem of finding a prey type that is only occasionally present and that changes its distribution within the habitat markedly in the space of a few weeks (Fig. 7.29). At the beginning of the A. dorsale period of field activity, aphids (S. avenae) are distributed more or less evenly from top to bottom of the wheat. By June this has changed so that nearly all aphids are at the top of the wheat plants feeding on the ears.

There are two hypothetically opposed strategies for dealing with this movement of aphids up the plant; the first is to be so adapted to aphids that the predator searches only those areas of the plant most likely to have aphids, and the second is to take a more general strategy and search the whole plant indiscriminately with the eventual discovery of aphids (this is essentially what A. dorsale did; see Chapter 5).

Fig. 7.29 The change in distribution of aphids (and Nematocera) on wheat with changing growth stage of the plants during the 1980 Damerham field season.

(Nos. show % of aphids found on parts of wheat, bars summarise these individual %'s)



These strategies will obviously involve the predator in searching different areas of wheat surface. The area of wheat surface per m^2 of ground was calculated in the way shown in Figure 7.30. The wheat stem and head were assumed to be cylinders, the dimensions of which were taken from the plants collected for the plant-clipping samples. Leaves were measured by drawing their outline on graph paper and then counting the squares and doubling (to take account of the upper and lower surfaces of leaves). The entire area of wheat per m^2 of ground was then estimated by multiplying the area of one plant of the appropriate growth stage by the number of wheat stems per m^2 of ground (as measured in the field). This gave the result that wheat area can be as high as about 20 m^2 per m^2 of ground area. This has a profound effect on the apparent densities of aphids on the plants as opposed to on the ground. The effect of expressing aphid densities as number per m^2 of plant area and number per m^2 of ground area is shown in Figure 7.31 for the usual "human" view, and the aforementioned specific and general predator searching strategies. The assumptions made and their effect on aphid densities (as measured by plant clippings and soil scrapings) are now summarised with an example (the early June sample).

Human view: Aphid densities on both plant and ground are simply quoted as numbers per m^2 of ground area. Thus for the early June sample these figures were:

Plant:	$1080/m^2$	($\equiv$ 96%)
Ground:	$40/m^2$	($\equiv$ 4%)

This gives the impression that 96% of the aphids per unit area sampled are found on the plant.

Aphid-specific predator view: The predator is assumed to search only the wheat head and flag leaf. The area of these two plant components was combined with the percentages of aphids found there (see Fig. 7.29) to give the numbers of aphids that a specific predator would perceive per m^2 of plant and ground. For the early June sample these figures were:

Fig. 7.30 The surface area of wheat per square metre of ground for the different growth stages.

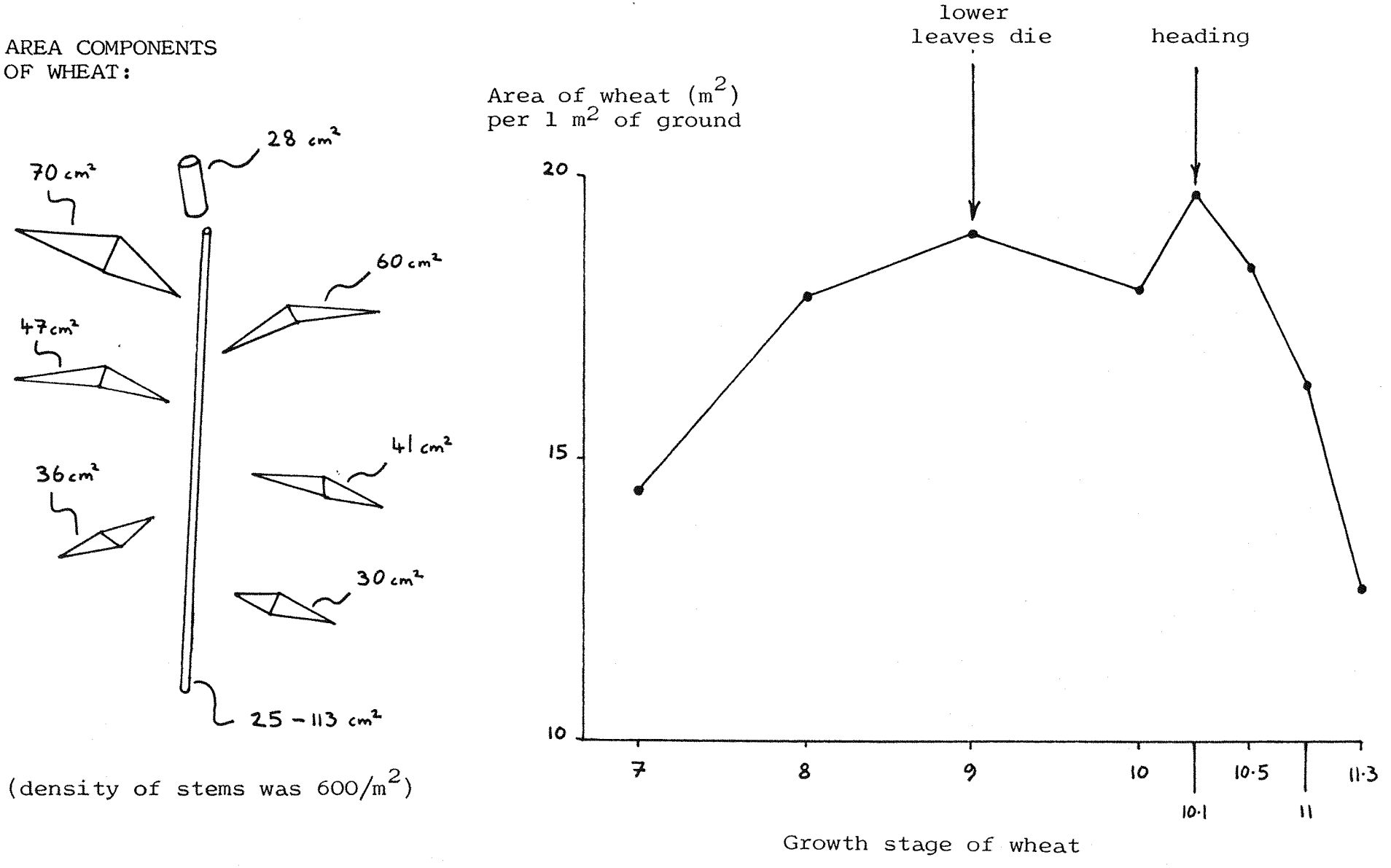
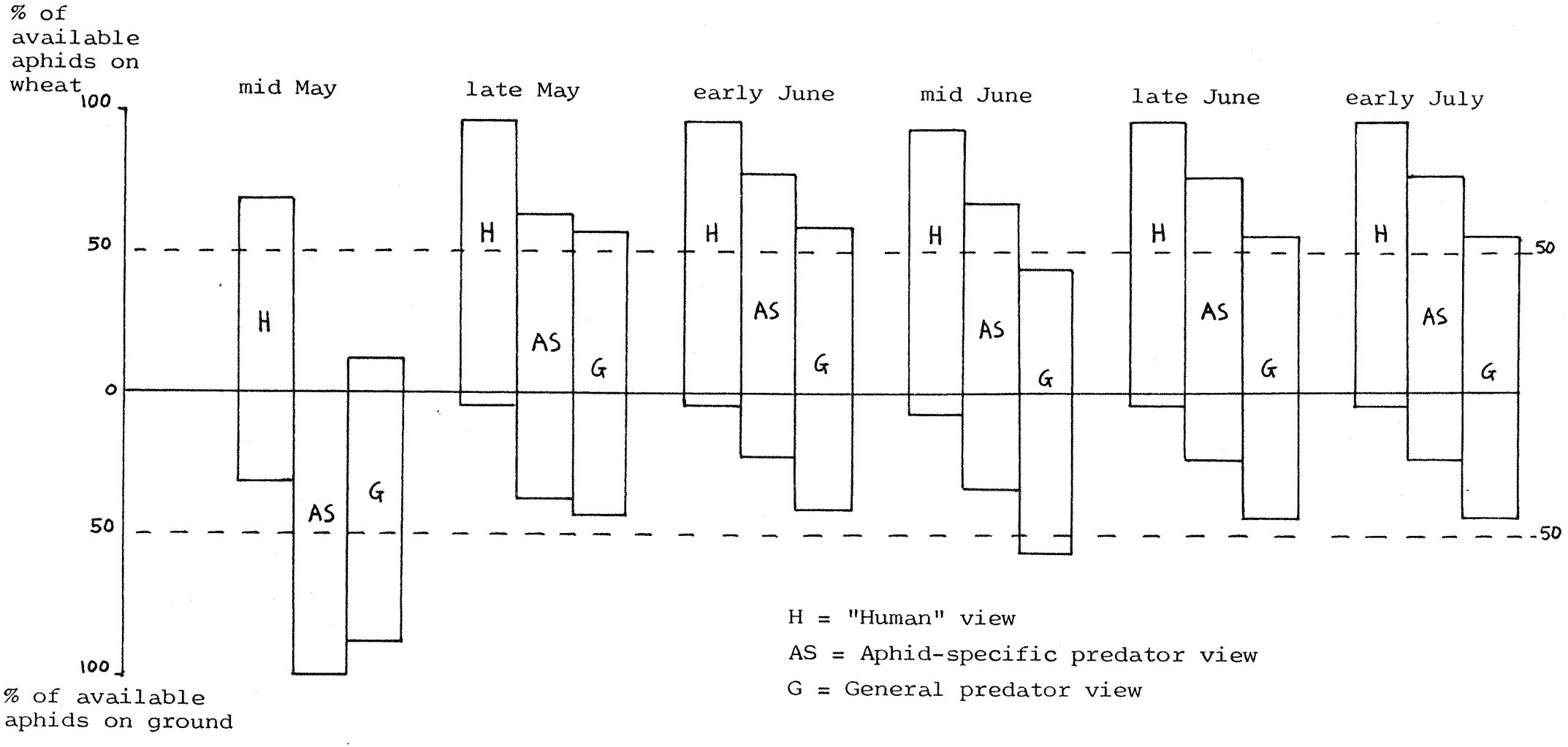


Fig. 7.31 The change in aphid distribution between wheat and ground through the field season from a human, aphid-specific or general predator point of view.



Plant: $1080 \times 0.78/5.88 = 143.3/m^2$ ($\equiv$ 78%)
Ground: $40/m^2$ ($\equiv$ 22%)

(where 0.78 is the proportion of aphids found on the flag leaf and head and 5.88 is the area (m^2) of flag leaf and head per m^2 of ground).

General predator view: The predator is assumed to search the whole wheat plant and the number of aphids on the plants (per m^2 ground) is divided by this total area of wheat per m^2 ground. For the early June sample a general predator would perceive the following densities of aphids per m^2 of plant or ground:

Plant: $1080/19.02 = 56.8$ ($\equiv$ 58%)
Ground: $40/m^2$ ($\equiv$ 42%)

It can now be seen that the apparent percentage of aphids available per m^2 of area to be searched decreases substantially from the human to the specific to the general predator view. This trend was constant through the season except for the mid May sample. Here, as there were no aphids on the flag leaf or head, the aphid-specific predator perceives all the available aphids as being on the ground. In addition soil scrapes showed a higher proportion of aphids on the ground than later in the season so that the general predator and human also perceive more aphids on the ground than in the rest of the season.

A human view presents the wheat field as being divided into a small density of aphids available on the ground and a large population on the wheat. For an aphid-specific predator this is essentially true but the same is not so for a general predator. As Figure 7.31 shows for a general predator there are about the same number of aphids per area (to be searched) on the plant and ground. If the other main prey types (Collembola and Nematocera for A. dorsale) were included in this calculation then a general predator would find a much higher density of prey on the ground as compared to the plant. If Collembola and Nematocera densities are included in the calculation for the general predator view then the percentage of prey available per m^2 of ground or plant searched ranges from 60% on the ground (early June) to 90%

(late June) showing that a general predator should search almost exclusively on the ground.

(ix) The proportion of aphids on the ground

The very constant proportion of aphids on the ground (Fig. 7.28) suggests that this may be a result of voluntary movement of aphids between plants. Both average wind speed (Fig. 7.20) and highest gust wind speeds were very variable over the 1980 season making it unlikely that they were the cause of aphids arriving on the ground (the same is true of rainfall in this period). No work was done in this project to establish the cause of aphids arriving on the ground but other work (Fraser pers. comm.) has also shown that this proportion of aphids is on the ground through the season. The importance of the percentage of the aphid population on the ground and the underlying mechanism controlling this will be discussed in relation to the biological control potential of A. dorsale in Chapter 9.

7.4 Final discussion of the 1979-81 S. Allenford Farm Fieldwork

Both the phenological and foraging data imply that A. dorsale has substantial potential for biological control. The following discussion draws on the points particularly relevant to biological control from this fieldwork.

A. dorsale migrates annually between field boundaries and the field; this conveniently allows sampling of the beetle when it is at high density in the boundaries (during the winter). This aggregation can create a false impression that A. dorsale occurs at a high field density; simple correction for the area of the field compared to the area of the boundaries shows that these aggregations when spread over the field (see below) lead to low densities of beetles.

The migration into the field occurs at an ideal time; early enough for A. dorsale to arrive in the field before large aphid populations build up but late enough to miss deleterious agricultural

practices such as rolling, early pesticide spraying and so on. The migration was extremely rapid with A. dorsale arriving in pitfalls some 50 m into the field in the same week as the migration started. Over this distance it took about two weeks for catches to even out completely from the hedge to the 50 m pitfalls implying that in very large cereal fields this dispersal time could limit the control potential of A. dorsale.

By the end of the cereal season most of the current generation of adult A. dorsale had died and the new generation emerged from pupation after the cereal harvest (measured by the appearance of callow beetles in pitfalls). This means that although the new generation do not suffer mortality due to the process of harvesting, they may be vulnerable to stubble/straw-burning, but this was not investigated here.

The factors controlling the timing of field emergence were not fully investigated; the hypothesis was put forward that daylength was the main factor and the extreme regularity of the emergence dates would confirm this (see also Chapter 1). It is possible however that crop microclimate and prey availability in the crop may also be important (both are also probably related to daylength); these aspects were not examined but manipulation of the crop could potentially lead to an earlier or later migration by A. dorsale. This may not be particularly desirable because S. avenae (the major aphid pest species in the South of England, Vickerman & Wratten 1979) populations develop comparatively late in the season (June).

Laboratory experiments (Chapter 4.8) showed that reproductively-mature A. dorsale ate more aphids per day than immatures but by the time the beetle emerges into the field most are mature so consumption rates should be at a maximum. In addition dissections suggested that mating had occurred before the migration into the field implying that little time is wasted by the A. dorsale population in looking for mates. Also females are known to lay their eggs on plants although this was observed only in the laboratory. This may increase aphid predation if the female A. dorsale climb far enough up the wheat to encounter aphids.

Dissections also showed that A. dorsale adults had started to feed in the boundaries before arriving in the field so there would be no delay in attacking aphid populations once the beetles had arrived in the crop. The three most common prey in the diet were aphids, Collembola and Nematocera. Laboratory experiments showed that of these, aphids were the most easily caught by A. dorsale and dissections showed that they could form a substantial part of the A. dorsale diet even when the aphids were at low field densities. There was no difference in the composition of the diet either between sexes or between reproductive stages within a sex. The number of aphids eaten by the A. dorsale population is affected by stage of reproductive maturity (Chapter 4.8) but not by elements of prey choice.

Laboratory work (Chapter 6) suggested that A. dorsale took prey as it encountered them; there was no element of choice. Laboratory work (Chapter 5) also suggested that this prey would be caught on the ground as A. dorsale hardly ever climbed. Correlative analysis of prey availability on the ground or plant in the field with prey in the gut contents of the beetle strongly suggested that A. dorsale was taking prey as it encountered them and that this was occurring on the ground. There was no real evidence to suggest a preference for aphids.

An analysis of the aphid densities on ground and plant (using the surface area that a general predator would have to search to find aphids to calculate the densities) showed that for A. dorsale the number of aphids per m^2 are approximately equal on ground and plant. When other prey types are considered in addition to aphids it is clearly adaptive for A. dorsale to search for prey on the ground on this basis alone. When this is combined with the infrequent and transitory nature of aphids as prey, it is no surprise that all evidence points to A. dorsale being a purely ground predator not specialised to feed only on aphids.

Summary

A. dorsale is resident in cereal crops at the right time to attack aphid populations but laboratory work shows that the beetle does not climb wheat plants and, although a general predator, will

preferentially eat aphids because they are the prey most easily caught by it. Correlative analysis of fieldwork would tend to support this. Clearly proof in the field of the lack of climbing by A. dorsale is required and this is the subject of the next Chapter (8). In addition the implications for the effectiveness of A. dorsale in the biological control of aphids if it does not climb need to be considered. In Chapter 9 this is done using a simple model incorporating the effect of changing the proportion of aphids on the ground (and hence available to A. dorsale). The modelling chapter ties together the laboratory and fieldwork of Chapters 3 to 8.

C H A P T E R 8

CHAPTER 8

FIELD OBSERVATION OF THE FORAGING BEHAVIOUR OF A. DORSALE

(See Chapter 2.8 for materials and methods)

8.1 Introduction

A combination of laboratory experimentation and field sampling has suggested that A. dorsale catches aphids more easily than other prey but that it catches them on the ground. These findings needed to be tested by observation of A. dorsale foraging in a natural field environment. The 1980 fieldwork (Chapter 7) showed that observation of A. dorsale at natural densities in the field was not possible. Instead higher densities of A. dorsale were confined to small arenas in a plot of wheat in the University's experimental grounds (Chilworth Manor). The plot had no natural population of A. dorsale so they were introduced using individuals from winter collections made at the S. Allenford farm site (Chapter 7). Although the use of small arenas does not entirely recreate the field situation it provides a vital link between the so far clearly separate laboratory and field work of this project. As field experiments are inherently more variable than those in the laboratory, this Chapter compares the foraging behaviour of A. dorsale in only two situations: in areas of high or low aphid density. More subtle experiments with several aphid densities were not possible given the short active season of the beetle.

8.2 A comparison between the 1980 S. Allenford farm site and the Chilworth 1981 site

The plot of wheat sown for the 1981 fieldwork at Chilworth was only 25 m^2 and although the plot had been sown with wheat for several years previously it was likely to be very different in prey density, species composition, etc. from larger more established farm site. To identify these differences a comparison was made between the 1980 S. Allenford field site and the Chilworth 1981 plot.

(i) The wheat crop

The wheat at Chilworth was broadcast sown, had fertiliser applied

to it, but no insecticides, fungicides or herbicides, nor was the crop rolled to encourage tillering. This may have led to differences in stem density, plant development and so on. Data on growth stage, height of crop and stem density are summarised in Table 8.1.

There were no real differences in growth stage or stem density between the Chilworth wheat plot and the 1980 commercially-grown crop at S. Allenford farm. Wheat at Chilworth was substantially (30 cm) shorter and this could have been important if A. dorsale had proved to be a frequent climber of the wheat.

(ii) Prey density and composition

Four factors could have caused prey density and composition at Chilworth to be very different from that at the S. Allenford site:

The Chilworth plot was not sprayed which may have increased prey density and diversity.

The Chilworth plot was not only small in area but also had no neighbouring arable land so numbers of prey migrating into the plot (e.g. cereal aphids) were likely to be low.

The arena walls may have prevented movement of prey within the plot and led to prey being depleted by A. dorsale in the observation arenas.

Half the arenas were caged; this increased aphid populations but may also have changed the density and composition of other prey.

Comparisons were made between the uncaged Chilworth arenas and the corresponding 1980 field data (late May to mid June), with caged arenas similarly being compared with the later 1980 field data for late June to early July. Average proportions of prey and total densities for the uncaged and caged comparisons are given in Figure 8.1; no statistical analysis was made.

The plant clipping data show that, unless caged, aphid populations on the Chilworth plot were much lower than at the farm site. There was little difference however in composition of prey between the plot and 1980 wheat field. This was ideal experimentally because prey species

Table 8.1 The Growth Stage, average height and average stem density of the wheat crop at the Chilworth 1981 site compared with the S. Allenford farm 1980 field site

	Growth stage of wheat crop	
DATE	FIELD 1980	CHILWORTH 1981
Late May	9 - 10	9 - 10
Early June	10.1 - 10.5	10.1 - 10.5.1
Mid June	10.5.1	10.5.1
Late June	10.5.1 - 10.5.4	10.5.1 - 10.5.4
Early July	11.1	11.1

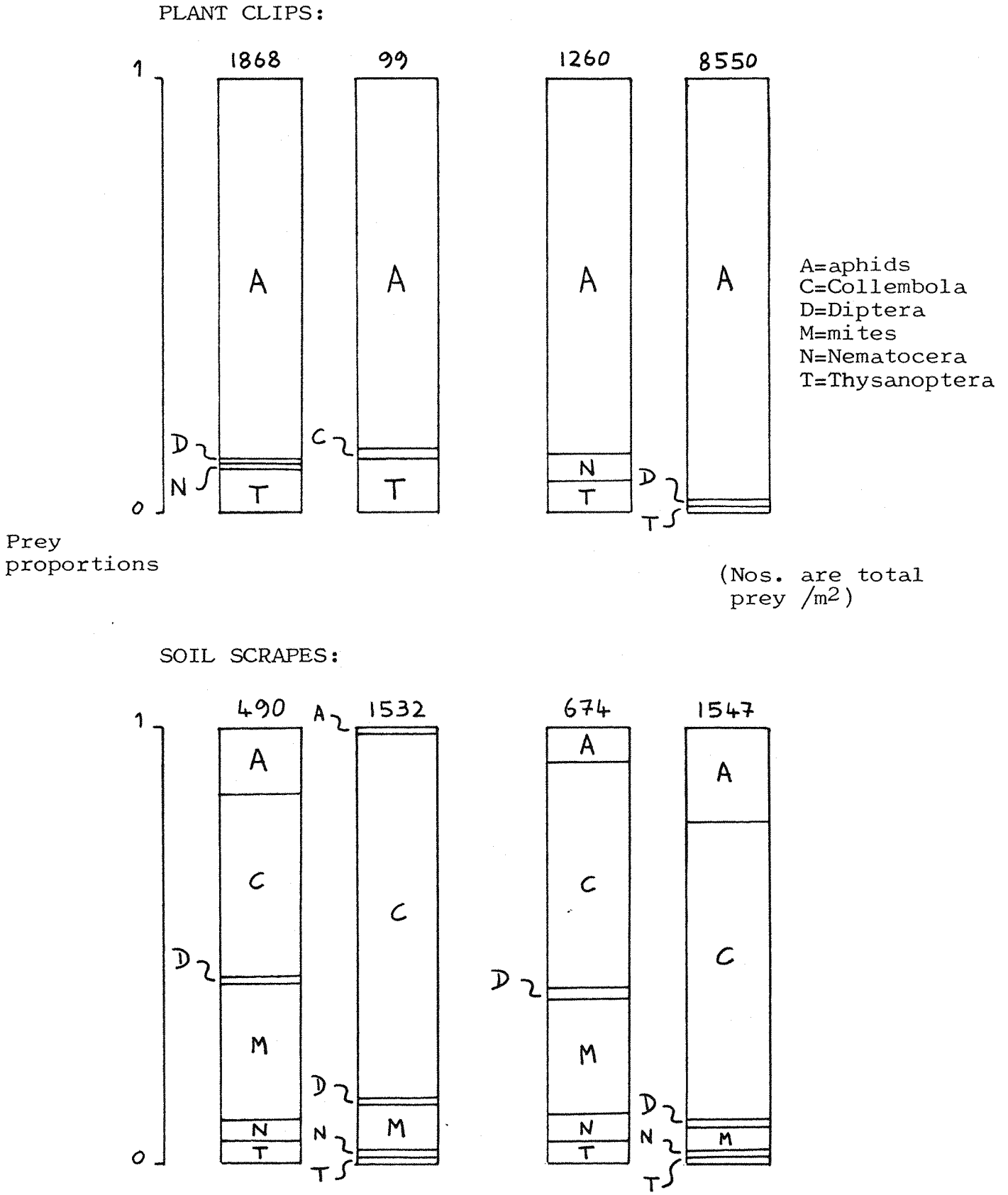
Average height of crop at G.S. 11.1

FIELD 1980: 100 - 110 cm
CHILWORTH 1981: 70 - 80 cm

Average density of stems ($/m^2$) of crop

FIELD 1980: 600
CHILWORTH 1981: 600

Fig. 8.1 The prey composition and density in uncaged and caged arenas in the 1981 wheat plot compared with the 1980 S.Allenford farm field site.



composition could be considered representative of that found in commercially grown wheat, while cages on the plot could be used to create areas of relatively high aphid density.

Soil scraping data showed that there were differences both in composition and density of soil fauna between the Chilworth plots and the S. Allenford field site. With the exception of aphids, which had increased, the prey composition and density in the caged arenas was the same as in the uncaged arenas. Prey composition and density remained the same for the two sample periods in the field 1980 samples revealing some consistent differences between the arenas and the wheat field.

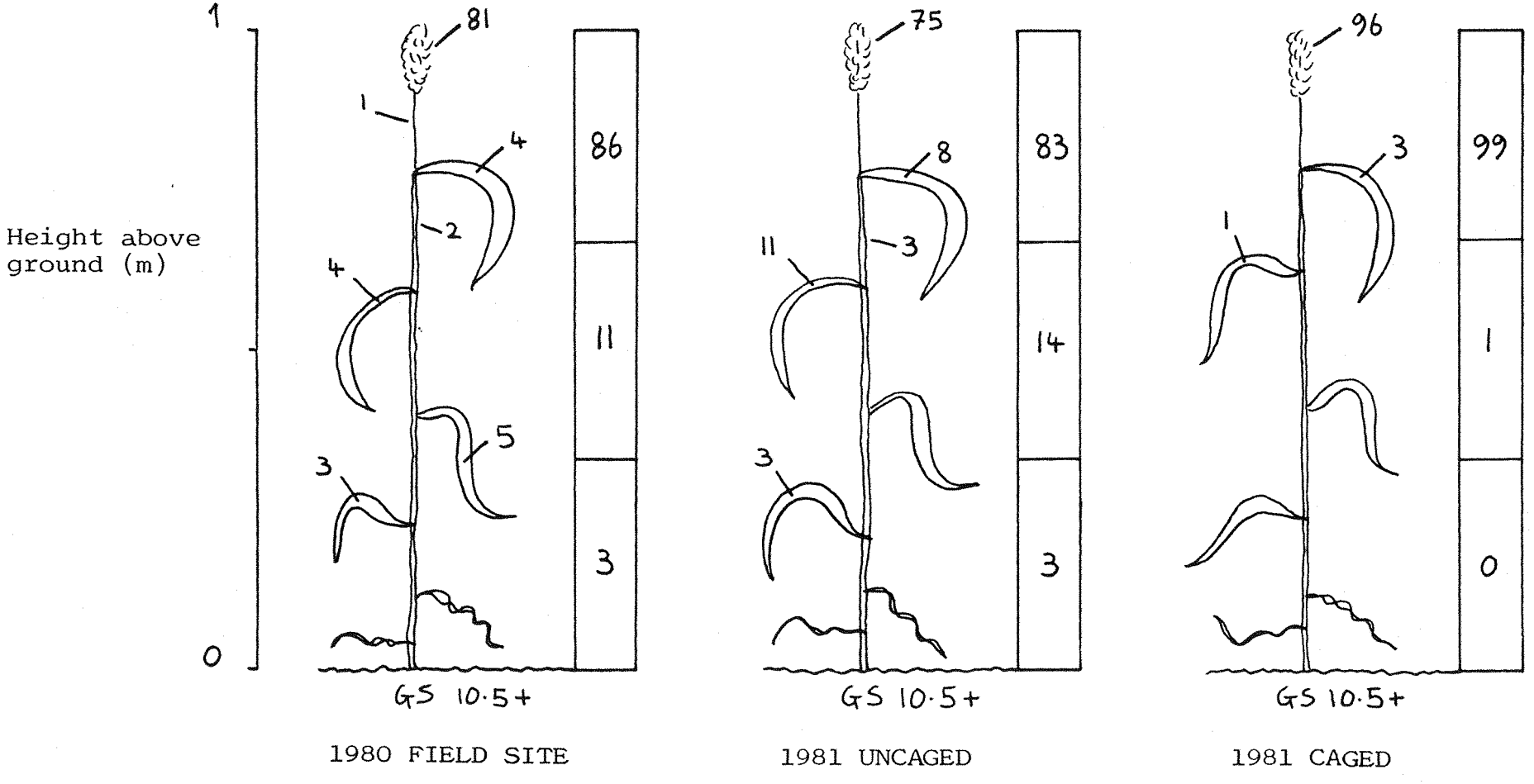
Overall prey density was about three times higher and Collembola a much larger proportion of the prey in the arenas than in the field. Again this was useful experimentally because the two predominant prey items in the diet of field-sampled beetles (Chapter 7.3), aphids and Collembola, were the two predominent prey types in the arenas. Also, because prey density was generally higher, over-exploitation of prey in the beetle observation arenas was unlikely to be a problem. At the consumption rates found in Chapter 4.7, A. dorsale (at a density of 10 beetles per arena) could consume only about 15% of the prey in an arena per day. This combined with the fact that the beetles took only a few days to escape from the arenas but were only replaced once a week means that depletion should have been minimal.

(iii) The distribution of aphids

Field sampling in 1980 showed that about 4% of the aphid population was on the ground at any one time. The samples also showed that by the time A. dorsale arrives in the field most of the aphids (S. avenae) are on the upper part (flag leaf and ear) of the wheat. Samples from the Chilworth plot showed a similar trend in the proportion of the aphid population on the ground. The proportion was high at first (about 20% in late May) but averaged about 8% for the rest of the sample dates (up to early July). Although this proportion is higher than in the field it is difficult to attach significance to this because the mechanism

Fig. 8.2 The distribution of aphids on wheat in uncaged and caged plots at the Chilworth 1981 field site compared with that on wheat at the 1980 S.Allenford farm site.

(Nos. show percentage of aphids found on parts of wheat, bars summarise these individual percentages)



underlying the arrival of aphids on the ground is not fully understood.

The distribution of aphids on the wheat plants in the Chilworth plot was essentially the same as in the field (Fig. 8.2). Aphids were even more concentrated on the head of the wheat plant in the caged arenas probably for two reasons; the cages caused lower leaves on the wheat to senesce at an earlier date and caged samples were taken at a later date (late June, early July) than uncaged samples (late May to mid June). In either case A. dorsale would have to climb up to the flag leaf or head to encounter significant densities of aphids.

(iv) The reproductive state of the A. dorsale population

The A. dorsale introduced to the Chilworth plots had been collected during the previous winter. They were kept in an outside insectary so that natural day length would induce them to mate and develop reproductively in synchrony with field populations. To check that this was so the individuals collected from Chilworth for gut analysis were also examined for reproductive state. Comparisons between males or females from the S. Allenford site and the Chilworth site (Table 8.2) showed no difference in their average reproductive state (see Chapter 7 for the calculation of this). Egg numbers in females at different reproductive states were also similar in the two sites. The differences between the sexes and between the different reproductive stages in voracity (Chapter 4.8) should have produced the same effect at Chilworth as in the field.

Summary

The structure and development of the crop at Chilworth was very similar to commercially-grown wheat. Prey composition and density, although different at Chilworth from the S. Allenford wheat field, should not be so artificial as to invalidate extrapolation of the foraging behaviour of A. dorsale in the arenas to a field situation. Aphid distribution both on the plant and between plant and ground was the same at Chilworth as in the wheat field. Finally the reproductive state of the Chilworth A. dorsale population was the same as that of a natural field population.

Table 8.2 The average reproductive state and average egg numbers of the A. dorsale population introduced to the Chilworth 1981 field site compared with a natural population sampled in 1980.

Average reproductive state

Sample	Early June	Mid June	Late June	Early July
Males				
FIELD 1980	2	2	2	2
CHILWORTH 1981	2	2	2	2.1
Females				
FIELD 1980	3.3	3.5	3.4	4.0
CHILWORTH 1981	3.4	3.6	3.7	4.1

Average egg numbers

♀ Reproductive state	FIELD 1980	CHILWORTH 1981
3	7.3	5.8
4	10.4	10.4
5	2.3	3.2

8.3 Changes in the behaviour of A. dorsale in the observation arena with increasing density

Continuous observation of the behaviour of small invertebrates is time-consuming for the amount of information gathered. As A. dorsale is a small nocturnal beetle it was essential to have a high density of beetles per arena so that time in the field was spent recording data rather than searching for beetles. The density must not be so high however that the behaviour of A. dorsale becomes atypical of the field situation where densities are less than one beetle per m^2 (Chapter 7.2). This section shows that a density of 10 A. dorsale per arena can be used (the equivalent of 40 beetles per m^2) without great changes in behaviour.

(i) The diel activity rhythm

A. dorsale was found to be nocturnally active both in the laboratory (Chapter 3.2) and in the field (Chapter 7.2). The effect of beetle density on this activity rhythm is shown in Figure 8.3; light readings were also taken at ground level in the arena.

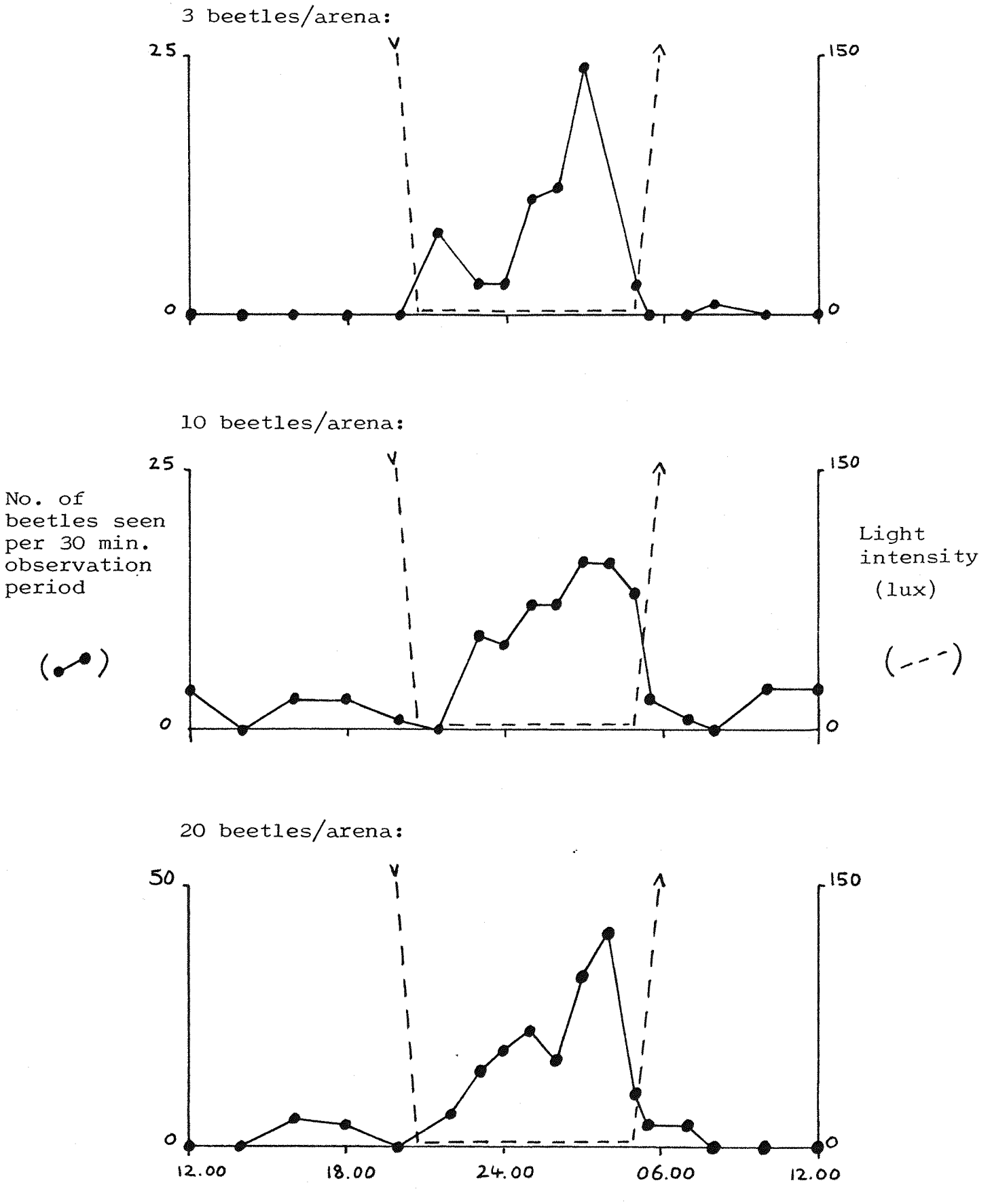
(N.B. In Figure 8.3 the number of beetles observed per 30 min period was taken to be the number entering a chosen quarter of the arena during the 30 min. Hence 24 beetles were observed at 03.00 h even though the total arena density of beetles was three.)

Peak activity was at about 02.00 to 04.00 for all three densities of beetles and although the main activity period was sharply delineated by sunset and sunrise there was more diurnal activity at the two higher beetle densities. The numbers of beetles seen per 30 min suggested that observations could be made throughout the night at any of the three densities.

(ii) The change in behaviour with changing density

During the recording of the above "activity" data the behaviour of each beetle was also noted at the time it entered the "observation area" (see Chapter 2.8). Behaviours were recorded using the categories established in Section 3.4 and used in all subsequent laboratory work.

Fig. 8.3 The diel activity rhythm of A. dorsale at densities of 3, 10 & 20 beetles per observation arena.



In addition individuals were classed as being in the "wall" or the "centre" area of the arena. The Wall area was defined as the strip of bare earth (c. 5 cm wide) around the perimeter of the arena resulting from the digging-in of the arena walls. The Centre area was the rest of the arena where the wheat was undisturbed. It was likely that behaviour would be atypical in the Wall area because individuals were likely to have recently come into contact with the arena walls. The average data for day or night, Wall or Centre are shown in Figure 8.4.

At a density of three beetles per arena no individuals were seen during day-time observations. At night only five observations were made of individuals in the Wall area and there were no observations of individuals coming into contact with each other. For these reasons it was assumed that the behaviour shown in the centre area at this density would be typical of the field situation. Behaviour shown in the Wall area was clearly very different from that in the Centre area.

At densities of 10 and 20 beetles per arena observations were again less frequent during the day (Fig. 8.4) and behaviour was very different from that shown at night. During the day individuals in the Centre area were mostly sitting still while individuals in the Wall area were mostly running; no searching behaviour was shown. At night a larger proportion of individuals were in the Wall area and their behaviour was very different from that shown in the Centre area, with most individuals showing running behaviour. At a density of 10 beetles per arena most individuals in the Centre were searching at night (as at a density of 3 per arena). At a density of 20 beetles per arena the proportion of beetles searching was much smaller (Fig. 8.4).

The differences in behaviour in the Centre area between beetle densities persisted throughout the night (Fig. 8.5). At a density of three A. dorsale per arena most of the night was spent searching; this was also so at a density of 10 per arena. At 20 beetles per arena as many individuals were running as were searching.

The average overnight differences in behaviour between the three densities of A. dorsale are summarised in Figure 8.6. Both in terms of the proportion of individuals in the Wall area and in the proportion of

Fig. 8.4 The difference in behaviour between night and day and the wall and centre areas of the arena at 3 densities of A. dorsale.

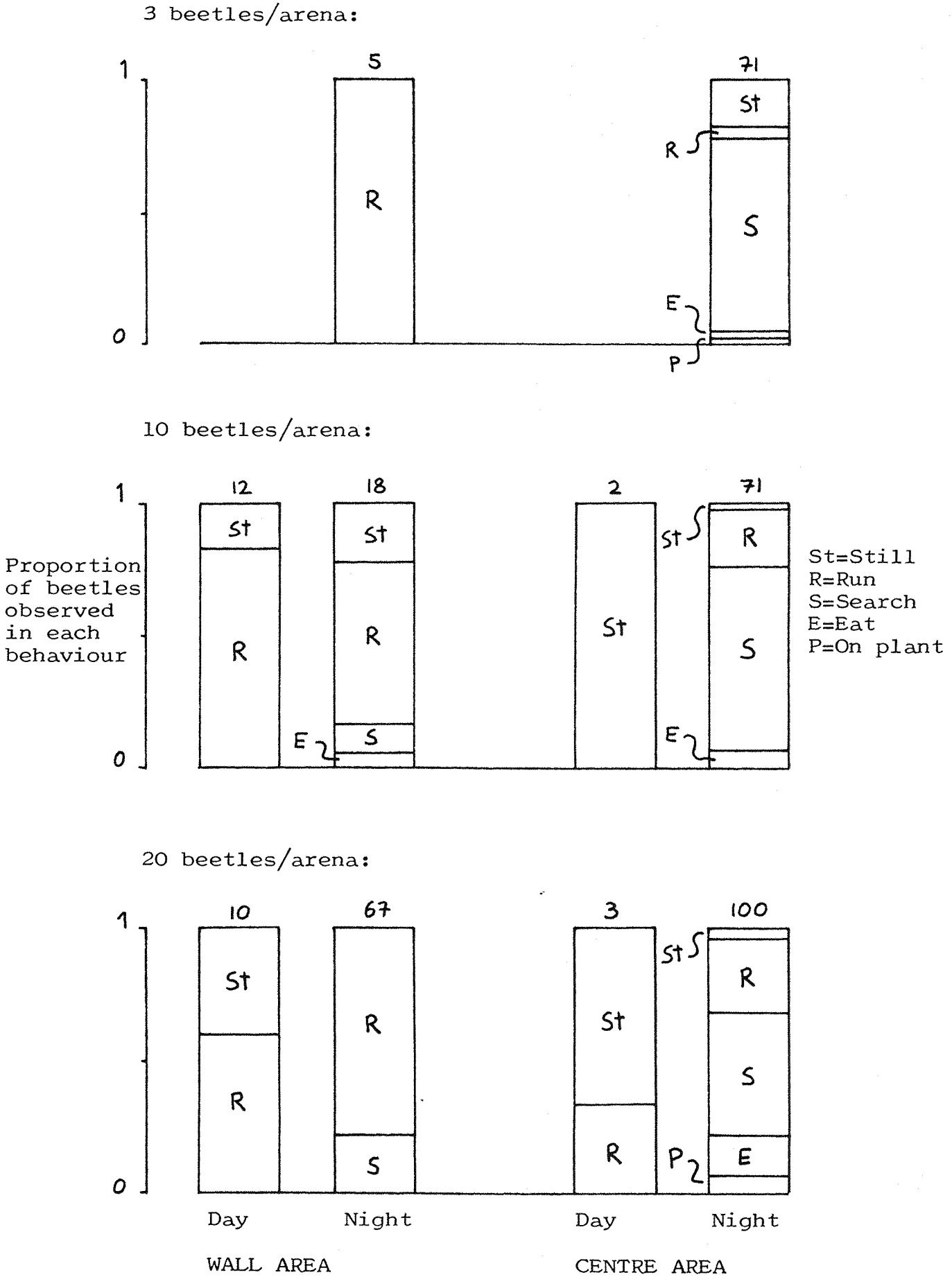


Fig. 8.5 The change in behaviour through the night in the centre arena area at 3 densities of A. dorsale.

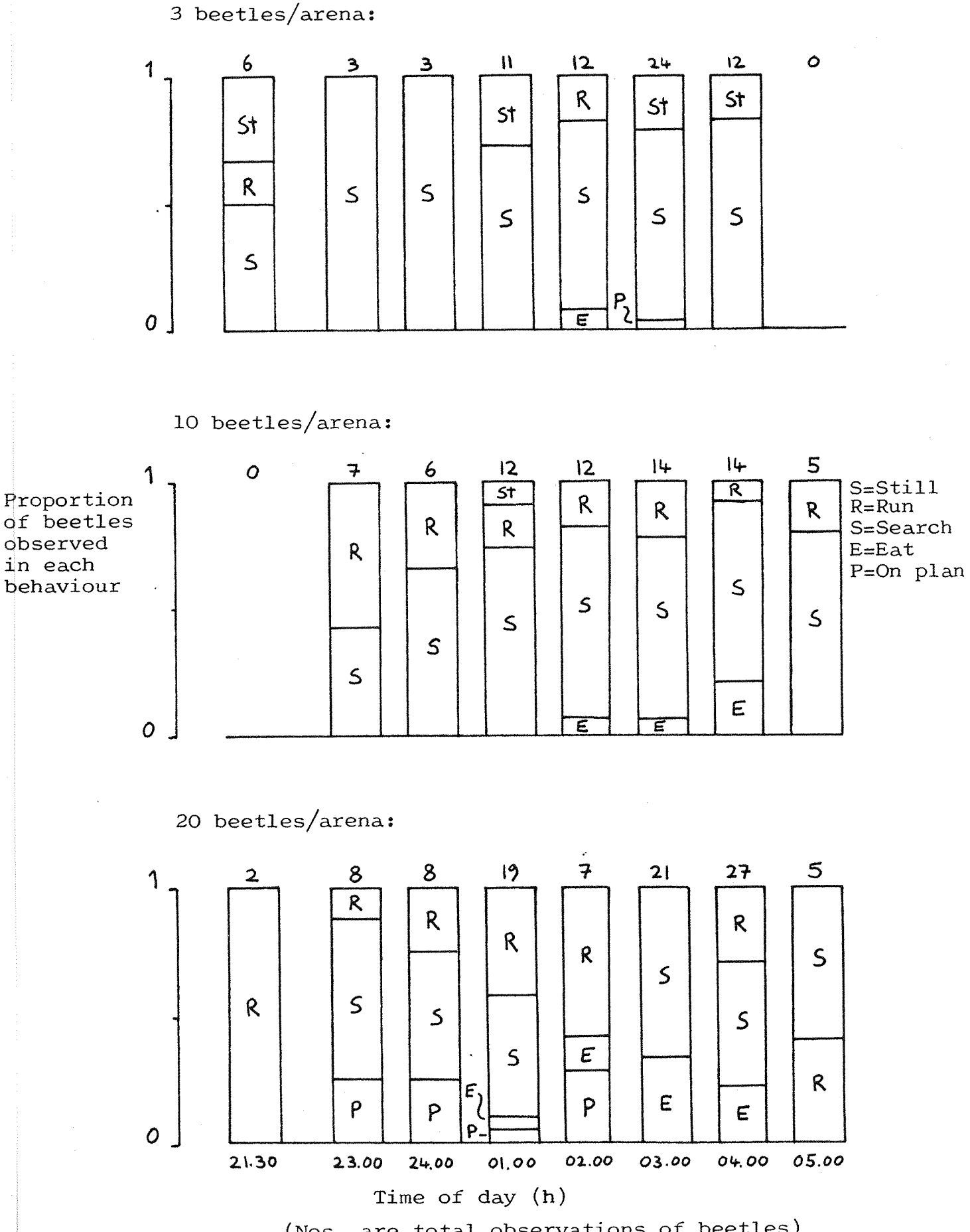
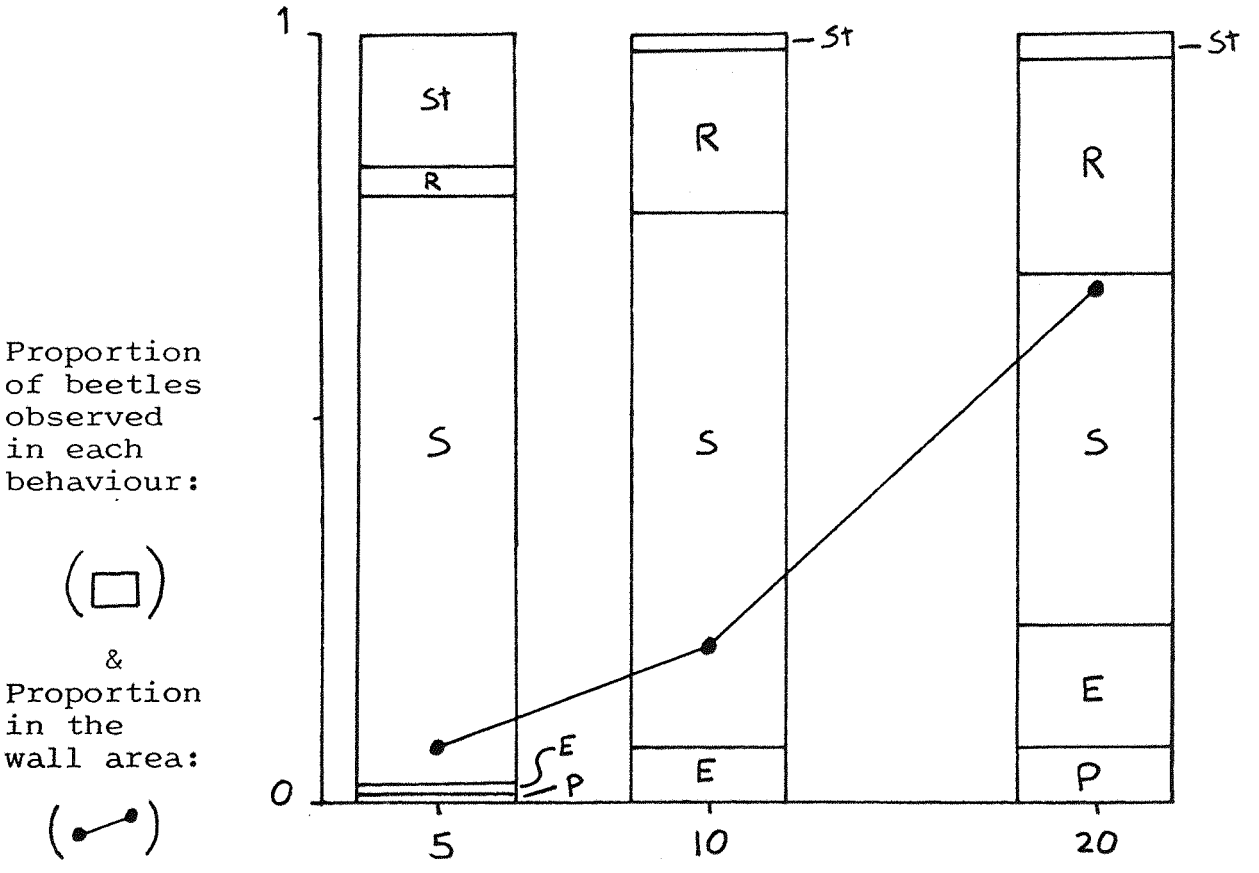


Fig. 8.6 The change in behaviour and proportion of individuals in the wall area with increasing arena density of A. dorsale.

St=Still, R=Run, S=Search, E=Eat, P=On plant.



Kolmogorov-Smirnov 2-sample test.
(on behavioural proportions)

Densities compared	n_1, n_2	p
3 vs 10	71,70	NS
3 vs 20	71,97	$p<0.05$

individuals showing each behaviour type in the Centre area, a large change occurred between a density of 10 and 20 beetles per arena. The change in type of behaviour shown could be tested statistically using the Kolmogorov-Smirnov 2-sample test (Siegel 1956). The proportions of beetles showing each behaviour at a density of three individuals per arena were taken to be typical of the behaviour that would be observed in a wheat field. The proportions observed at a density of 10 or of 20 individuals per arena were then compared with the "field" behaviour recorded with three beetles per arena. Note that because both of these comparisons use the data from the three individuals per arena trial, for statistical rigorousness the probability level of significance should be halved, i.e. $p = 0.05/2 = 0.025$. At a density of 10 beetles per arena there was no difference in the proportions of beetles showing each behaviour from the density of three beetles per arena; at a density of 20 beetles per arena there was a significant difference (Fig. 8.6).

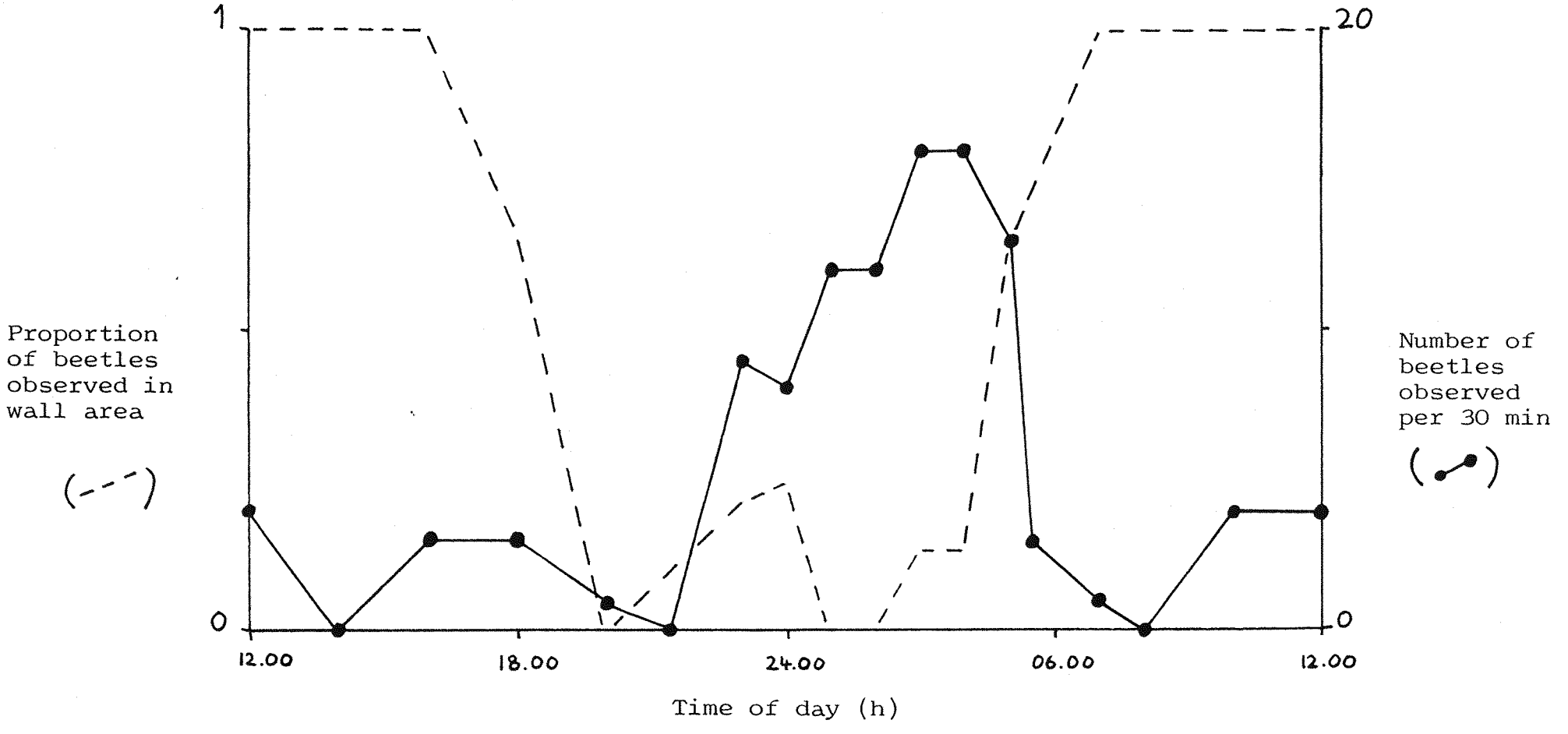
Confirmation that the high density of 10 A. dorsale per arena was not causing individuals to attempt to escape from the arena is shown in Figure 8.7. Although activity is highest at night the proportion of individuals in the Wall area was lowest at this time; the beetles were not so crowded that they were trying to escape from the arena all the time.

Summary

A. dorsale was almost exclusively nocturnally active for all trial densities of beetles per arena. Diurnal behaviour was characterised by being mainly still or running, nocturnal behaviour was mostly searching. Behaviour in the Wall area of the arena was very different from that in the Centre, being mostly running or still. Behaviour changed slightly but not significantly when the density of A. dorsale was increased from 3 to 10 per arena, but there was a significant change when the density was further increased to 20 beetles per arena.

In the following trials, where continuous observation was made of individual A. dorsale behaviour, a density of 10 individuals per arena was used. No observations were made during the day and behaviour in

Fig. 8.7 The change in activity and proportion of beetles in the wall area through the day at a density of 10 A. dorsale per arena.



the Wall area was not included in the data presented. The proportion of individuals in the Wall area was recorded throughout the observation period as this seemed to be a convenient measure of whether overall behaviour patterns were changing (Fig. 8.6).

8.4 The change in the foraging behaviour of A. dorsale between areas of low and high aphid density

This Section comprises the main body of observational work in which individual beetles were watched for a maximum of 30 min each but were usually lost before this time elapsed. All trials were with a density of 10 A. dorsale per arena. The low aphid density trials ran from late May to mid June and the high aphid density trials from late June to early July.

Two main questions were asked:

What is the general behavioural time budget of A. dorsale in the wheat field environment?

How does the behaviour of A. dorsale change between areas of high and low aphid density?

In general, statistical analysis of results was of proportions of time spent in each behaviour only. The actual times from different observational periods could not be used because they were affected by several factors which were difficult to allow for: beetles gradually escaped from the observation arenas so that the total observation time was likely to be less at the end of a 3-day experimental period than at the beginning; on some nights there was heavy rain while others were so dry there was hardly any dew, and so on. There was not enough time to collect data to show the effect of these variables so analysis could only be in terms of proportion of time spent in each behaviour.

(i) Climate data

During observation periods the daily maximum and minimum temperatures on the ground in the arenas were recorded. These temperatures were then correlated with daily maximum and minimum temperatures

recorded at Hurn weather station (N.G.R. SU115980). Both the daily maxima and minima correlated significantly between the two sites ($r = 0.657$, d.f. = 1,8, $p < 0.05$ and $r = 0.733$, d.f. = 1 & 15, $p < 0.001$ respectively). As temperature was likely to be the most variable weather statistic between the two sites it was assumed that as it correlated well other weather statistics would also be comparable.

The weekly averages for the six main climate statistics are shown in Figure 8.8; the hatching in the diagram shows above average values for the 7 wk experimental period. Superficial examination of these data suggests the following overall picture. Rainfall was heavy in the first 4 wk and the overcast skies led to mostly very warm nights. As rainfall ceased in later weeks the skies cleared, wind speed dropped and night temperatures were much lower, particularly in early July.

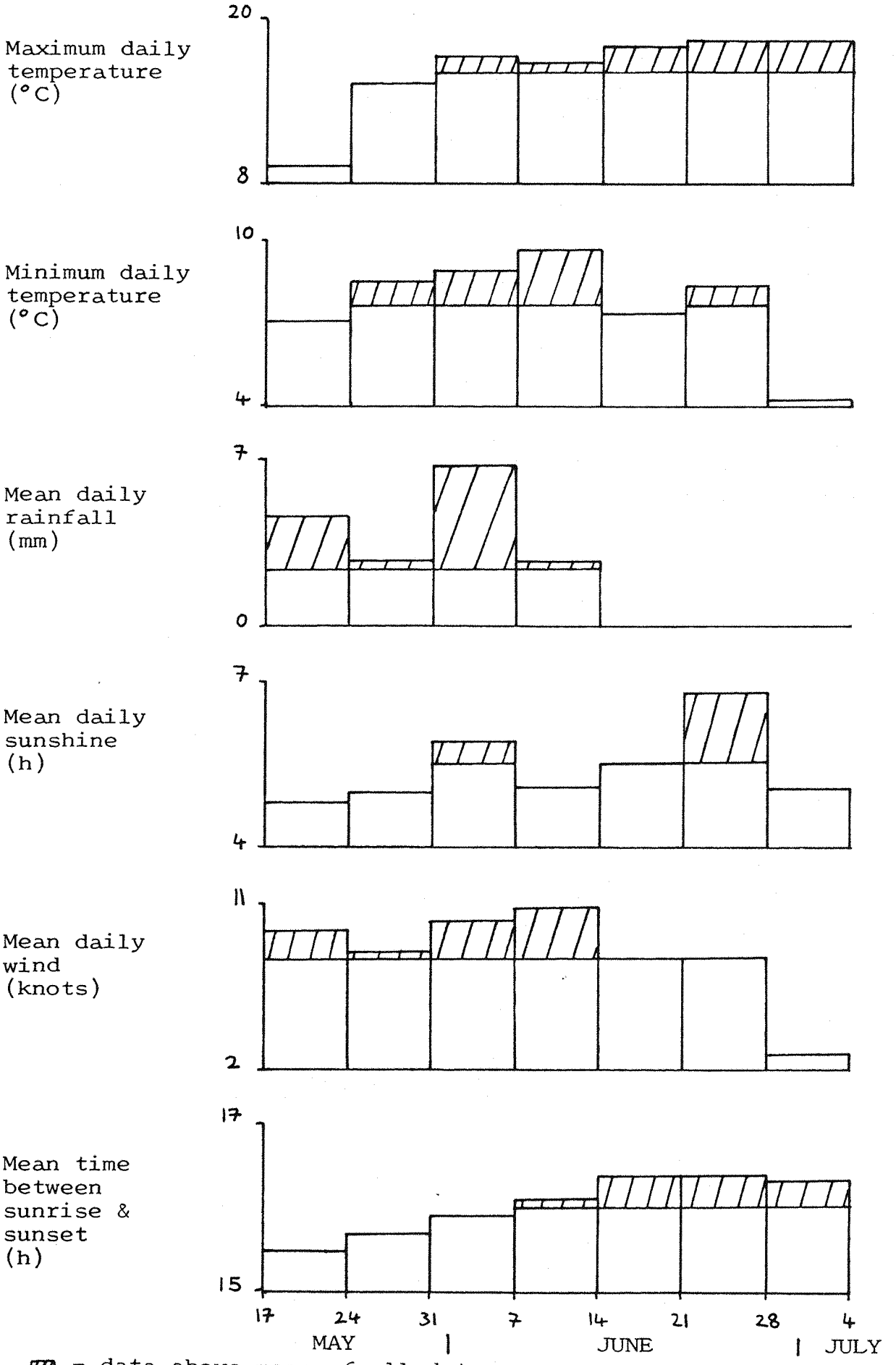
Climate data will be referred to in interpreting changes in activity or foraging behaviour that are not obviously related to changes in prey (especially aphid) abundance.

(ii) The proportion of individuals and time spent by individuals in the Wall area of the arena

The initial observations of A. dorsale behaviour (8.3) showed that behaviour in both the Wall and the Centre areas of the arenas changed with density. The proportion of individuals in the Wall area of the arena was an indicator of this change in behaviour: the higher the density of beetles in the arena, the more time they spent running and the more often they arrived in the Wall area.

The proportion of individuals and the proportion of time spent by individuals in the Wall area were recorded on each observation night. These proportions were then used as crude indicators of whether the behaviour of A. dorsale was changing over the observation period as a whole, i.e. from Figure 8.6, if the proportion of individuals in the Wall area was much above 0.2 then behaviour was likely to be changing from that shown during the initial trials.

Fig. 8.8 The change in 6 weather statistics during the 1981 period of field observation of A. dorsale.



▨ = data above mean of all data for 17th May - 4th July

These data for the observational period are shown in Figure 8.9 and as might be expected, changes in the proportion of time spent by individuals in the Wall area mirror changes in the actual proportion of individuals in the Wall area. The mean proportion of time spent in the wall area was 0.12 while the mean proportion of individuals was 0.25. Although the mean proportion of individuals entering the Wall area was higher than the 0.2 criterion established in Section 8.3, the difference is small compared with the value of 0.6 which reflected the significant change in behaviour when A. dorsale was at a density of 20 per arena. It was assumed that overall behaviour was consistent for all observation periods.

The only wide fluctuations in the proportions were over the period of 1 - 3 June; reference to the climate data (Fig. 8.9) shows that rainfall during this period was very high. The rain fell during the night and was probably directly responsible for these fluctuations in beetle behaviour. The mechanism by which rainfall affected the behaviour of A. dorsale is not known; rain drops rarely hit the ground directly but splashing from the wheat may have disturbed the beetles.

(iii) Behaviour on the ground and on the wheat

Behaviours were divided into the categories used in Chapter 3.4 and presented as proportion of total time spent in each behaviour by all beetles observed on each sample night. Figures 8.10 and 8.11 present the average proportions for each of the sample weeks for behaviours on the ground and on the plant respectively. In Figure 8.10 plant behaviours are combined to give a single "On plant" category.

Comparisons were made of the proportion of time spent in each behaviour per night, between the low aphid density arena (uncaged) and the high aphid density arena (caged), using the Mann-Whitney U-test (Siegel 1956). This unmatched sample test was used because only six nights of observation were possible in the caged arena while 12 nights of observations were made in the uncaged arena. The results of these tests are shown in Table 8.3.

Fig. 8.9 The change in the proportion of observed beetles and time spent in the wall area through the season.

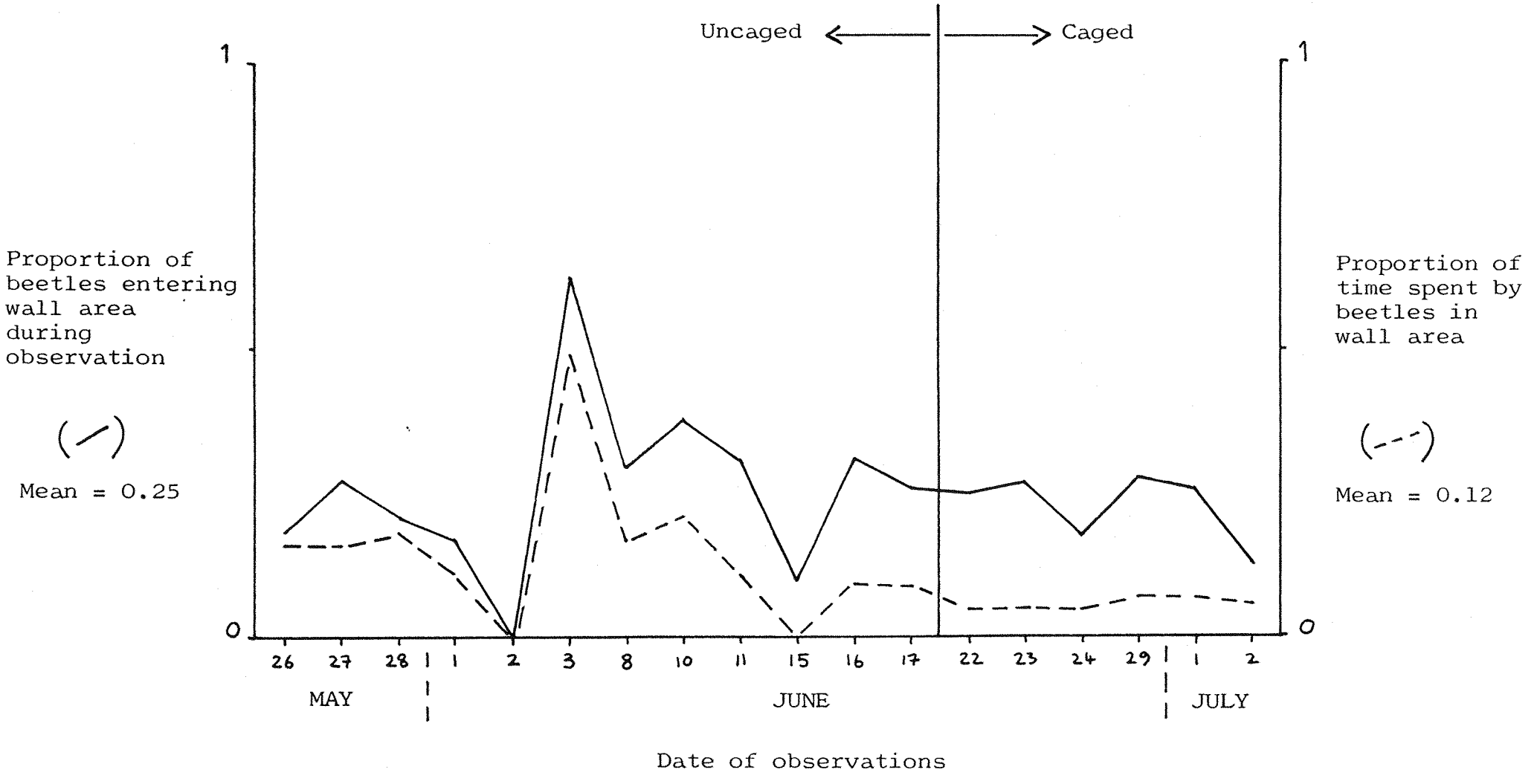


Fig. 8.10 The average proportion of time spent in each behaviour on the ground or "on plant" by A. dorsale for the 6 sample weeks of the Chilworth 1981 season.

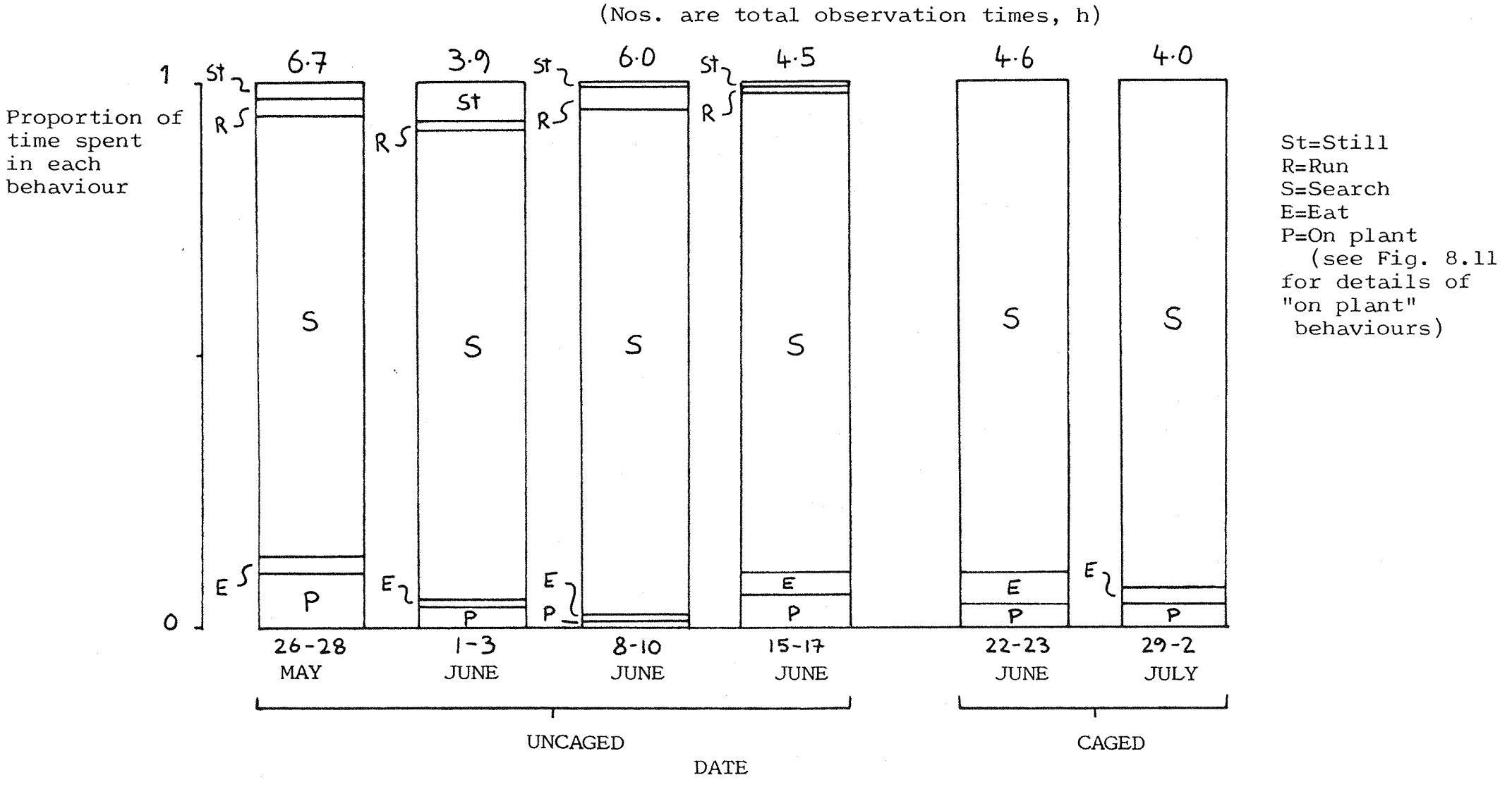


Fig. 8.11 The average proportion of time spent in each behaviour on the plant by A. dorsale for the 6 sample weeks of the Chilworth 1981 season.

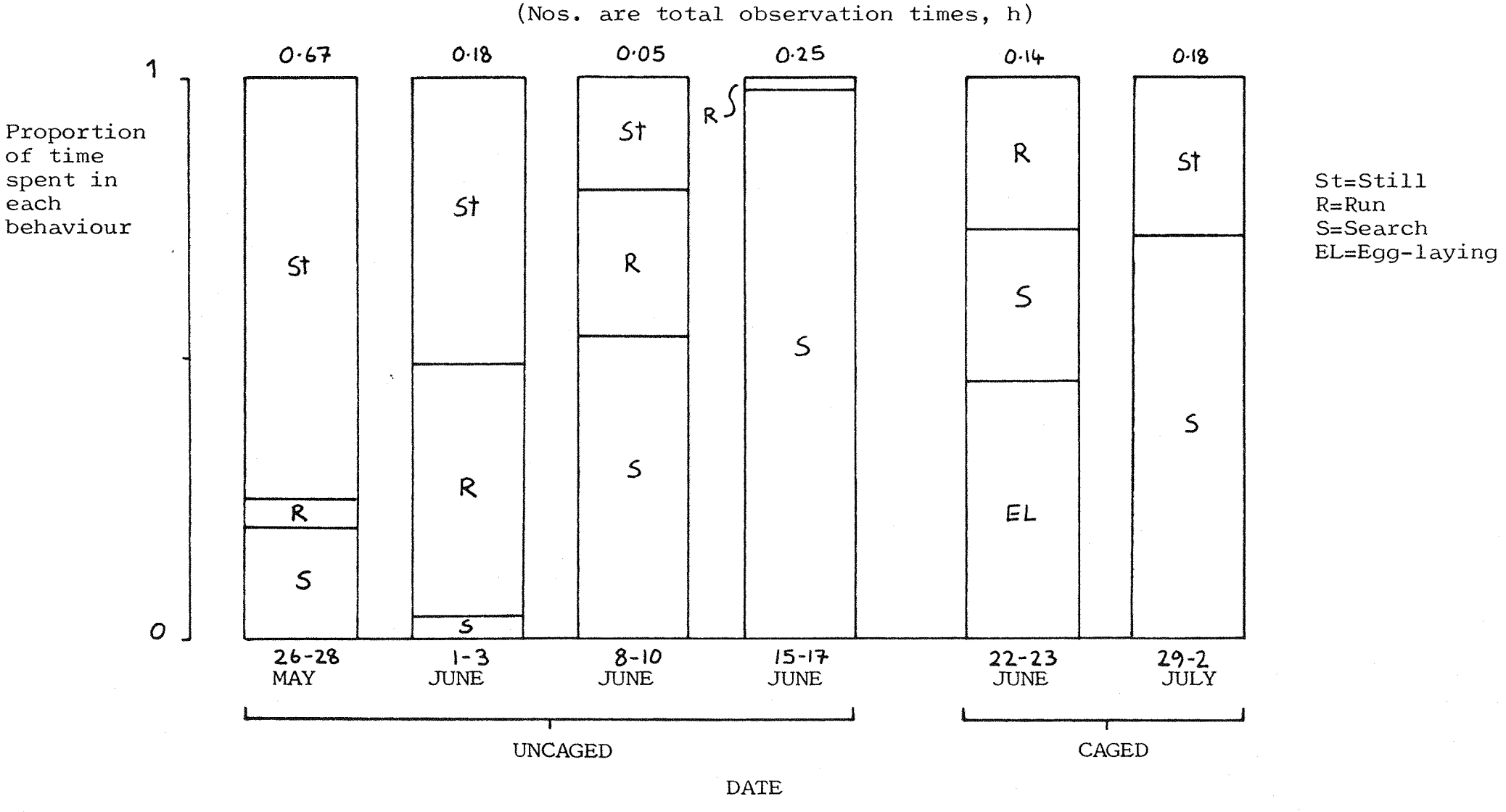


Table 8.3 The results of Mann-Whitney U-tests comparing proportion of time spent in each behaviour in areas of low and high aphid density

	Behaviour compared	Significance
Ground behaviours (as a proportion of total observation time)	Still	$p < 0.05$
	Run	$p < 0.05$
	Search	NS
	Eat	NS
	On plant	NS
Ground behaviours (as a proportion of ground observation time)	Still	$p < 0.05$
	Run	$p < 0.05$
	Search	NS
	Eat	NS
Plant behaviours (as a proportion of total observation time)	Still	NS
	Run	NS
	Search	NS
Plant behaviours (as a proportion of plant observation time)	Still	NS
	Run	NS
	Search	NS

(For all tests $n_1 = 6$, $n_2 = 12$)

The only significant differences between the high and low aphid density arenas were that a higher proportion of time was spent either still or running in the low aphid density arena. As Figure 8.10 shows both of these categories formed a very low proportion of the total observation time making the importance of this difference minimal.

None of the more important categories, search, eat and "on plant", changed between the low and high aphid density arenas. There was no difference in the on-plant behaviour between low and high aphid density either.

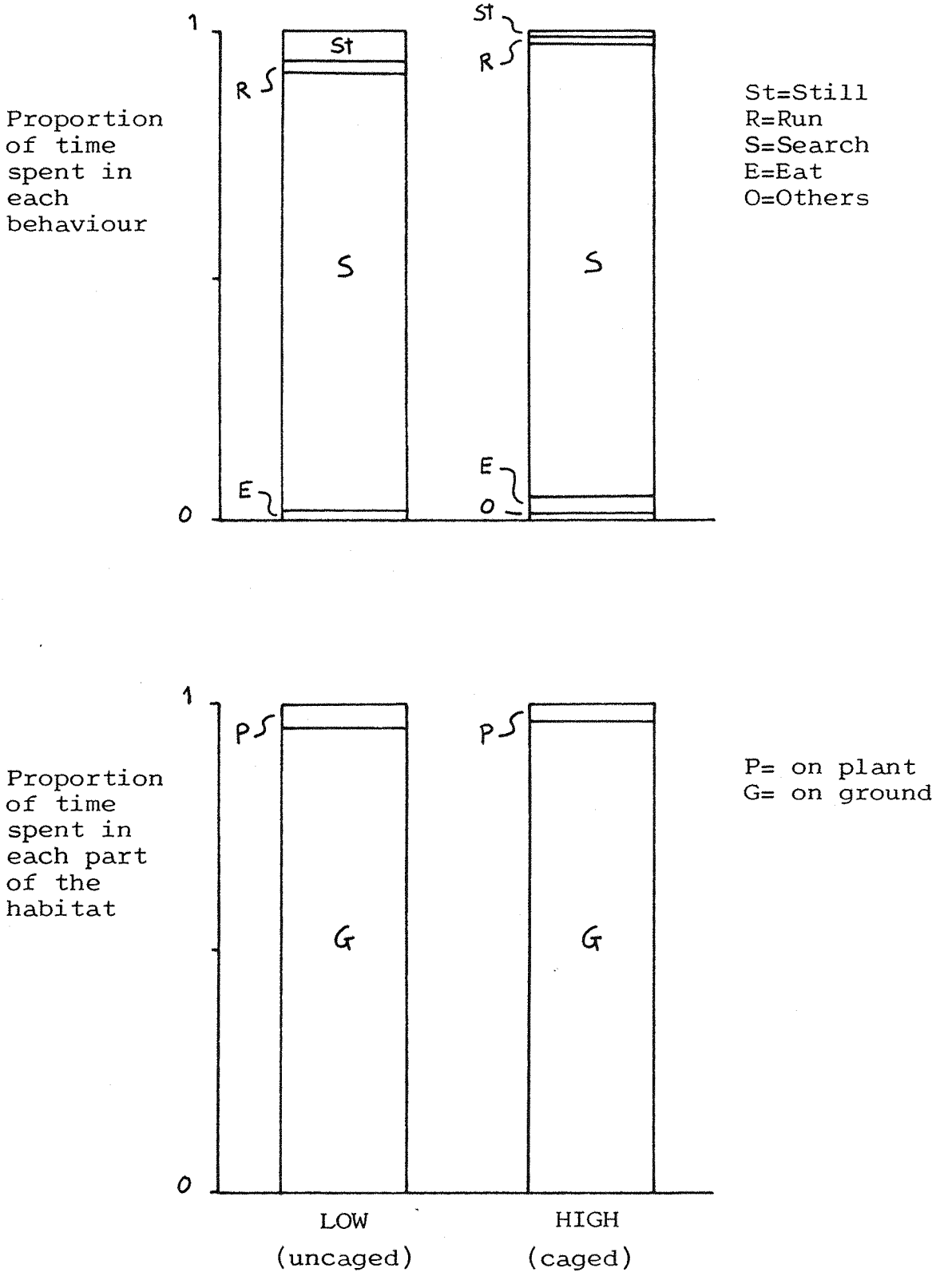
The proportions of time allocated to each behaviour (for ground and plant combined) and to each area (plant or ground) are summarised for the low and high aphid density arenas in Figure 8.12 . Nearly all of the period of nocturnal activity of A. dorsale was spent searching for prey and this did not change with aphid density. Nearly all the time was spent on the ground and again this did not change with aphid density.

Although this is strong evidence that A. dorsale does not respond to increased aphid density by spending more time on the wheat there are three points that need to be checked to confirm this hypothesis.

The data have been analysed as proportions and although A. dorsale may not have increased the proportion of time it spent on the plants, it may have increased the actual time spent on the plant by increasing the total period of nocturnal activity. Figure 8.10 shows that this did not happen; since A. dorsale was limited in activity to the hours of darkness (this was rechecked in early July) the total observation hours reflect the total activity time of A. dorsale. This activity time actually gets shorter in the caged arenas not longer.

N.B. The total period of observation of behaviour was quite short on each night (about 1.7 h) because a substantial amount of time was occupied by ensuring that the wheat was searched by the observer as rigorously as the ground (see Chapter 2.8, Materials and Methods). Also comparison between the climate data (Fig. 8.8) and Figure 8.10

Fig. 8.12 The average proportion of time spent in each behaviour and on the wheat or on the ground by A. dorsale in a low or high aphid density arena.



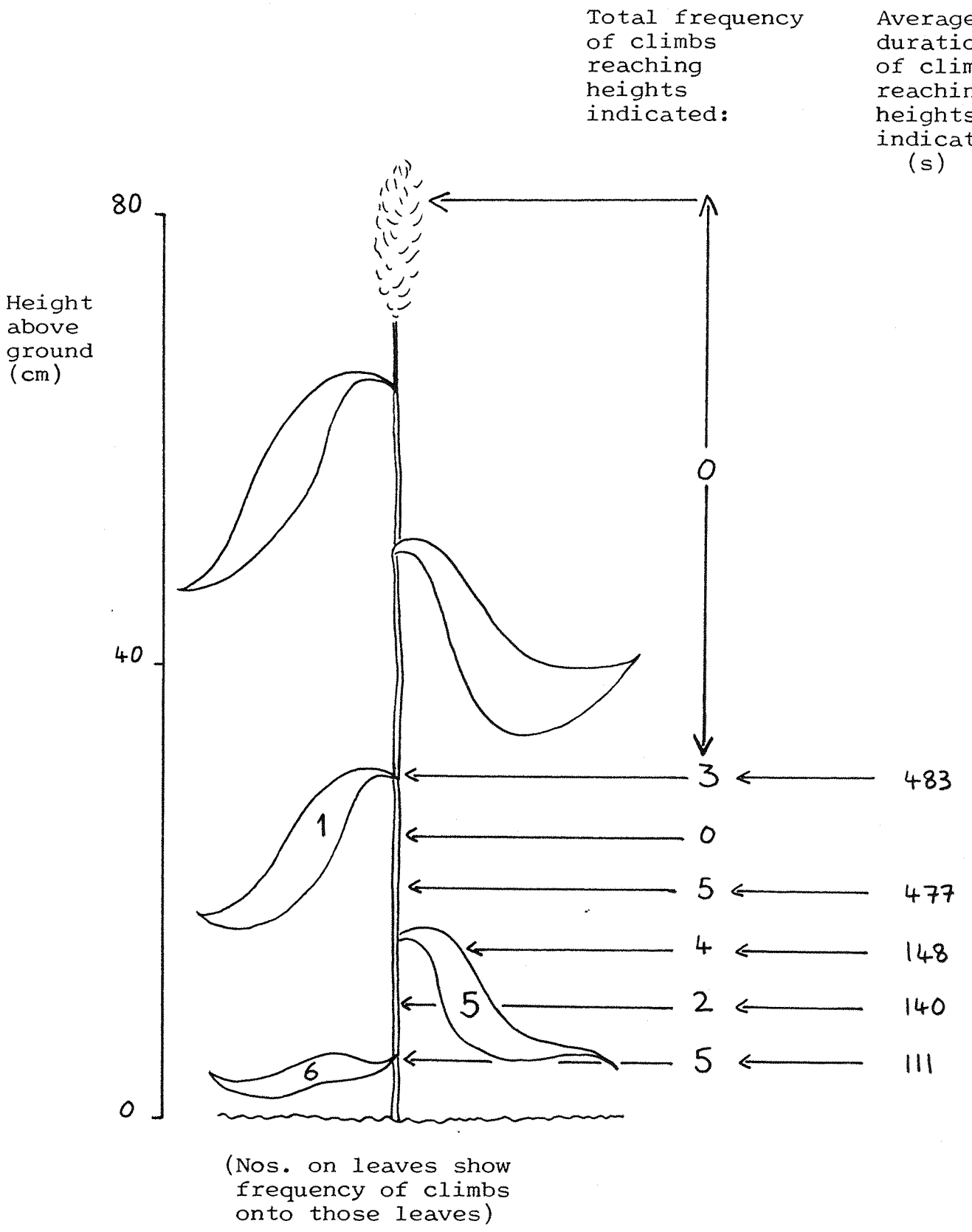
shows that the longest total weekly observation times occurred only when average night minimum temperatures were high (over 8°C) and average rainfall was low (below 3 mm) for that week.

Although the time spent on the plant was short so was time spent eating, so A. dorsale may still have eaten aphids on the wheat despite spending only short periods there. There are two forms of data which show this to be unlikely or of little consequence. Firstly A. dorsale was never seen to eat or encounter prey on the wheat; to be an efficient aphid predator it should have spent nearly all of its short time on the wheat feeding. Secondly the heights and durations of climbs by individuals were recorded and are summarised for both low and high aphid density arenas (Fig. 8.13). The data were combined because the Mann-Whitney U-test showed that there was no significant difference between low and high aphid density for height or duration of climbs (where $n_1 = 4$, the number of observed climbs in the high aphid arena and $n_2 = 15$, the number of climbs in the low aphid arena). Referral to the distribution of aphids on the wheat in the two types of arena (Fig. 8.2) shows that nearly all the aphids were on the flag leaf or higher. From Figure 8.13 it is clear that none of the beetles climbing in the caged arena would have reached high enough to encounter aphids. In the uncaged arena only the 5% of beetles reaching the third leaf would have encountered aphids and even they would have encountered only 3% of the total aphid population.

(As might be expected, the duration of climbs increased with the height of the climb and one of the longest climbs (in time) was made by a female to deposit an egg on the wheat stem at 15 cm up. This single observation indicates that the egg laying behaviour of female A. dorsale is also unlikely to increase their encounter rate with aphids.)

Finally, fieldwork has shown that an increasing proportion of A. dorsale sampled from the field contained aphids as the field density of aphids increased (Chapter 7.3). The combination of this information with field sampling data showing that a constant proportion of aphids are present on the ground (Chapter 7.3), and laboratory behavioural

Fig. 8.13 The frequency distribution and duration of climbs up wheat stems in the arenas at the Chilworth 1981 site.



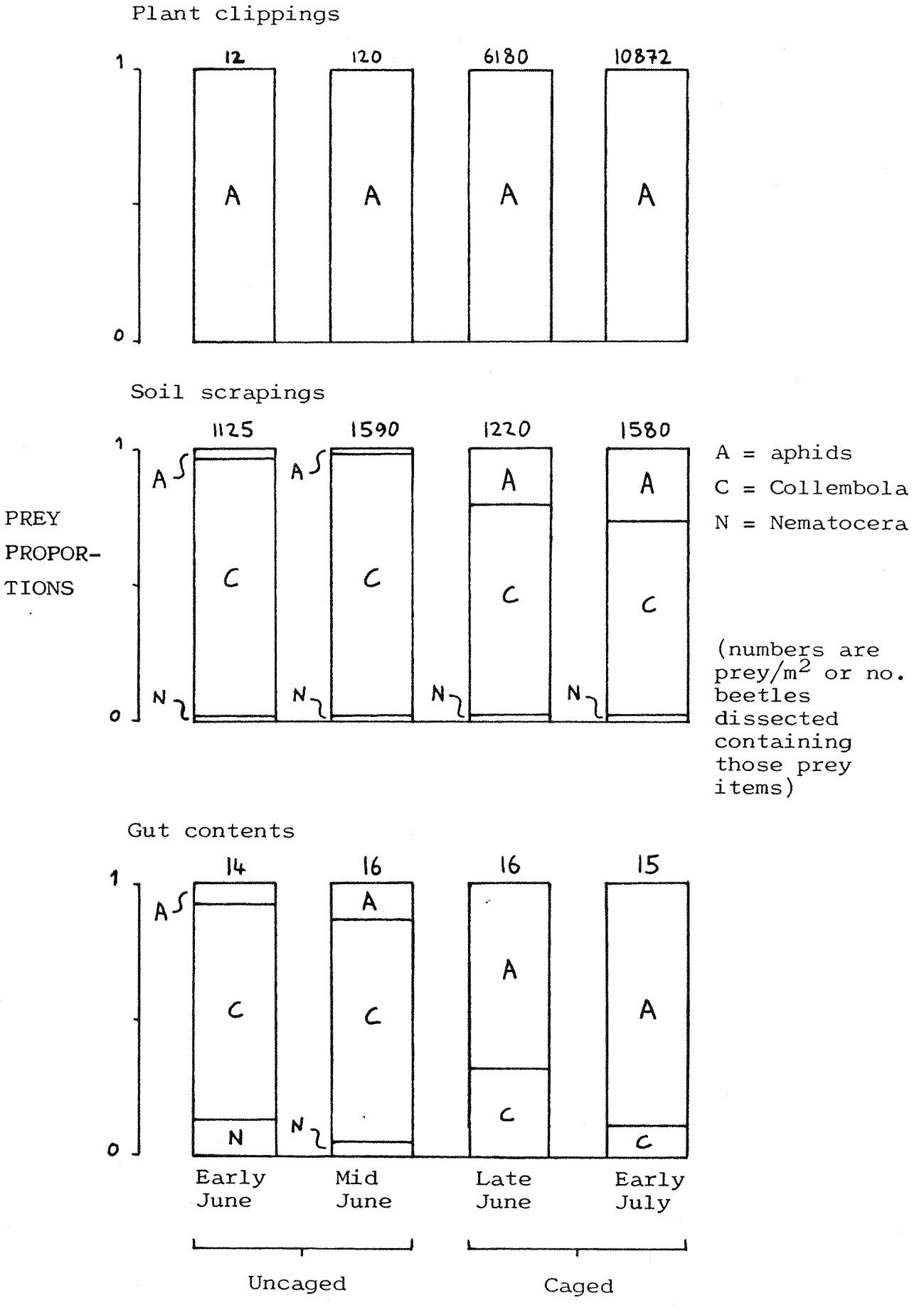
studies showing that A. dorsale hardly ever climbed (Chapter 5.6), suggested strongly that the beetle was eating aphids that it encountered on the ground. The work of this Chapter has shown that A. dorsale was unlikely ever to encounter aphids on the plant and that it did not respond to increased aphid density with increased climbing. Sampling in the Chilworth plot showed that the density of aphids on the ground was much higher in the caged than the uncaged plots. If this system fully mirrored the field system then the A. dorsale in the high aphid density arenas should have eaten more aphids than the beetles in the low aphid density arenas.

It was not possible to observe directly which prey were taken by A. dorsale. Instead about 30 individuals had to be introduced into separate high or low aphid density arena and collected 2 days later to be dissected in the laboratory. There were only sufficient beetles to do this a total of four times. Remains in the gut were visually identified and as with A. dorsale sampled from S. Allenford farm (Chapter 7.3) three prey types were predominant; aphids, Collembola and Nematocera. In the four samples of A. dorsale that could be taken for gut dissection these three types made up over 90% of the gut contents, so only these prey types are referred to from now on.

The proportions of prey available on the wheat and on the ground are shown with the proportions of prey in the gut in Figure 8.14. As expected there was no obvious relationship between the gut contents of A. dorsale and the prey on the wheat. There were, however, some clear links between the prey in the gut contents of A. dorsale and the prey available on the ground. As aphids increased (density or proportion) on the ground they increased (frequency or proportion) in the gut contents and the same trend was apparent for Collembola. Nematocera were too low in numbers for any trend to be apparent.

Analysis of these results was made by correlating the frequency or proportion of prey in the gut on each sample date with the density or proportion of prey on each sample date. This meant that each correlation consisted of four points only (the four sample dates in Figure 8.14). The small sample size results from the gut data being

Fig. 8.14 The proportions of the three main prey types available on the wheat, on the ground and found in the gut contents of A. dorsale through the Chilworth 1981 field season.



qualitative only (i.e. each prey item was present or absent in the gut) and no other statistical analysis could be applied to the data because of this.

Correlative analysis was used to establish two points:

As aphid density or proportion increased on the ground the frequency or proportion of aphids in the gut contents of A. dorsale increased.

A. dorsale was foraging like a random predator and not like a predator specialising on aphids.

The correlations and significance levels are summarised in Table 8.4 for both of these analyses.

To establish the first point it was assumed that A. dorsale would respond directly to the density of aphids on the ground or to the proportion that aphids formed of all prey on the ground. This means that for the former

frequency of aphids in gut	vs.	density of aphids on ground

should correlate, or for the latter

proportion of gut contents that are aphids	vs.	proportion of ground prey that are aphids

should correlate.

In fact both give significant positive correlations (see upper half of Table 8.4) showing that A. dorsale did eat more aphids as aphid density on the ground increased. This is final confirmation that the Chilworth arena system behaved like the wheat field system; a substantial proportion of A. dorsale can contain aphid remains without ever having encountered aphids on the wheat.

Table 8.4 Correlative analysis relating prey availability in the Chilworth arenas to prey in the gut contents of *A. dorsale* foraging in those arenas.

Aphid feeding only

Quantities correlated			r	Significance of r
Frequency in gut	vs	Density in field	0.957	$p < 0.05$
Proportion in gut	vs	Proportion in field	0.985	$p < 0.02$

Foraging models

	Uncorrected	Capture rate corrected
	(Significance of r)	
Numbers model		
Aphids (Normal)	$p < 0.05$	$p < 0.02$
(log)	$p < 0.05$	$p < 0.05$
Collembola	NS	NS
Nematocera	NS	NS
Average r-value	0.319	0.172
Proportions model		
Aphids	$p < 0.02$	NS
Collembola	$p < 0.01$	NS
Nematocera	NS	NS
Average r-value	0.843	0.849

(d.f. = 2 for all correlations)

The prey availability and gut content data from the 1980 S. Allenford farm fieldwork were used to show wheather A. dorsale was responding directly to the density of aphids in the field (the "Numbers model") or taking aphids in the proportion presented to it (the "Proportions model") (see Chapter 7.3). In addition, the prey data fed into these two models were also corrected for the temperature-dependent success with which each prey type was captured by A. dorsale (Chapter 6.7). This capture success correction was used because the laboratory work of Chapter 6.7 showed it to be the single most important factor governing the relationship between prey appearing in the gut contents of A. dorsale and prey availability.

The details of the way in which data were prepared for the two models are given in Chapter 7.3 so only the bare essentials are given here.

For the Numbers model to fit the prey availability and gut data the following three correlations must all be significant at $p < 0.05$:

1. Frequency of aphid remains in gut contents vs. Density of aphids on ground

   (this relationship could be linear or curvilinear so the correlation was performed with normal and logged axes)

2. Proportion Collembola form of gut contents containing Collembola & Nematocera vs. Proportion that Collembola form of the total density of Collembola & Nematocera on the ground

3. Proportion Nematocera form of gut contents containing Collembola & Nematocera vs. Proportion that Nematocera form of the total density of Collembola & Nematocera on the ground

i.e. A. dorsale "chooses" aphids but forages "randomly" on Collembola and Nematocera.

For the Proportions model to fit, these three correlations must all be significant at $p < 0.05$:

1.	Proportion aphids form of gut contents containing aphids + Collembola + Nematocera	vs.	Proportion that aphids form of the total density of aphids + Collembola + Nematocera on the ground
2.	Proportion Collembola form of gut contents containing aphids + Collembola + Nematocera	vs.	Proportion that Collembola form of the total density of aphids + Collembola + Nematocera on the ground
3.	Proportion Nematocera form of gut contents containing aphids + Collembola + Nematocera	vs.	Proportion that Nematocera form of the total density of aphids + Collembola + Nematocera on the ground

i.e. A. dorsale takes all three prey types "randomly"; there is no element of choice.

The fit of these two models both for uncorrected and Capture-rate-corrected data is given in Table 8.4 (lower half). Using the criterion that all three correlations must be significant the fit of the Numbers model was always poor. Aphids correlated significantly but the overall fit (shown by the average of the three correlation coefficients) was not good.

The uncorrected data fitted the Proportions model with good correlations for aphids and Collembola but the fit for Nematocera was poor. The corrected data did not give significant correlations for any of the prey types but gave a better overall fit because the r-value for Nematocera was much higher than with uncorrected data.

With the provisos that correlations are not proof of a causitive link, and that to use so many correlations means that some will be significant just by chance alone, it is clear that the Proportions

model provides the best fit to the data. This is the same conclusion as reached for this analysis using field data in Chapter 7.3. This is a field-based confirmation of the laboratory findings of Chapter 6 that A. dorsale is a general predator, neither optimally foraging nor specialising on cereal aphids, but taking prey in the proportions presented to it.

8.5 The fate of aphids arriving on the ground

If A. dorsale consumes aphids only on the ground then the way in which aphids arrive on the ground and what happens to them in the absence of predators becomes very important in deciding the biological control potential of A. dorsale. There are two basic systems which include the arrival of aphids on the ground, but they have very different implications for biological control:

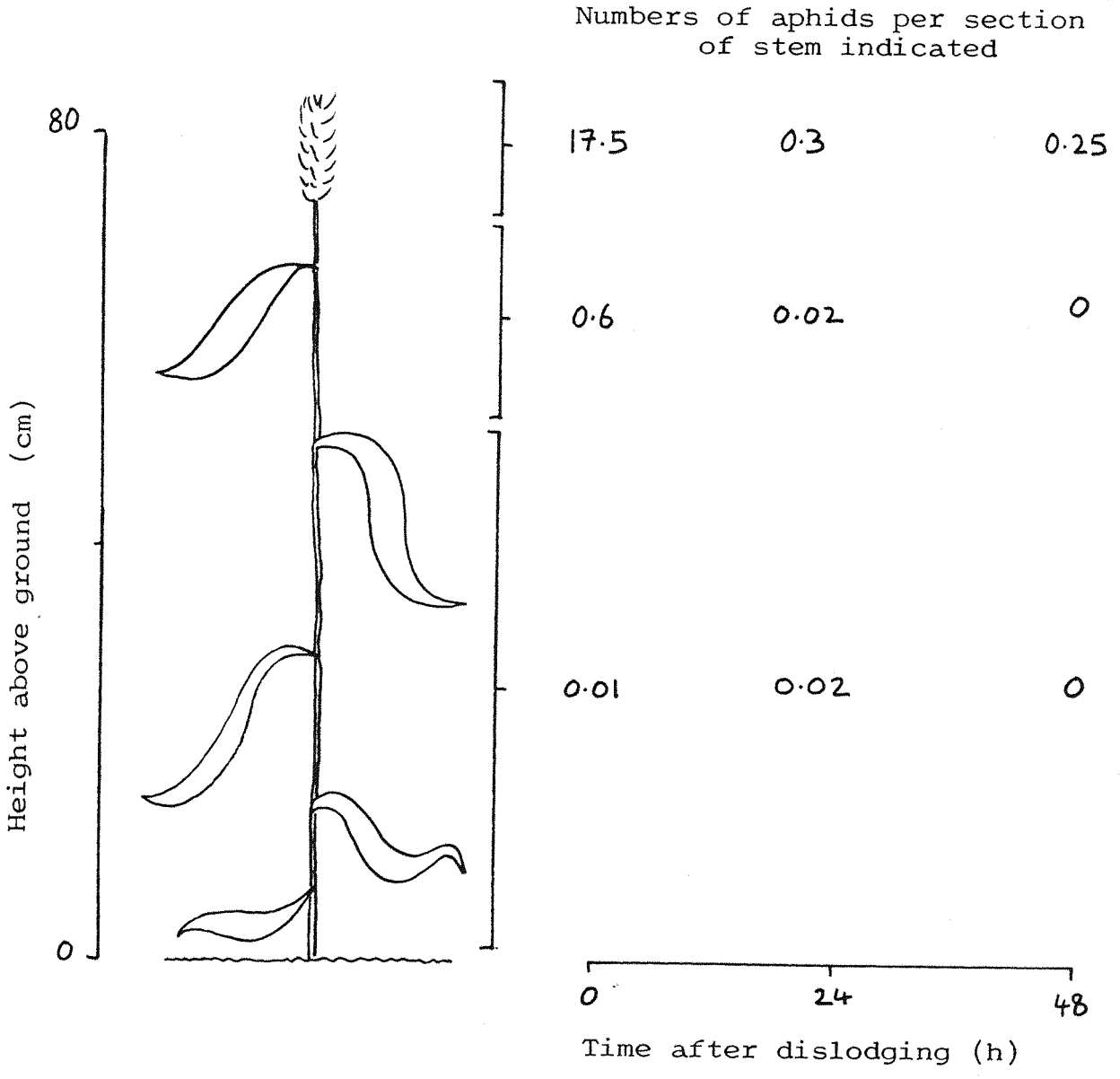
1. Aphids are constantly moving from wheat stem to wheat stem via the ground. Here the number that are eaten by ground predators could be a substantial source of mortality in the aphid population.

2. Aphids move or are knocked off the wheat stems but die on the ground (due to causes other than predation) before reaching another stem. In this system as the aphids would die anyway the number that are eaten by ground predators is irrelevant to the normal development of the aphid population.

At the end of the observation period at Chilworth (early July) the high aphid populations in the caged sample arenas (i.e. arenas without A. dorsale) were used to test the fate of aphids arriving on the ground. After an initial count of the density of aphids per arena the aphids were dislodged and counts made of the numbers returning after 24 and 48 h. The data are shown in Figure 8.15, each number being the mean of 200 counts (20 stem counts in each of the 10 cages). Aphids were clearly not returning to wheat stems, including the lower parts, in detectable numbers.

No further analysis was made of this result as the methodology is open to several criticisms that were not answered by experiment:

Fig. 8.15 The number of aphids per wheat stem 24 and 48h. after dislodging the original population.



Aphids may have been damaged by dislodging and so unable to reclimb wheat stems.

Aphids once on the ground may have left the arena rather than climb other wheat stems.

Aphids may have been eaten by predators other than A. dorsale once on the ground in the arena.

This suggests that aphids die on the ground whether or not A. dorsale is present. It is interesting to note that the aphid populations in the two caged arenas which had A. dorsale introduced into them (Fig. 2.16, Chapter 2) were as high (about 18 aphids per stem) as the 10 caged arenas without A. dorsale. In the next Chapter the importance of the proportion of the aphid population arriving on the ground and their fate there is investigated using a simple simulation model.

8.6 Discussion

(i) The use of arenas in fieldwork

The advantage of direct observation of the behaviour of animals in the field is that it gives confidence in the results not being an artifact of the experimental system. The disadvantage is that usually only small amounts of data can be gathered for large amounts of time spent observing in the field. This disadvantage was partially overcome with A. dorsale because it was possible to have a very high density of the beetle in observation arenas without producing behaviour atypical of the low density field situation. Meetings between individuals were observed on a total of 15 occasions in the arenas and these encounters all lasted about 1 - 2 s with no obvious signs of aggression. The five encounters observed between other species of Carabidae lasted longer (5 - 6 s) and involved aggressive behaviour (pushing, biting etc.). The habit of overwintering as large aggregations in field boundaries may be responsible for the more "placid" interactions between A. dorsale individuals. Whatever the reason, the arena technique used here may not be equally successful with all species of Carabidae.

(ii) Laboratory vs. field behavioural observation

Chapter 5 included the laboratory version (c.f. Section 5.6: "Late season" trials) of this fieldwork. A comparison between the two illustrates some important points about the extension of laboratory results to field situations.

(a) Climbing data.

The mean number of climbs per hour of observation was higher in the laboratory (3) than the field (1.5). But the frequency distribution of the height of climbs up the plant was similar in the laboratory (Chapter 5, Fig. 5.20) to that in the field (Fig. 8.13). The net result is that although laboratory beetles climbed more often than those in the field they also did not climb high enough to encounter aphids. The overall conclusion from Chapter 5 was that the amount of climbing by A. dorsale did not change in response to changing aphid distribution. This was also the conclusion of this Chapter.

(b) Time budget data

A comparison of the average proportion of time occupied by each of the main behavioural categories between the Chapter 5.6 results and these field results would produce the following figures:

	Section 5.6	Chilworth
Search	0.25	0.90
(Run and Still)	0.65	0.03
Eat	0.15	0.05
"On plant"	0.05	0.03

The proportion of time spent on the wheat was about the same but clearly the laboratory results would lead to an overestimate of the time spent eating and an underestimate of the time spent searching. The laboratory results could be interpreted as evidence of both an efficient predator; it spends a relatively long time eating for a small amount of searching, and an inefficient predator; it spends only one quarter of its time searching.

In the laboratory experiments, searching time on the plant was not increased by the addition of aphids to the arena (Chapter 5, Fig. 5.16). This was essentially the conclusion of the fieldwork; A. dorsale does not respond to an increase in density of aphids on the ground by searching more on the wheat.

These comparisons show that it is possible to extend relative measures from laboratory to field, i.e. the comparative effect of low and high densities of aphids on the ground, on the proportion of time allocated to searching on wheat plants. But it is not possible to use laboratory results to make absolute statements about behaviour in the field, i.e. A. dorsale will climb wheat three times an hour, will spend one quarter of the night searching and so on. Gilbert et al. (1976) make a similar point about the time budget of coccinellid larvae in the field; laboratory estimations would suggest that they spend long periods in the field searching; field observations show that search time is curtailed by long periods of "doing nothing in particular" (exactly the reverse of the A. dorsale situation).

(iii) The implications for cereal aphid control

The fieldwork at Chilworth confirmed the earlier laboratory and field findings that A. dorsale is a ground forager. This does not mean that it has no role to play in the control of cereal aphids. This will be decided by the fate (in the absence of predation) of aphids arriving on the ground, a question which could not be conclusively resolved in this thesis. The answer to this question may also decide the role of Carabidae other than A. dorsale; representatives of the genera Amara, Carabus and Pterostichus were seen in the arenas but never observed climbing. Araneae, Dermaptera and Staphylinidae were all seen to be actively exploring wheat plants, the two former in particular were often observed on the flag leaf or wheat head. Clearly work on the small scale movements of aphids within the wheat crop will be vital in deciding the contribution to aphid mortality of these various taxa.

C H A P T E R 9

CHAPTER 9

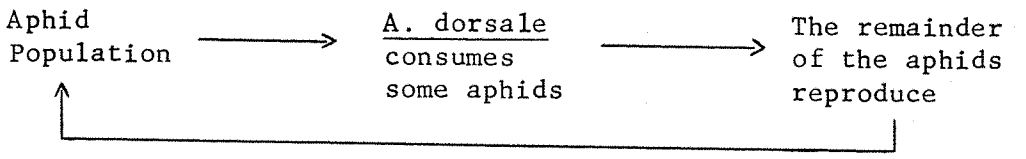
A MODEL TO SHOW THE POTENTIAL OF A. DORSALE TO REDUCE CEREAL APHID POPULATIONS

The format and parameters of the equation underlying this simulation model were decided upon by myself. All credit for the computer program which actually produces the results must however go to Allan Watt who kindly volunteered to write it, thereby saving me a considerable amount of time and not a little frustration.

9.1 Introduction

The preceding Chapters have dealt with what might be termed the immediate interactions between A. dorsale and cereal aphids, i.e. the number of aphids eaten per day, possible preference for aphids and so on. While these questions are essential to understanding the relationship between A. dorsale and its prey, they do nothing to reveal the effect of this beetle on the population dynamics of cereal aphids. In Chapter 4, for example, it was shown that as A. dorsale matured reproductively, its voracity (expressed in number of aphids eaten per day) increased, but would this increase be enough to prevent a small aphid population developing into an outbreak?

The ideal way to show whether these "immediate interactions" have an effect on an aphid population would be by large-scale field experiment; practical considerations (time, manpower etc.) make this approach impossible. It is possible, however, to construct a mathematical model of the immediate interactions between A. dorsale and the aphid prey in terms of the number of aphids eaten by the A. dorsale population on a single day. This model can then be transformed into a computer program which will show how this daily interaction affects the size of the aphid population over several days. The model developed here is of a simple iterative type with the number of aphids left at the end of a day being fed back into the model to produce the numbers at the start of the next day:



The model can be simple largely because the interaction between A. dorsale and cereal aphids is one way. That is, A. dorsale may reduce cereal aphid populations but the reverse does not occur either within a season (the period covered by the model) or between seasons (see Section 9.6 for further discussion of this point).

A combination of laboratory and fieldwork (Chapters 5, 7 and 8) showed that although most of the aphid population is on the wheat, A. dorsale searches for prey almost entirely on the ground. The proportion of the aphid population moving from plant to plant via the ground may decide the potential of A. dorsale to control aphid numbers. The principle aim of the model is to assess the importance of the proportion of aphids arriving on the ground in relation to other parameters (such as aphid reproductive rate and voracity of the A. dorsale population) in deciding the degree to which the A. dorsale population controls aphid outbreaks.

9.2 Classification of the model

Models can be classified in a number of different ways, classification of the type of model to be used here will help point to the drawbacks and aims of the model. The classification is based on that of Southwood (1978).

This model is a form of systems analysis known as "strategic modelling", the aim of which is to predict not only the output from a system for a given set of initial conditions, but also to identify those parts of the system which play the key roles in producing the output. In order to do this some simplification must occur and some components of the model are treated very superficially.

The components of this model are based on both general theory and field observations. This mixed deductive-inductive approach has been used extensively to explore arthropod predator-prey relationships and has provided valuable insights (for instance see Hassell 1978). The aphid population is allowed to grow exponentially rather than logistically, but this increase is taken to occur in discrete steps on a daily basis (aphid reproduction is probably much lower at night than in the day, D. Dent pers. comm.). In addition, mortality imposed by the A. dorsale population must also occur on a daily basis (i.e. A. dorsale feeds only at night). This means that the model is more easily described by a difference equation, which expresses the change in population size per unit of time, rather than a differential equation, which assumes that the population changes continuously with time (see Hassell 1978 for further discussion of this). The field observations showed which of the parameters that could be included on the basis of a priori reasons and laboratory work were in fact worth including and more importantly provided a realistic range of values for these parameters. The next Section describes in detail how the choice of parameters was made.

Finally, this model is deterministic; it has a fixed and unique outcome for each set of initial conditions. In a real situation this is not so and it is possible to allow several outcomes for a given set of initial conditions by making the model stochastic. Stochastic models are, however, very complex mathematically and the output they produce is very similar to deterministic models unless the population involved is small (Southwood 1978). Even at below-outbreak levels, aphid populations contain large numbers of individuals so it was deemed justifiable to use a less realistic but more manageable deterministic model.

9.3 The model

There are three components to this model; the capacity of the aphid population to increase, the capacity of the A. dorsale population to eat aphids and the actual density of aphids available to the A. dorsale population (i.e. the number of aphids arriving on the ground).

The capacity of the aphid population to increase is represented by an initial starting density of aphids (N_t) which is multiplied by a daily rate of increase of the population (r) to give the density of aphids on the next day (N_{t+1}):

$$N_{t+1} = N_t\, r$$

The capacity of the A. dorsale population to consume aphids is given by multiplying the density of the beetles (B) by the number of aphids that one beetle could eat per day (A). This total number of aphids eaten per day (AB) is then subtracted from the initial density of aphids:

$$N_{t+1} = (N_t - AB)\, r$$

The actual density of aphids available to A. dorsale is given by multiplying the total density available (N_t) by the proportion that are available to be eaten (P). The A. dorsale population is constrained to eat aphids from the available proportion (N_tP) only, the number eventually eaten being subtracted from the initial aphid density (N_t) before reproduction (r):

$$N_{t+1} = \left[N_t - (N_tP - AB) \right] r$$

Where

N_t	=	initial density of aphids
N_{t+1}	=	final density of aphids
P	=	proportion of aphids available for predation (i.e. aphids reaching the ground)
A	=	number of aphids eaten per beetle
B	=	density of beetles
r	=	daily reproductive rate of aphid population

N.B. Biological "realism" is maintained by including the condition that,

if $AB > N_tP$, then $(N_tP - AB) = 0$

i.e. once all the aphids in the available proportion have been consumed the A. dorsale population cannot then go on eating to produce "negative aphids".

This equation was translated into a computer program, in the BASIC language, which would repeat the above computations for the requested number of days. Options were provided for a print out of the aphid population at the end of each day or just on the final day. Options were also provided for specifying a number of simulations to be run sequentially by allowing the user to enter a range of values for the starting density of aphids and the beetle density. A program listing is given in Appendix 2.

9.4 The range of values for the model parameters

For the output of the model to have any biological meaning the values of the parameters making up the model must cover ranges that can be found in the field. These ranges are now given together with the sources on which they are based; further explanation of these values is given in the next Section.

(i) Initial density of aphids (N_t)

Aphid densities in a wheat field in mid May can range from close to zero in non outbreak years to close to 500 per m^2 in outbreak years (A.D. Watt and S.D. Wratten pers. comm.).

(ii) Proportion of aphids available (P)

Since there are no comprehensive field measurements of the proportion of aphids arriving on the ground this parameter was varied from 0 to 100% of the aphid population arriving on the ground.

(iii) Number of aphids eaten per beetle per day (A)

Laboratory work (Section 4.7) showed a linear relationship between temperature and numbers of aphids eaten per beetle per day. The gradient of this line (0.62) gives the number of aphids eaten per beetle per

day degree (C). Calculation of field day degrees over several years from local weather station data (Chapter 7.3) shows that for the mid May to mid June period (see "time period" below) used in this model voracity could range from 8 to 16 aphids eaten per beetle per day.

(iv) The density of A. dorsale (B)

Fieldwork at S. Allenford farm (Chapter 7.2 and N.W. Sotherton pers. comm.) suggested that field densities of A. dorsale are usually less than 1 per m^2; other work (Sunderland & Vickerman 1980) has shown a mean density over several years of just over 1 per m^2. The model was allowed to range from 0 to 2 per m^2 to cover likely values.

(v) Aphid reproductive rate (r)

Fieldwork has shown that the daily rate of increase of an aphid population can range from just over 1.1 to 1.4 (Dean 1973b; N. Carter, N.W. Sotherton & A.D. Watt pers. comm.). The model was used over a range of 1.1 to 1.5 to cover all likely values.

(vi) The time period of the model (t)

Fieldwork (Chapter 7) showed that cereal aphids had already arrived in the crop before the A. dorsale population; other work (A.D. Watt & S.D. Wratten pers. comm.) confirms this. In consequence the A. dorsale population could start to feed on aphids from when it first migrated into the crop, i.e. mid May. The model should run from this date until the aphid population has reached a point in time where either an outbreak will or will not occur. This point has been defined in terms of the developing aphid population, the growth stage of the wheat, the yield of grain and the costs of spraying (George & Gair 1979). They found by field experiment that spraying of wheat was economic, in terms of increased grain yield, if the number of aphids per ear was at least five and increasing at G.S. 10.5.1. This plant growth stage is reached at about mid June, so if the model was run for 30 days (mid May to mid June) and at the end the aphid population has reached 2500 per m^2 (i.e. c. five per ear) and increasing, the A. dorsale

population had not successfully controlled the aphids. If the aphid population was below 2500 per m^2 after 30 days, then the A. dorsale population could be considered to have controlled an aphid outbreak.

The time period of the model is, therefore, 30 days, constrained at the beginning by the time of migration of A. dorsale and constrained at the end by the economic outbreak criterion of George & Gair (1979).

To summarise:

Parameter	Range
N_t	0 - 500/m^2
P	0 - 100%
A	8 - 16/day
B	0 - 2/m^2
r	1.1 - 1.5/day
t	30 days

9.5 Comments on the range and choice of parameters

There are several properties of the equation underlying this model which seem biologically unrealistic:

The model is unstable; only a small range of values of each parameter will produce slow changes in the aphid population, all others lead to rapid extinction or uncurbed exponential growth. The latter two outcomes are the least common in the field!

The model uses parameters which do not change with time; in the field, temperature changes with time and temperature is known to affect both aphid reproductive rate and the voracity of A. dorsale.

There is no effect of the aphid population on the A. dorsale population; there are many documented cases of the density of invertebrate prey affecting the density of their predators by a variety of mechanisms (Hassell 1978).

These three major points will now be discussed in the context of the wheat field system:

(i) The instability of the model

No animal populations increase exponentially indefinitely but a large number do undergo exponential growth in their early stages (see Southwood & Comins 1976). The criterion used to establish an outbreak, and hence the end of the model run, is an economic one. This "economic" decision is taken before aphids reach such high populations that their reproductive rate is limited by crowding, production of alates, etc. For the time period we are interested in the aphid population is not regulated by density dependent mortality factors and hence has the potential to increase very rapidly.

Some of the reproductive rates used in the model produced unrealistically high aphid densities by the end of the simulation. Although in reality population growth would have been slowed or stopped by density dependent factors (e.g. crowding) before the end of the simulation period, as these factors only operate at higher densities (see Vickerman & Wratten 1979; Carter et al. 1980) the populations would still be classified as having reached outbreak level.

(ii) Parameters that are constant with respect to time

(a) Aphid population parameters

The growth of an aphid population on wheat is dependent on several factors (crowding, temperature etc.) but is described by just two parameters in this model; the initial size of the population and its daily reproductive rate. This was a deliberate simplification to allow easier interpretation of the effects of the mortality caused by A. dorsale. There is however some justification for this simplification. No allowance need be made for the effects of crowding for the reasons discussed in the section above. Temperature affects reproductive rate (Dean 1974) but day degree data over several years from Hurn Weather Station (N.G.R. SU 115980) showed no consistent increase or decrease from mid May to mid June, making it reasonable to assume an average reproductive rate over this period. The growth stage of the wheat can

affect the aphid reproductive rate (Carter et al. 1980); this was not allowed for and is a potential source of error. In effect the model will slightly underestimate the potential of A. dorsale because in mid to late May the aphid reproductive rate will be lower than the average rate used in the model (this is due to the cereal aphid of principal interest, S. avenae, feeding on the less favourable flag leaf at first but then moving up to the ear). This will be examined further in the final discussion.

(b) A. dorsale population parameters

As with the aphid population, the factors controlling the number of aphids eaten by the A. dorsale population were simplified to two; the daily voracity of an individual beetle and the density of beetles. Again this may not be too much of a simplification. Field sampling (Chapter 7.2) showed that the decline in numbers of A. dorsale begins in late June so that the model's assumption of a constant density of the beetle is reasonable. The assumption of a constant level of voracity is less justifiable; three aspects of this are now considered.

1. Maximum voracity: Laboratory work (Chapter 4) showed that both temperature and reproductive state affect the voracity of A. dorsale. Field sampling (Chapter 7) showed that the reproductive state of the population was constant for the time period of the model. Although voracity did change with temperature, weather data showed no significant increase or decrease in day degrees over the period mid May to mid June so the assumption of a constant voracity level is reasonable. The model does allow for this constant level to be changed as might be expected in a "cold" or a "hot" summer.

2. Time spent searching: Some invertebrates actually spend very little time searching for prey, e.g. coccinellid larvae (Gilbert et al. 1976), and this can severely restrict their potential for biological control. Field observation (Chapter 8) showed that A. dorsale spends about 90% of its active period searching and that although this period is shortened by very heavy rain no other weather factors had any effect. Time spent searching will not normally vary sufficiently to invalidate the model's assumption of a constant number of aphids eaten per day.

3. Satiation of A. dorsale: The voracity of A. dorsale individuals was determined in the laboratory with an abundance of prey (aphids). The model uses these voracity results and hence assumes that A. dorsale finds sufficient aphids during one night's foraging to become satiated. This need not be the case for two main reasons; aphids may be at such low density that A. dorsale cannot search a large enough area to catch sufficient to become satiated or alternative prey may be so abundant that aphids form only a small part of the diet. The likely effects of these two factors are analysed below.

Search area: Voracity was shown to vary with temperature by laboratory experiment (Chapter 4.7). Further experiments showed that the success of A. dorsale in catching prey is also strongly linked to temperature (Chapter 6.7). The two cannot, however, be evaluated in the field by one simple measurement of temperature. Field night-time temperatures (which control capture success) are obviously lower than day time temperatures (which combined with night temperature set the level of voracity). The relationship between the two is straightforward when day time and hence night time temperatures are low. The discontinuity occurs when day time temperatures are high; the subsequent night time temperature can be high (if the sky is overcast) or low (if the sky is clear). The former will lead to a situation where high day temperatures have produced a high level of voracity but because the night temperature is also high A. dorsale can feed until satiated. In the latter situation, however, voracity is high but low night temperatures prevent A. dorsale from feeding until satiated. This will result in a lower potential for controlling cereal aphid populations.

It is possible to crudely analyse this system for a range of voracity levels (set by the average 24 h temperature) and capture successes (set by the average night time temperature) by the following method:

1. For a given average 24 h temperature there is a level of voracity in number of aphids eaten per day (Chapter 4.7).
2. For a given average night temperature A. dorsale catches aphids with a certain efficiency (Chapter 6.7).

1. and 2. can be combined to show how many aphids A. dorsale must encounter to catch sufficient aphids to become satiated. For instance if the voracity level was 10 aphids per day (for satiation) but only 0.7 (or 70%) of all aphids encountered were captured, then A. dorsale must encounter at least

$$10 \times 1/0.7 = \underline{14.3 \text{ aphids}}$$

to catch the 10 aphids required for satiation.

We then need to calculate the area that A. dorsale can search for the night temperature used above. This is given by:

$$\text{Width of search path} \times \text{Speed of movement} \times \text{Total time spent searching}$$

For A. dorsale at 15°C the speed of movement is 3 cm per s and the width of the search path (distance between antennae when swept across ground) and time spent searching are constant at 0.5 cm and 4.5 h (or 16200 s) respectively, i.e.

$$0.5 \times 3 \times 16200 = \underline{2.43 \text{ m}^2} \text{ searched per night}$$

It can now be seen that the density of aphids must be at least

$$14.3/2.43 = 5.9 \text{ per m}^2$$

if A. dorsale is to catch enough aphids to achieve satiation.

The range of values used in these calculations was wider than would occur normally in the field so as to cover all probable conditions (Table 9.1). The resultant required ground densities of aphids for A. dorsale to become satiated at various combinations of night and average 24 h temperatures are given in Figure 9.1.

If night temperatures average 10-15°C then A. dorsale can reach satiation with low densities of aphids on the ground even when voracity is high. Once night temperature drops below 10°C a much higher density

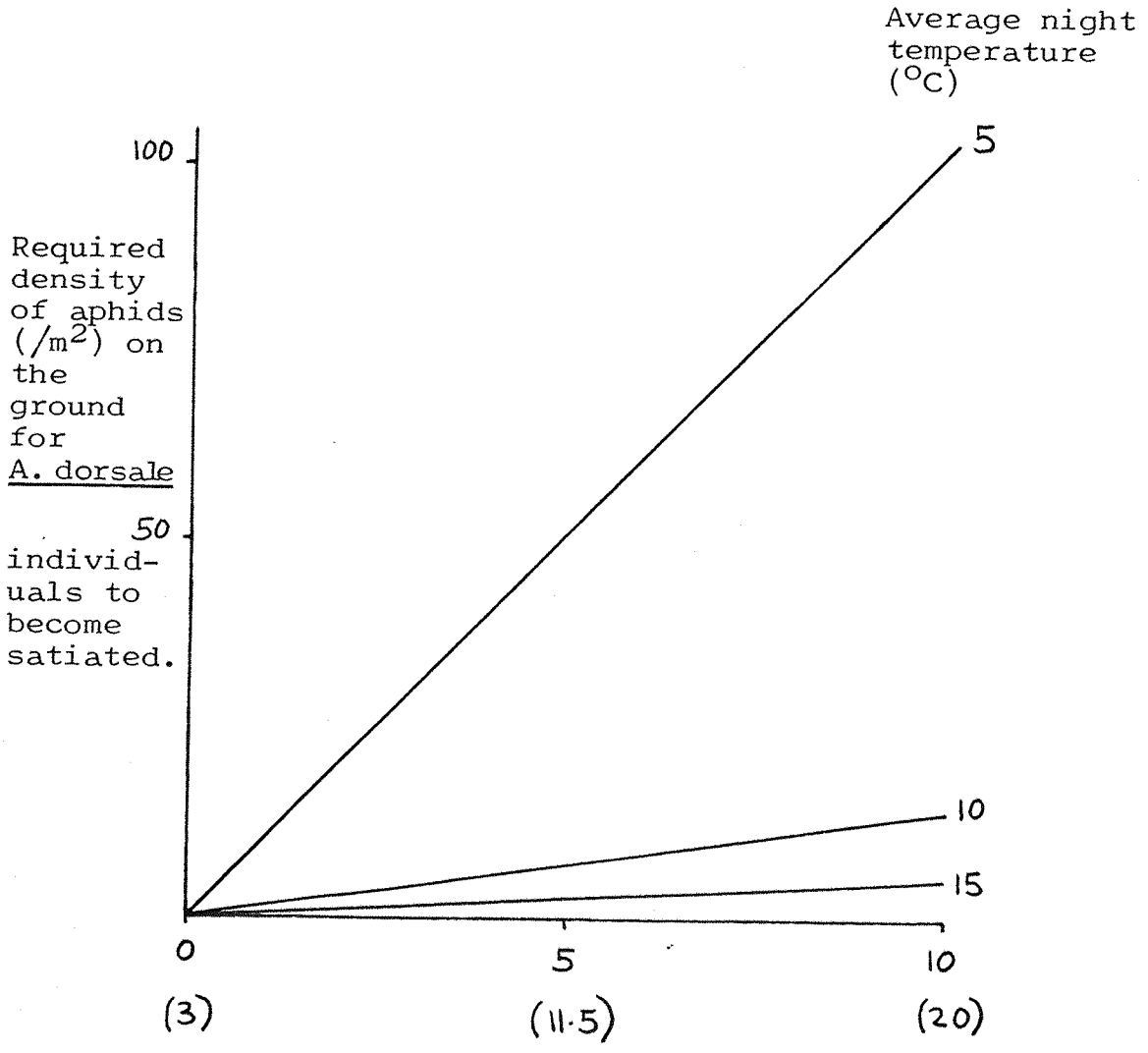
Table 9.1 The range of values and the source of the parameters used to calculate the required density of aphids for *A. dorsale* to feed until satiated for a range of night only combined with 24 h average temperatures.

	Average 24 h temperature (°C)					(Source)
	3	5	10	15	20	
Voracity (aphids/day)	0	0.8	3.9	7.0	10.1	(Chapter 4)

	Average night temperature (°C)				
	3	5	10	15	
% successful captures of aphids encountered	0	24	47	66	(Chapter 6)
Width of search path (cm)	0.5	0.5	0.5	0.5	(Chapter 3)
Speed of beetle (cm/s)	0	0.5	1.75	3	(Chapters 4 and 6)
Search time (h)	4.5	4.5	4.5	4.5	(Chapter 8)

N.B. Speed was assumed to vary linearly with temperature between the two recorded values of 0 cm/s and 3 cm/s.

Fig. 9.1 The change in the density of aphids on the ground required by A. dorsale to catch sufficient in one night to become satiated, for a range of voracity levels and night temperatures.



(figures in brackets are the average 24h temperatures (°C) producing that level of voracity).

of aphids is required on the ground with increasing voracity. The field sampling of Chapter 7.2 showed that about 4% of the aphid population is on the ground. If voracity was 20 aphids per day and night temperature was 5°C then A. dorsale could only encounter enough aphids to become satiated if total aphid density was about 2500 per m^2. Using the economic criterion of five aphids per ear (see Section 9.4) this means that A. dorsale would only be eating to maximum potential (satiation) when aphids had already reached outbreak level.

In summary, in conditions of high day and low night temperatures (as occur in summer), if the proportion of the aphid population on the ground is small (i.e. 5%), A. dorsale will not encounter sufficient aphids to reach satiation (thus reducing the beetles' biological control potential) unless the aphid population has already reached the aforementioned outbreak level.

Alternative prey: Field sampling (Chapter 7.3) showed that aphids were not the predominant prey type for all of the mid May to mid June period with which the model is concerned. Collembola, for instance were very abundant during some weeks of sampling and this was reflected in the diet of A. dorsale by this prey type forming the major proportion of prey taken. Clearly if the A. dorsale population is largely feeding off alternative prey even though there are aphids available, then its potential to control the aphid population is reduced.

This situation has also been analysed crudely for the three main prey types; aphids, Collembola and Nematocera (see Chapter 7.3); N.B. no account is taken of differences in calorific content/size of prey. If all three prey types were considered at the same time the analysis would become more complicated than is necessary to show the approximate effects of alternative prey. Accordingly two situations were considered; aphids with Collembola as the alternative prey and aphids with Nematocera as the alternative prey.

The two situations were analysed by considering five ratios of aphid density to alternative prey density (in terms of prey per m^2 of ground), these being:

9:1, 7:3, 5:5, 3:7, 1:9

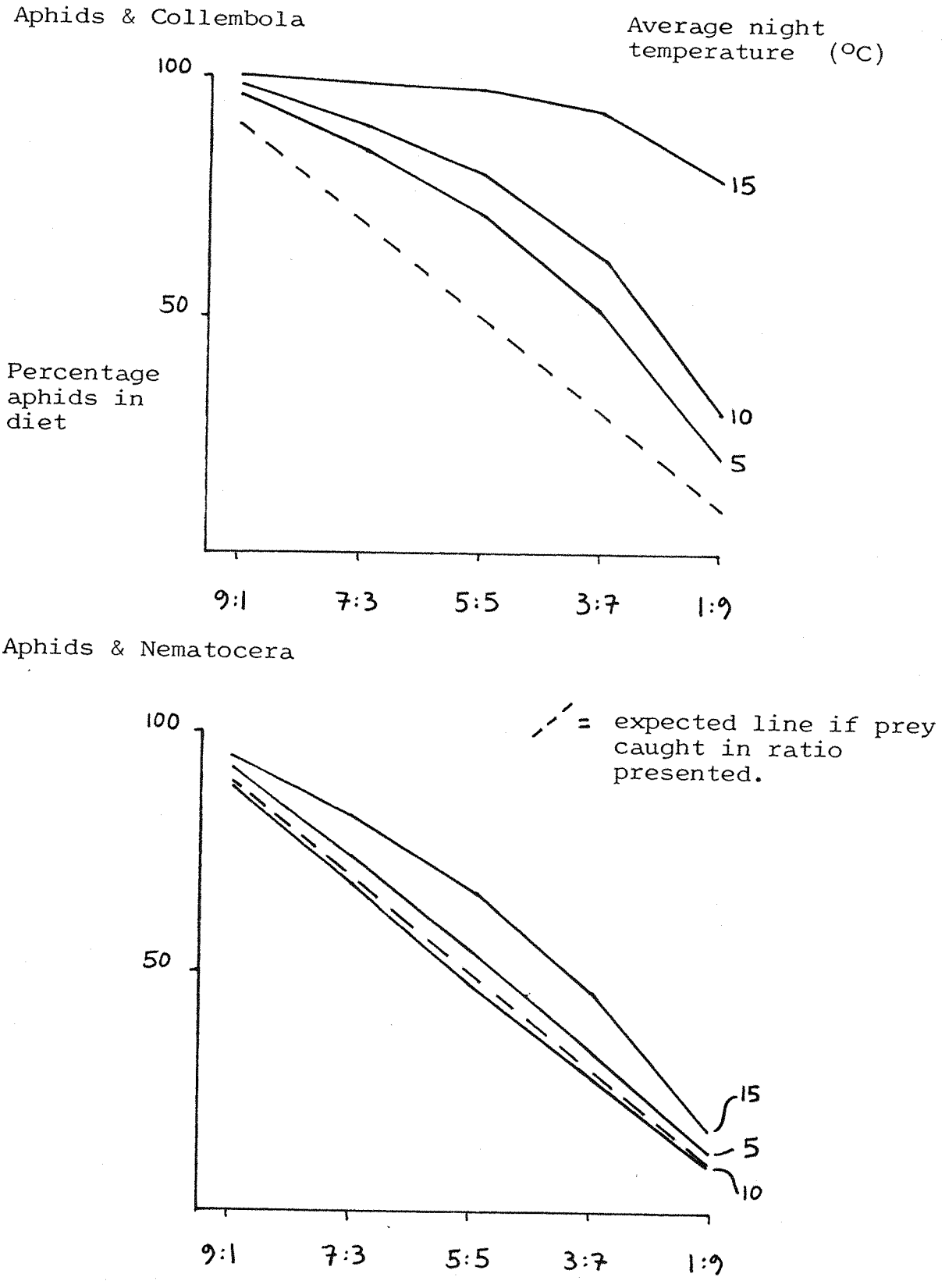
(aphids : alternative prey)

The laboratory work of Chapter 6 and analysis of field sampling in Chapters 7 and 8 suggested that the most important factor controlling the ratio in which these prey are actually taken is the temperature-dependent capture efficiency of A. dorsale for the various prey types. The above ratios were adjusted for these capture efficiencies at temperatures of 5, 10 and 15°C. The resulting ratio was taken to be the ratio of aphids : alternative prey actually eaten by A. dorsale. For instance, if aphids were in a 9:1 ratio to Collembola and the temperature was 5°C, adjustment for capture efficiencies would produce the below ratio of the two prey types actually captured:

	Aphids	:	Collembola
Ratio of prey density	9		1
Capture efficiency adjustment (from Chapter 6)	x 0.24		x 0.10
Ratio of prey actually caught	2.16	:	0.1
Prey capture ratio as %	96	:	4

The change in the percentage of aphids in the diet (i.e. prey capture percentage) for the five prey density ratios with the alternative prey of Collembola or Nematocera is shown in Figure 9.2. If Collembola are the alternative prey then at higher temperatures (15°C) the A. dorsale population eats mostly aphids even when there are nine times as many Collembola available. A reduction of temperature to 10 or 5°C produces a substantial decrease in the proportion of aphids in the A. dorsale diet as Collembola become more abundant. If Nematocera are the alternative prey then there is a substantial reduction in the proportion of aphids in the A. dorsale diet, regardless of temperature, as the Nematocera become relatively more abundant.

Fig. 9.2 The effect of alternative prey on the percentage of aphids in the A. dorsale diet.



(c) The specific interaction between the aphid and A. dorsale populations

1. The spatial distribution of aphids and A. dorsale

This model deals with the situation where A. dorsale is already encountering aphids and so makes one of two assumptions: either both aphids and A. dorsale are distributed evenly throughout the crop or the aphids are patchily distributed within the crop and A. dorsale has already arrived in the patch. There is some evidence to suggest that the latter type of aphid distribution is the case (Dean 1973), so it must be remembered that the model assumes that A. dorsale can by some means arrive in the patches of aphids efficiently. Again this assumption may be reasonable, work by Baars (1979) has shown that carabids are capable of movement over distances of at least 50 m in a single night. Work by Bryan (pers. comm.) has shown that A. dorsale can aggregate (although the underlying mechanism is not known) to artificial patches of aphids in wheat fields.

2. The fate and proportion of aphids arriving on the ground

A. dorsale hunts for prey almost exclusively on the ground and so catches only those aphids that have arrived there; the rest of the aphid population is inaccessible. The model makes two very important assumptions that have yet to be fully tested in the field and which could work both for and against control of aphid numbers. The first is that all aphids arriving on the ground, unless eaten by A. dorsale, climb back onto the wheat that day and continue to reproduce normally. The second is that the proportion of aphids arriving on the ground is not density dependent but constant over the range of aphid densities covered by the model. In the case of the first assumption, if aphids are incapable of climbing back on to the wheat anyway then A. dorsale plays no part in limiting aphid populations; alternatively if aphids take some days to return to the wheat plants and begin normal reproduction, then their potential to reproduce will be less than the model suggests.

3. The size of aphid prey eaten

The voracity of A. dorsale in this model was expressed as the number of aphids eaten per day based on the laboratory experiments of Chapter 4. The aphids used in these experiments were all large, i.e.

III instar to adult, so a smaller total number of aphids were eaten per day than might be eaten in the field where a large proportion of the population are I or II instar nymphs (Dixon et al. unpubl.). In terms of control of the aphid population, however, the potential of A. dorsale is greatly increased if it eats only adults for the following reason:

Measurements in the field (Dean 1973b) have shown that it takes 10 days from birth for cereal aphids of the species S. avenae to reach maturity and produce the first offspring. Adults were found to live for about 22 days during which time they produced 38 nymphs. (More general references (Dixon 1973; Blackman 1974) suggest that these statistics have about the same values for the majority of aphid species). So for each adult aphid consumed by A. dorsale reproduction is effectively halted until nymphs in that area have matured (i.e. up to 10 days). If A. dorsale eats only nymphs then aphid population growth will be slowed but as the adult aphids are producing nymphs at an average rate of 1.7 per day the overall effect is much less.

Laboratory experiments (Chapter 4.5) have shown that A. dorsale catches adult aphids more successfully than it does small nymphs but as the precise age structure of aphids arriving on the ground is not known, it is not possible to say what effect this will have in the field.

4. The temporal separation of aphid mortality and reproduction

Finally, the model works by imposing mortality on the aphid population and then the aphid population reproduces. In some predator-prey systems this temporal separation of the mortality induced by predation and reproduction of the prey would clearly not be realistic. In this case however there is justification for the following reasons: aphid reproductive rate increases with temperature (Dean 1974; Dent pers. comm.) so at night in the field, when temperatures are low, reproduction will also be low. A. dorsale only forages at night, producing the temporal separation of mortality and reproduction in the aphid population assumed in the model.

(iii) Effect of the aphid population on A. dorsale

Where a predator has a similar generation time to the prey, prey numbers can immediately affect the reproductive rate of the predator. The density of prey can also affect the larval survival, fecundity, adult survival and so on of predators whose main food source is that prey type (Hassell 1978). A. dorsale has a much longer generation time (1 yr) than the cereal aphid (about 1-2 wk) so prey effects on the beetle population's rate of reproduction would be extremely delayed. But, more importantly, A. dorsale is polyphagous and in the absence of aphids would simply catch alternative prey. There is no obvious mechanism for aphid numbers to affect the numbers of A. dorsale.

Summary

A number of statements have been made about how various parameters not included in the model could affect the potential for biological control of aphids by A. dorsale. These are now briefly summarised:

Parameter not included in model	Effect on control potential.
Maturing of wheat	Increases potential for control.
Area searched by A. dorsale	If night temperature is below $10^{o}C$, this severely restricts potential.
Alternative prey: Collembola	If night temperature is below $15^{o}C$ and Collembola abundant control potential is reduced.
Alternative prey: Nematocera	If abundant, potential is severely reduced regardless of temperature.
Patchy distribution of aphids	If A. dorsale cannot detect patches, potential is reduced.
Fate of aphids arriving on ground	If all aphids on ground would die independently of A. dorsale, the beetle has no potential for control.

Size of aphid prey	If a large proportion of aphids on the ground are nymphs this will reduce potential.

This summary makes it clear that the model over- rather than under-, estimates the potential of A. dorsale to limit aphid populations. It is easy to incorporate most of these parameters into the model by expressing them as a reduction in one of the parameters used in the model. For instance if night temperature was 10°C and Nematocera were equally abundant with aphids on the ground then only 50% of the A. dorsale diet would consist of aphids. This could be expressed in the model as a halving of the density of A. dorsale (i.e. only half the beetles were feeding on aphids) or as a halving of voracity (i.e. all the beetles fed on aphids but only for half the time). This means that these important parameters although left out of the model are in effect included in the final discussion of the model simulations and their implications for control of cereal aphids.

9.6 Simulations with the model

(i) Parameter range and step size

The range in values of each parameter has already been discussed (9.4). The increments by which each parameter was changed (step size) were chosen on pragmatic grounds; the increment had to be small enough to produce smooth "curves" on the graphs plotted (i.e. rounding errors were minimised) and show the full effect of each parameter, but not so small that graphs became a mass of lines. The parameters, their value ranges and step sizes were:

Parameter	Value range	Step size
Initial aphid density (/m^2)	0 - 500	10
Aphid rate of increase(/day)	1.1 - 1.5	0.1
A. dorsale density (/m^2)	0 - 2	0.4
A. dorsale voracity (No. eaten/day)	8 - 16	2
Percent aphids available	0 - 100	5%, 10% then steps of 10

The "curves" plotted were in fact a series of straight lines because parameters did not vary continuously. This was an advantage because the area under each curve could be calculated by simply treating the curve as a series of polygons (see section below).

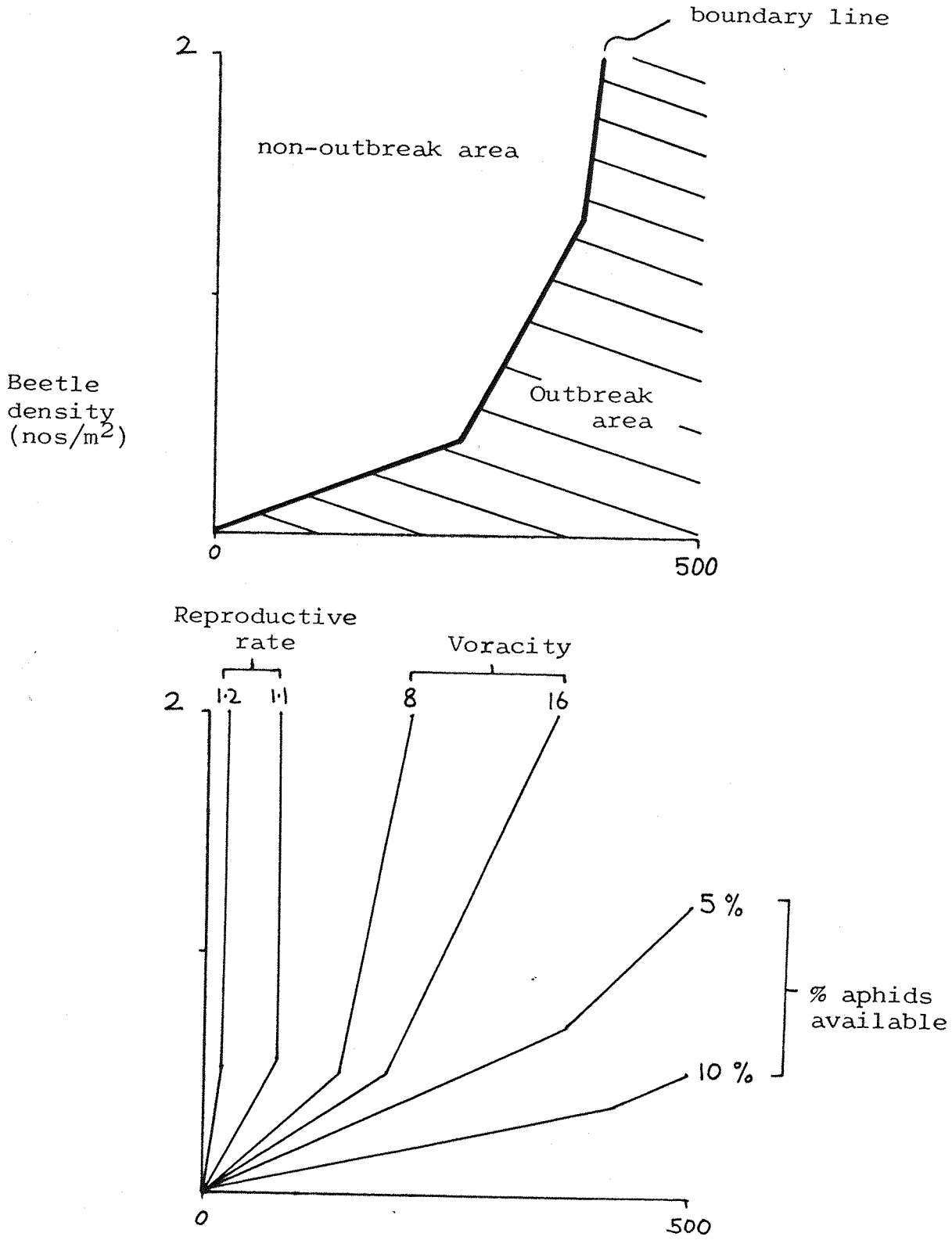
(ii) Plotting graphs from the simulation model output

In Section 9.4 the criterion for deciding whether an aphid outbreak had occurred was established as: if the population reached "five aphids per ear (i.e. c. 2,500 per m^2) and increasing" at the end of the simulation then an outbreak had occurred. The values of the five parameters in the model which produced outbreaks were recorded and used to plot boundaries on graphs between "outbreak" and "non-outbreak" areas. The axes of the graphs were initial aphid density vs. density of A. dorsale; note that these two parameters are treated essentially as independent variables creating a "graph area", the division of which into the outbreak and non-outbreak areas is decided by the values of the three other parameters (aphid reproductive rate, % aphids available and voracity of A. dorsale). This means that for the likely range of A. dorsale and aphid field densities it is possible to show the relative importance of reproductive rate, % aphids available and voracity in decreasing aphid outbreaks.

The top graph in Figure 9.3 shows a hypothetical example of the boundary line, outbreak and non-outbreak areas. As the axesa are the same for all graphs plotted the outbreak area is not shaded from now on. Instead it is taken that for all lines plotted, above and left of the line (i.e. high beetle but low aphid densities) is the non-outbreak area and below and right of the line (i.e. low beetle but high aphid densities) is the outbreak area. Note that because the line represents the last set of values for which outbreaks occurred it should strictly be included in the outbreak area, also that all lines must go through the origin.

For any one aphid reproductive rate both beetle voracity and the percentage of aphids available can be varied. Similarly for any one voracity both reproductive rate and percentage available can be varied and so on. In some cases increasing a parameter beyond a certain point did not change the boundary line; this is illustrated

Fig. 9.3 Hypothetical examples of graphs from the simulation model output to show outbreak/non-outbreak areas and how reproductive rate, voracity and % aphids are indicated.



in Figure 9.3 for reproductive rate and percentage aphids available (the other two parameters are assumed to be held constant in each case). Note that for reproductive rate "1.2+" means 1.2 up to the maximum rate used in the model (1.5) and for percentage aphids available "10%+" means 10 up to the maximum percentage used (100).

Alternatively, a parameter may change the boundary line but by plotting the boundaries produced by the minimum and maximum values of that parameter it is clear what effect intermediate values of the parameter will have on the boundary. This is shown in Figure 9.3 for a change in voracity with all other parameters held constant. The other voracity levels of 10, 12 and 14 are spaced more or less evenly between the 8 and the 16 boundary lines and hence are not shown.

These short-hand representations are used on all graphs from now on and are made possible because each of the five parameters always has the same effect on the boundary line, i.e.

Parameter increased	Effect on boundary	Effect on extent of outbreak area
Aphid reproductive rate	Moves up	Increases
A. dorsale voracity	Moves down	Decreases
Percentage aphids available	Moves down	Decreases

N.B. for all these parameters the line or area may move in the direction indicated or not change, as shown in the hypothetical Figure 9.3.

(iii) Comparing the relative effects of the parameters

It would be advantageous to have one method to compare the effect of all three parameters on the boundary line. Such a comparison can be made by calculating the maximum amount by which each parameter reduces the outbreak area (the shaded area in Figure 9.3) while the other two parameters are held constant. An example will show how this is done:

In Figure 9.4 a hypothetical example is given of the effects of aphid reproductive rate, % aphids available and voracity of A. dorsale on the boundary lines and hence outbreak areas on the graph. For simplicity's sake the boundaries are represented as straight lines. Note that in this example when reproductive rate reaches 1.2, further increases in the rate do not change the boundary. This is also true for both % aphids available and A. dorsale voracity when reproductive rate = 1.2. With a reproductive rate of 1.1 however both % aphids available and voracity change the outbreak area. Casual inspection of the graph shows that the following pairs of lines (the solid lines on the graph) give the biggest changes of outbreak area for each parameter:

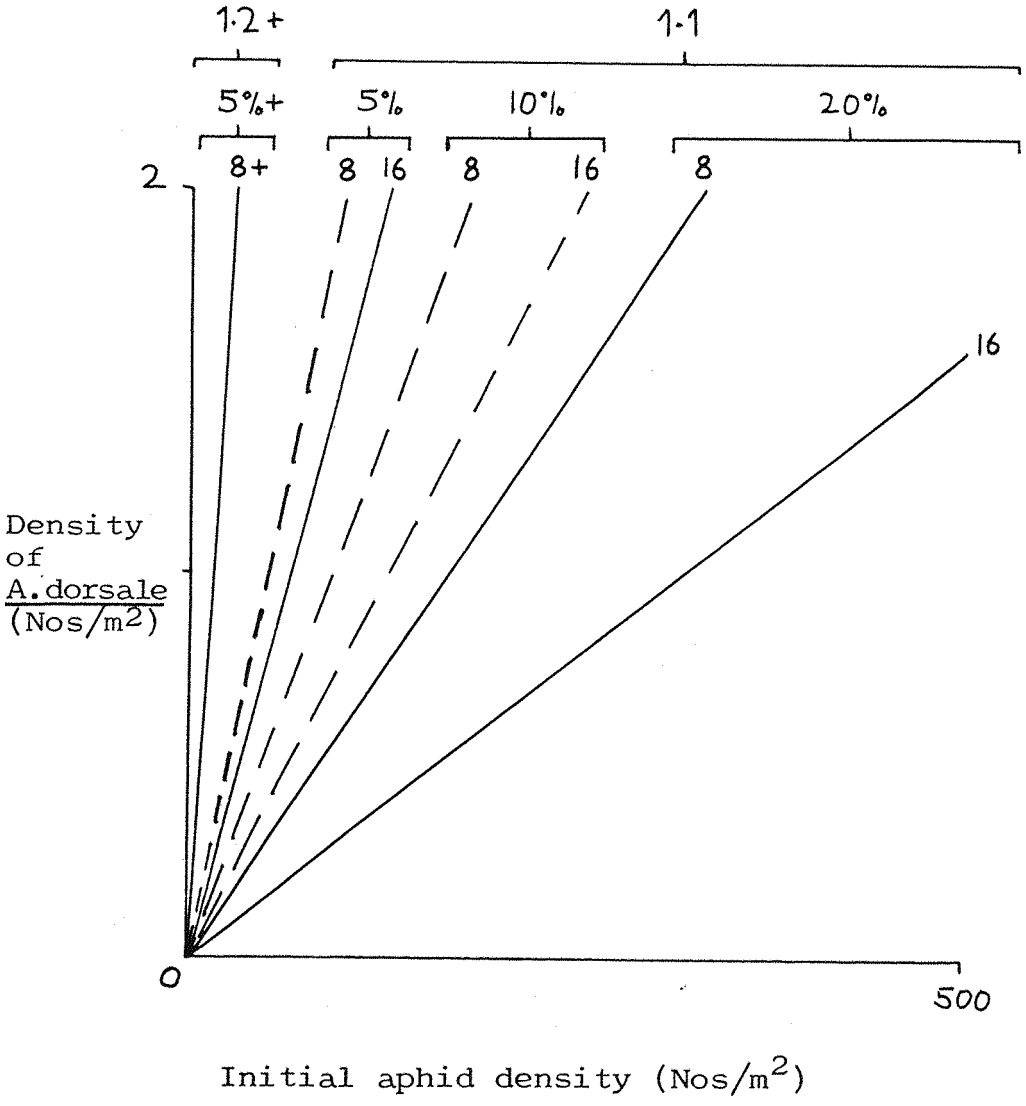
Reproductive rate	1.2 +		1.1
	5% +	compared with	20% +
	8 +		16
% aphids available	1.1		1.1
	5%	compared with	20% +
	16		16
Voracity	1.1		1.1
	20% +	compared with	20% +
	8		16

N.B. Only the underlined parameters change and each line is referred to by the values of the three parameters determining it.

This visual impression can be checked by calculating the outbreak area under each line of the graph and showing which of the comparable pairs of lines gives the biggest change in this area.

Note that the total area of the graph in Figure 9.4 is 500 x 2 = 1000 and that the area "under" each boundary line is expressed as a proportion of this (proportions are needed for comparisons between graphs).

Fig. 9.4 Hypothetical example to show how the effect of parameters can be compared using the amount by which they change the outbreak area of the graph.



Figures above lines are: x = aphid reproductive rate

y = % aphids available

z = voracity of A. dorsale

For significance of dotted and solid lines see text.

Boundary Line	Outbreak area	Outbreak area as a proportion of total graph area
1.2+, 5%+, 8+	975	0.975
1.1, 5%, 8	900	0.900
1.1, 5% 16	875	0.875
1.1, 10%, 8	825	0.825
1.1, 10%, 16	750	0.750
1.1, 20%+, 8	675	0.675
1.1, 20%+, 16	400	0.400

These proportions can now be used to show not only which parameters produced the biggest changes in the outbreak area but also by how much the area was changed:

Parameter	Lines compared			Change in outbreak area
Reproductive rate	1.2+ 5%+ 8%	with	1.1 20%+ 16	0.975 - 0.400 = 0.575
% aphids available	1.1 5% 16	with	1.1 20%+ 16	0.875 - 0.400 = 0.475
Voracity	1.1 20%+ 8	with	1.1 20%+ 16	0.675 - 0.400 = 0.275

Using these values it is now possible to say that changes in reproductive rate produced the biggest changes in the outbreak area and that voracity produced much smaller changes than either reproductive rate or % aphids available and so on. This technique of graphical analysis will be used for the following simulations to show how the three parameters change in importance with respect to one another.

N.B. In Figure 9.4 all the boundary lines were drawn in, but some (the dotted lines) were in fact unnecessary as they did not indicate the largest changes in outbreak area. In the following graphs these unnecessary lines will be omitted in the interests of clarity.

(iv) The simulation model output

This section is divided into three; firstly graphs are presented and discussed showing the overall picture for control over the complete range of parameter values used in the model; secondly an "outbreak area" graphical analysis is made of this overall control picture, and thirdly the "outbreak area" analysis is used to show how the relative importance of the three parameters changes if reproductive rates are excluded from the analysis one at a time progressing from 1.1 up to 1.5.

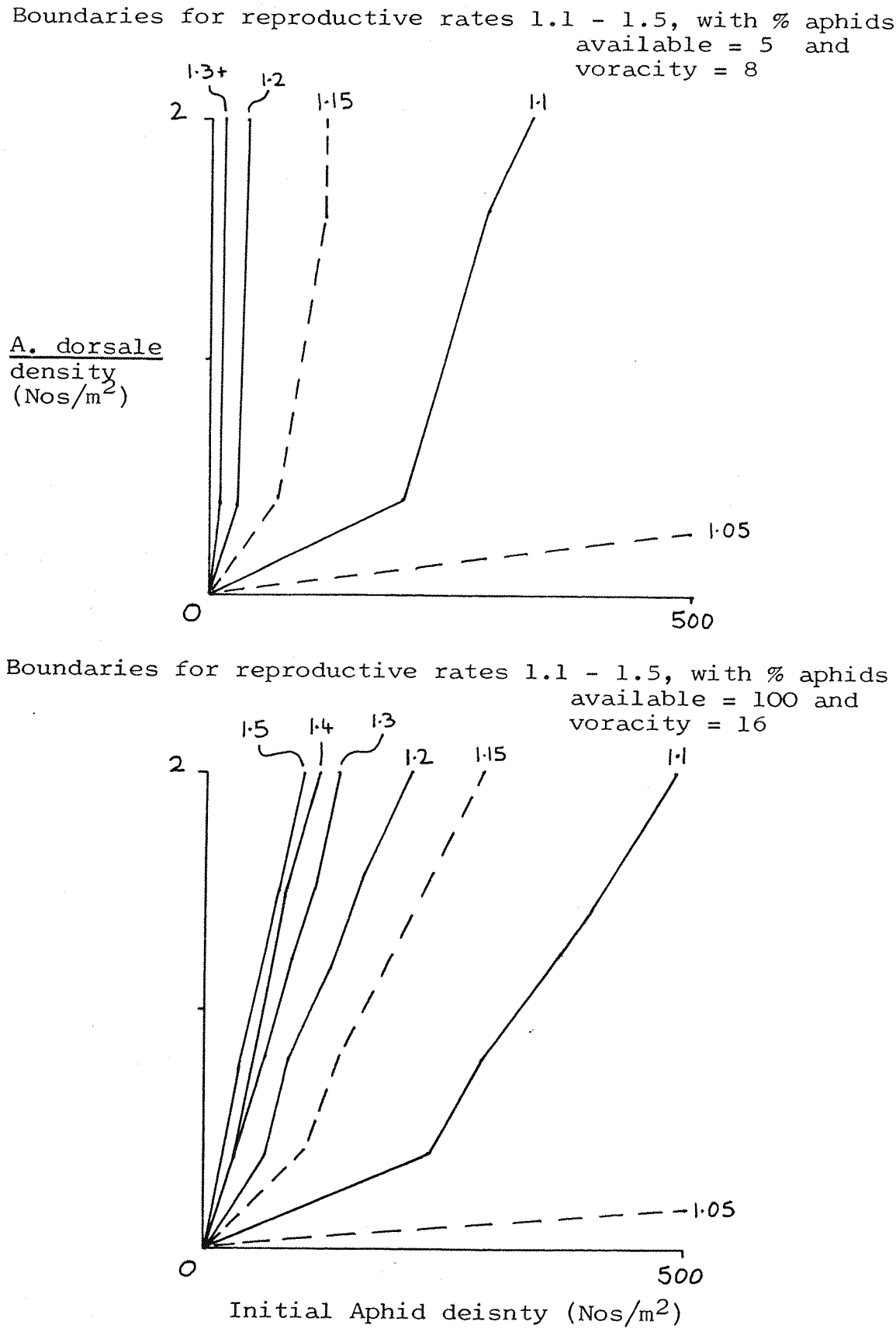
(a) The overall control picture

The range of values allowed in the model for each parameter was chosen to cover most values that would be measured in wheat fields in Great Britain. By graphing the outbreak areas for different aphid reproductive rates when aphid mortality is at a minimum (i.e. % aphids available = 5, Voracity = 8) and when aphid mortality is at a maximum (i.e. % aphids available = 100, Voracity = 16) it is apparent that reproductive rate is most important in determining outbreak area (Fig. 9.5). In Figure 9.5 outbreak areas in the top graph are essentially the same as those in the lower graph; the area increases rapidly as reproductive rate changes from 1.05 to 1.15 and above 1.15 there is little change. In control terms A. dorsale will only be useful over the full range of aphid and beetle densities if the aphid reproductive rate is 1.1 or lower. Changes in voracity or % aphids available do not significantly alter this conclusion.

Some comments on the following graphical analysis:

In Figure 9.5 two extra reproductive rates were included (1.05 and 1.15) to show how quickly the outbreak area changed with small changes in reproductive rate. For simplicity these are excluded from the actual graphical analysis. Also note that when reproductive rate

Fig. 9.5 The effect of reproductive rate on "outbreak area" when aphids are subject to minimum and maximum predation by A. dorsale.



Figures beside lines are reproductive rates, the dotted lines are extra reproductive rates included to show the rate of change.

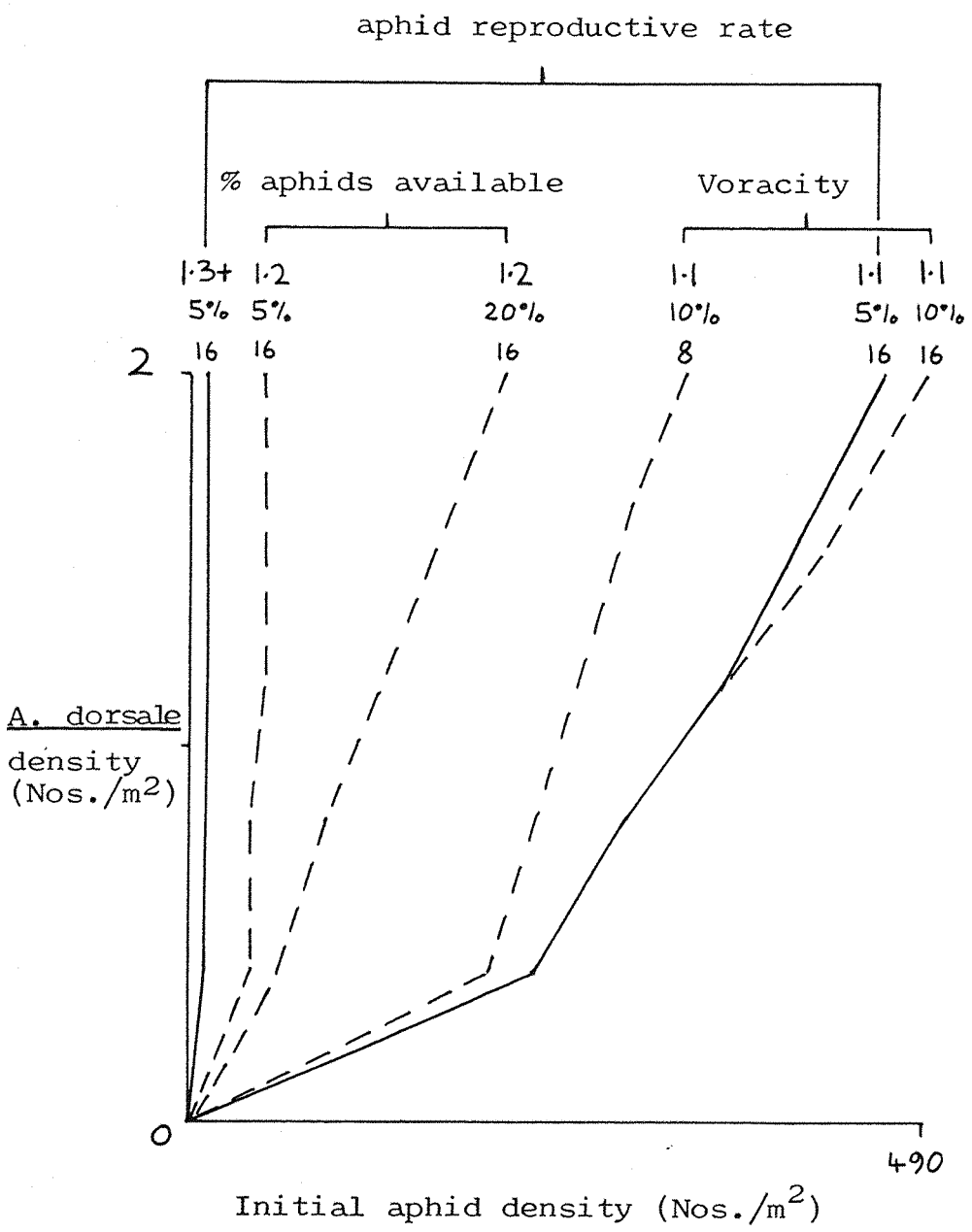
was 1.1, the furthest to the right the boundary line reached on the graph was 490 aphids per m^2 (see lower graph). In effect the maximum control area reaches only to 490 aphids per m^2 and calculation of outbreak area was up to this density only and not to 500 aphids per m^2. This was also done in the subsequent analyses where reproductive rates were excluded one by one. The reason for this is because we are interested in the relative effects of reproduction, % aphids available and voracity and so need extend the graph area only as far as the maximum aphid density reached by any boundary line included in the analysis. Extending the graph area further to the right does not change the relative differences between outbreak areas.

(b) Graphical analysis of the overall picture

The initial impression from 1. above was that aphid reproductive rate was the most important parameter in deciding the size of the outbreak area. Figure 9.6 summarises this by showing the maximum change in outbreak area caused by each one of the three parameters while the other two parameters are held constant. Following the hypothetical example given in the previous section these changes can be represented as the change in outbreak area as a proportion of the total graph area:

Parameter	Lines compared			Change in outbreak area
Reproductive rate	1.3+		1.1	0.982 - 0.380
	5%	with	5%	= 0.602
	15		16	
% aphids available	1.2		1.2	0.916 - 0.773
	5%	with	20%+	= 0.143
	16		16	
Voracity	1.1		1.1	0.533 - 0.380
	10%+		10%+	= 0.153
	8		16	

Fig. 9.6 The relative effects of aphid reproductive rate, % aphids available and A. dorsale voracity on the outbreak area.



Figures above lines are: x = aphid reproductive rate

y = % aphids available

z = A. dorsale voracity

A decrease in reproductive rate can cause about a 60% reduction in the size of the outbreak area; by contrast increases in % aphids available or voracity give only about 15% reductions in outbreak area. This confirms that over the whole range of aphid and A. dorsale densities used in the model, aphid reproductive rate is the primary parameter deciding whether A. dorsale successfully prevents an aphid outbreak.

(c) Further graphical analysis with the successive exclusion of reproductive rates

Having shown that aphid reproductive rate is most important when the complete range of beetle and aphid densities is considered, it now becomes useful to successively exclude reproductive rate values from the analysis (starting with 1.1, then 1.2 and so on) and examine whether reproductive rate is still the most important parameter. This is an essential next step because the model has the dual purpose of establishing whether A. dorsale has any potential for controlling cereal aphids, but also of showing which parameters primarily determine the extent of this potential and hence which parameters require careful measurement in the field. Measurements in the field would themselves have two purposes; to add to the realism of the model by providing more detailed information on the range of values of parameters, and in a forecasting situation measurement of a few important parameters in the field may lead to a prediction of whether the aphid population will be controlled by A. dorsale.

The successive exclusion of reproductive rates may make it possible to produce statements such as "If aphid reproductive rate is 1.3 or above then the most important factor determining control potential is % aphids available, but below 1.3 the aphid reproductive rate itself is most important". To produce the statement the following quantities must be calculated for each of the five ranges of reproductive rates (i.e. 1.1 - 1.5, 1.2 - 1.5, 1.3 - 1.5, 1.4 - 1.5 & 1.5) produced by the successive exclusions:

the maximum change of outbreak area produced by a change in aphid reproductive rate;

the maximum change of outbreak area produced by a change in % aphids available at each of the reproductive rates in the range;

the maximum change of outbreak area produced by a change in voracity at each of the reproductive rates in the range.

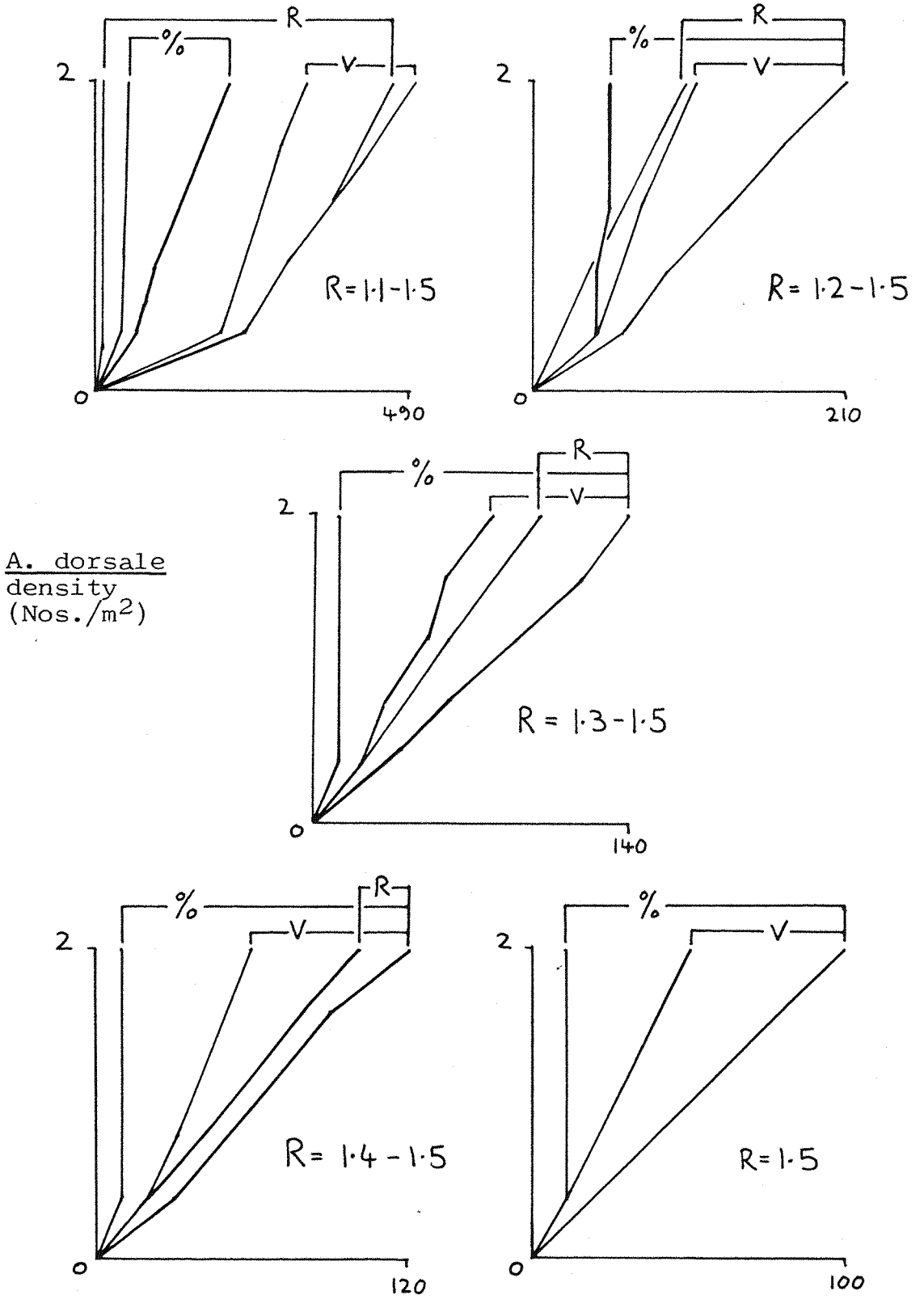
By calculating maximum changes in outbreak area at all reproductive rates within a range for both % aphids available and voracity, it becomes possible to say at what point all maximum changes for these two parameters (i.e. changes at reproductive rate 1.1, 1.2, 1.3 etc.) become larger than the largest change of area produced by a change in reproductive rate.

The largest changes of outbreak area produced by changes in all three parameters are summarised in Figure 9.7. Only the largest changes for each parameter are shown in this Figure; Table I of Appendix 2 gives the complete range of changes of area, together with the individual boundary lines describing each area (each line is represented in the Appendix by the usual three figures representing; reproductive rate, % aphids available, voracity).

In general, for any one range of reproductive rates, the lowest reproductive rate in the range gave the biggest changes of outbreak area for changes in % aphids available and voracity. (Not surprisingly the lowest and highest rates of reproduction in a range gave the biggest change of outbreak area for a change in reproductive rate.) This was so except for the reproductive range 1.1 - 1.5 where the largest change with % aphids available was with reproductive rate at 1.2 (see Table I; Appendix 2).

The graphs in Figure 9.7 show that if reproductive rate is low (1.1), then the starting density of aphids must be very high (over 490 per m^2) before the A. dorsale population exerts no control over the aphid population growth. When reproductive rate is increased (1.2 and above) even quite small initial aphid populations (100-200 per m^2) are beyond the control of the A. dorsale population. In any case the outbreak area covered about half of the total graph area at minimum for all of the graphs (i.e. ranges of reproductive rates). Control of

Fig. 9.7 The changing relative effects of aphid reproductive rate, % aphids available and A. dorsale voracity on outbreak area as successive reproductive rates are excluded from the analysis.



R = reproductive rate; % = percent aphids available;
V = voracity.

aphid populations by A. dorsale is clearly limited to the half of the graph representing high beetle but low aphid densities.

It was noted earlier that sometimes increasing the value of a parameter did not change the boundary line/outbreak area. This happened consistently only with % aphids available with voracity making no difference to the trend below:

Reproductive Rate	% aphids available above which no further change in outbreak area occurred
1.1	10%
1.2	20%
1.3	30%
1.4	30%
1.5	40%

There were similar but less consistent trends in reproductive rate (where again voracity made no difference):

% aphids available	Reproductive rate above which no further change in outbreak area occurred
5%	1.3
10%	1.4

and voracity, where both % aphids available and reproductive rate affected the trend:

Reproductive rate	% aphids available	Voracity above which no further change in outbreak area occurred
1.3	5%	8
1.4	5%	8
	10%	8
1.5	5%	8
	10%	8
	20%	8

The significance of these trends will be examined in the discussion of these model simulations.

Figure 9.7 shows how, as the range of reproductive rates contracts to 1.5, the relative importance of the three parameters changes. When all reproductive rates are included (and hence the full range of beetle and aphid densities), it is the reproductive rate itself which produces the biggest changes in graph area. For reproductive rates of 1.2 and above, % aphids available produced the biggest decrease in outbreak area. And for reproductive rates of 1.3 and above, voracity became the parameter producing the second biggest decreases in outbreak area.

There is a change both in the ranking of parameters and in the amount by which they decrease the outbreak area for the different ranges of reproductive rates. These changes can be summarised from Table I; Appendix 2 as:

		Average decrease of outbreak area produced by change in:		
Range of reproductive rates	Range of initial aphid densities	Reproductive rate	% aphids available	Voracity
1.1 - 1.5	0 - 490	0.60	0.10	0.10
1.2 - 1.5	0 - 210	0.30	0.30	0.15
1.3 - 1.5	0 - 140	0.10	0.40	0.20
1.4 - 1.5	0 - 120			
1.5	0 - 100			

The simulations show that between the reproductive rates of 1.1 and 1.3 the relative importance of the three parameters in determining outbreak area changes substantially. For reproductive rates of 1.3 and above the relative importance of the parameters remained essentially the same. (N.B. In Figure 9.7 there is no change of outbreak area due to reproductive rate changes in the graph for R = 1.5 because only this reproductive rate is considered on the graph.)

9.7 Discussion

The discussion will be divided into three sections:

The underlying causes of the results of the simulation model.

The potential of A. dorsale to control cereal aphid populations.

Implications of the model for future studies on natural enemies.

(i) The underlying causes of simulation results

The simulation model allows the aphid population to increase geometrically while the total number of aphids eaten by the A. dorsale population increases only arithmetically. In effect this means that even quite small increases in the aphids' reproductive rate will result in the A. dorsale population being unable to control the aphid population. This is the reason for the sudden change in outbreak area with reproductive rate in Figure 9.5 and why reproductive rate produced the largest change in outbreak area over the whole range of beetle and aphid densities.

In the previous Section it was found that increasing the value of some parameters past a certain point did not produce any further effect on the outbreak area. In addition, as reproductive rate increased, its relative effect on the outbreak area decreased while the relative effect of both voracity and % aphids available increased. These trends arise for the following reasons:

When the reproductive rate is a low as 1.1, if 10% or more of the aphid population are available for predation then effectively all the aphids produced by the previous day's reproduction are available to be eaten. So it makes no difference, in terms of control of the aphid population, whether 10 or 100% of aphids are available for predation. Increases in voracity, however, may lead to a larger proportion or all of the previous day's aphid offspring being eaten with a resulting increased reduction in the outbreak area.

As aphid reproductive rate increases a larger percentage of aphids must be available if all offspring are to be exposed to predation by A. dorsale. If the % aphids available is very low (5-10%) then only a

small proportion of the previous day's offspring are exposed to predation; this has two consequences. For reproductive rates of 1.3 and above, all aphid populations reach outbreak level and secondly, increased voracity has no effect on the outbreak area. In effect, % aphids available becomes the major parameter deciding the size of the outbreak area but with voracity becoming more important as the % aphids available increases.

(ii) The control potential of A. dorsale

The most obvious point arising from the simulations is that the A. dorsale population cannot "catch up" with the aphid population in the way that specific predators would by immigration or reproduction. This reflects the biology of the two populations in that the aphids reproduce rapidly while the A. dorsale population although capable of consuming large numbers of aphids, cannot itself increase in numbers. A. dorsale will play an important part in regulating cereal aphid populations only when their reproductive rate is low (1.1) or when the initial density of aphids in the crop is small (100 per m^2 or less). The changing growth stage of the crop will favour this as it will lead to aphid populations breeding slowly when the A. dorsale population first enters the field. If control is not established at this stage then the increase of aphid reproductive rate as the growth stage of the crop becomes more favourable will put the aphids quickly beyond the control of the A. dorsale population.

At higher reproductive rates (1.2 and above) the % aphids available becomes important in deciding whether A. dorsale exerts any control over the aphid population. Field sampling (Chapter 7.3) showed that at any one time about 4% of the aphid population were on the ground and hence available. Other work (Shiyomi 1967; Fraser pers. comm.) has shown that a total of about 20 to 30% of the aphid population arrives on the ground at sometime during the course of a day. This may mean that during the hours of darkness (i.e. about 5 h) only about 4-6% of the aphid population are actually exposed to predation by A. dorsale. In this case A. dorsale will exert no control over aphid populations with reproductive rates of 1.2 or over and control will be limited even at lower reproductive rates (see upper graph, Fig. 9.5).

Laboratory experiments (Chapter 4) showed that for A. dorsale, voracity increased with temperature and also as the beetles matured reproductively. Both were allowed for in the model and in general voracity had only a small effect on the potential of A. dorsale to control aphid populations.

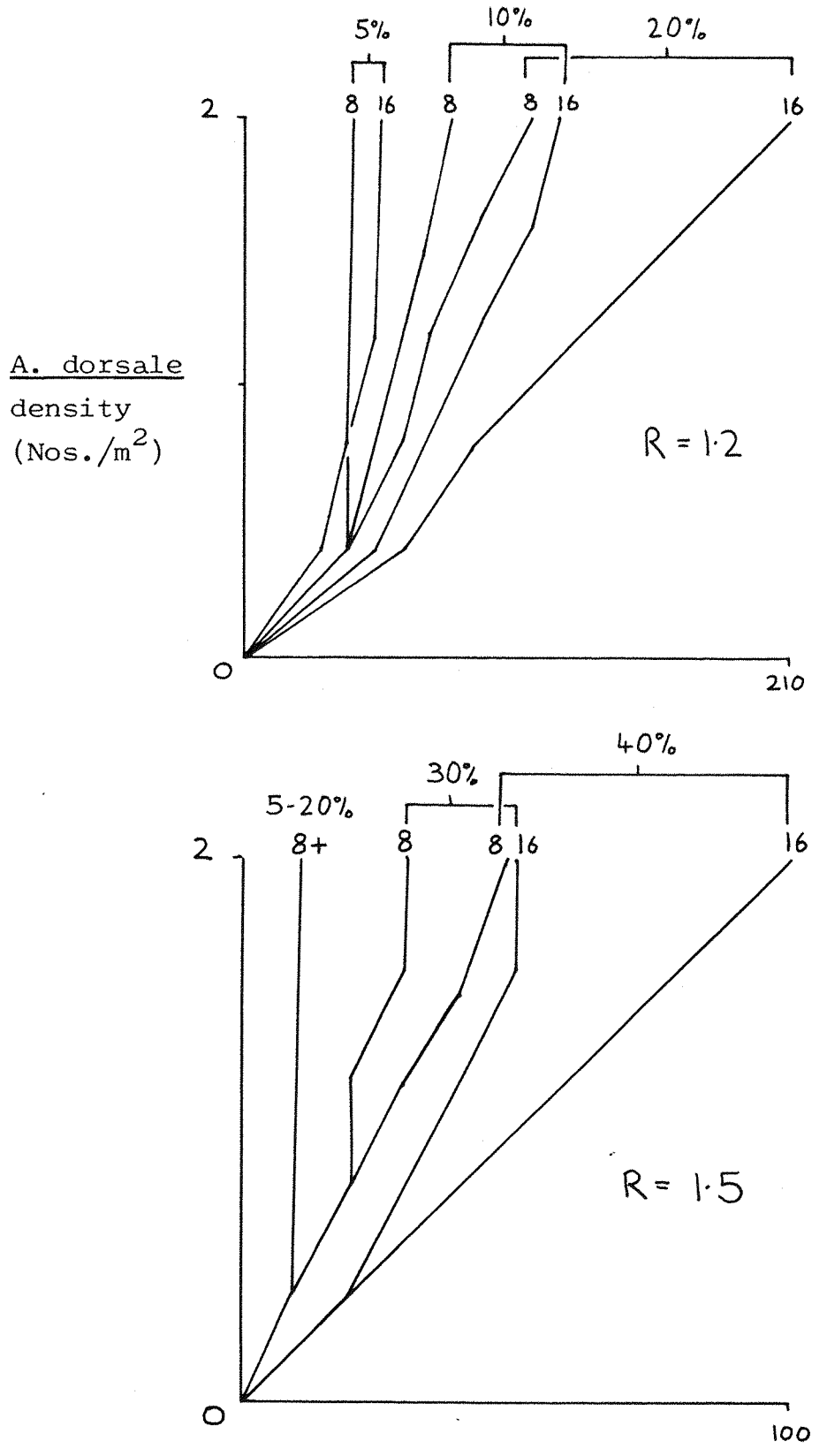
In summary, A. dorsale only has potential to control cereal aphid populations with low reproductive rates or, if reproductive rate is high, the initial aphid population must be small and a large proportion must arrive on the ground and hence be available for predation. The control potential of A. dorsale is determined by parameters of the aphid population (reproductive rate, % aphids available) not by its own parameters (voracity and density).

Implications for field monitoring of control potential:

The biological control potential of A. dorsale is clearly limited to a small number of situations in the field. The accuracy with which the parameters used in the model would have to be measured to show whether conditions were right for control changes according to aphid reproductive rate.

If reproductive rate is 1.1 then neither % aphids available or voracity are important, only a measure of reproductive rate and initial aphid density is required. For reproductive rates of 1.2 and above, it becomes important to know the initial field density of aphids and the % aphids available. If the field density of aphids is above c. 200 per m^2 then A. dorsale exerts no control over the cereal aphid population. Measurement of one field density of aphids gives a definitive statement of control potential. The situation is less simple with measurements of % aphids available; if the percentage is over 40 then it has the same effect on control potential for all aphid reproductive rates. If the percentage is less then 40 then the accuracy of measurement of % aphids available changes with reproductive rate. This is illustrated in Figure 9.8 for the highest and lowest reproductive rates for which % aphids available is important; 1.2 and 1.5. If reproductive rate is 1.2 (upper graph) and % aphids available was measured in the field as greater than 20, then the exact percentage

Fig. 9.8 The changing effect of % aphids available on outbreak area with changing aphid reproductive rate.



R = aphid reproductive rate; figures above lines are:

x = % aphids available
y = Voracity

is not important. If below 20% then the percentage must be measured accurately because the outbreak area increases substantially from 20% available to 5%. Similarly if the reproductive rate is 1.5 and the % aphids available falls between 20 and 40 it must be measured accurately as its precise value will change the outbreak area substantially. Work on Aphis fabae Scop., the black bean aphid, (Holt per. comm.) has shown that it is possible to detect differences in daily reproductive rate as small as 0.1 (the step size used in these simulations). Such sensitivity if achieved with cereal aphids could then show the accuracy with which the % aphids available would need to be determined.

Voracity clearly affects the outbreak area (Fig. 9.7) and as the level of voracity is determined by temperature this can easily be monitored by temperature measurements in the microclimate of the beetle. Such measurements could also be used to calculate decreases of voracity due to A. dorsale being unable to search a sufficiently large area to catch enough aphids to become satiated (Section 9.5). In addition, the effect of alternative prey in reducing voracity could also be determined by measurements of temperature and the two other major components of the diet, Collembola and Nematocera.

The last component is a measure of the density of A. dorsale. Accurate measures of the density of small invertebrates with relatively small population sizes have proved difficult and time-consuming (Southwood 1978). This may be partially overcome by measuring the density to an accuracy of 0-1 or 1-2 per m^2 and adjusting statements about control of the aphid population to include only the lower or the upper half respectively of the graph area.

As the different parameters require very different amounts of time and effort to measure, it is important to establish an order of priorities of the parameters. The next section deals with this.

(iii) Implications for future studies of predators

The simulation model has shown that some parameters are more important than others in deciding whether the A. dorsale population has any potential to prevent cereal aphid outbreaks. Although the

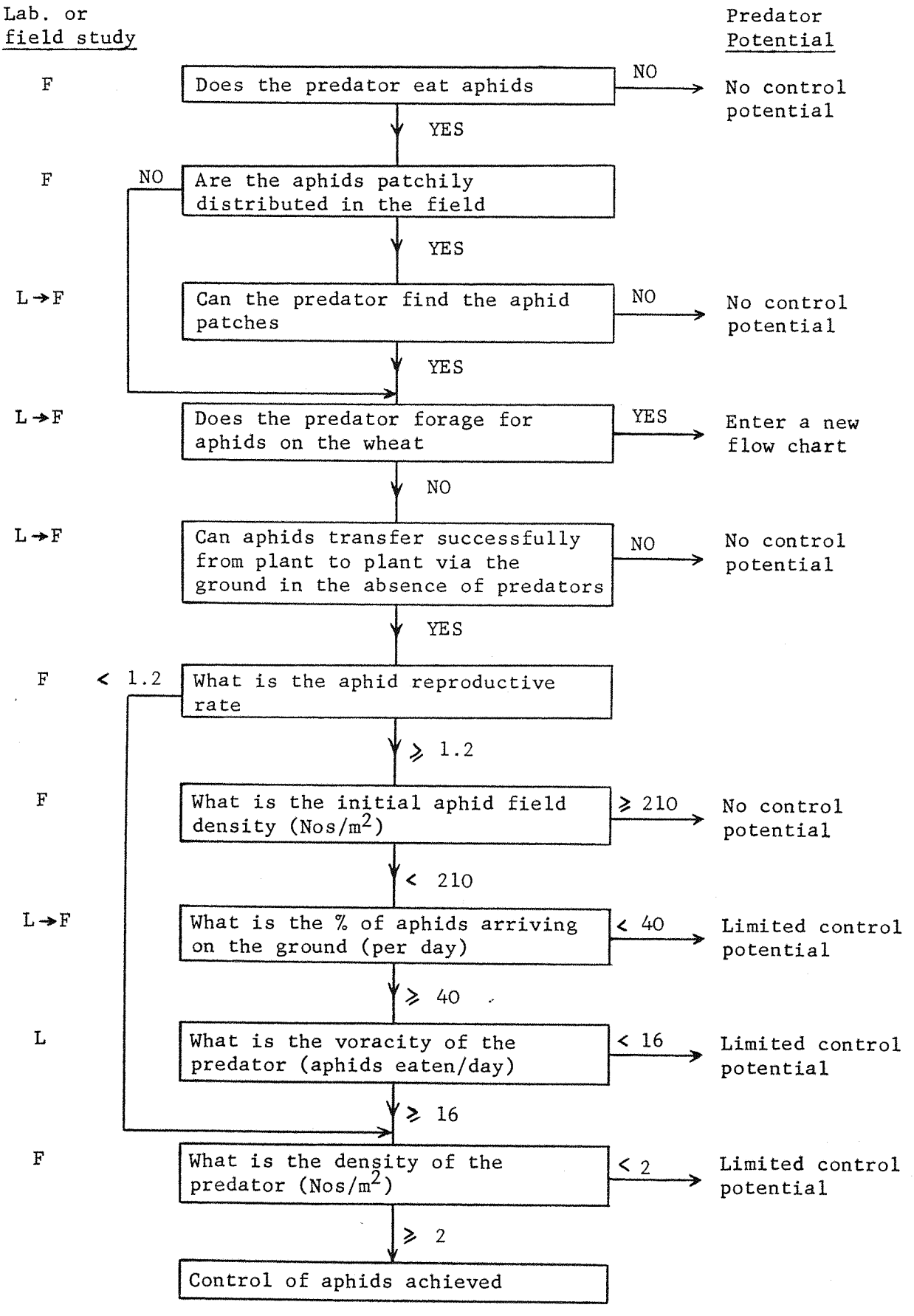
ranking of these parameters changed for the different simulations it is possible to construct a flow chart of their order of importance. The flow chart is in the form of a series of questions which would be asked, in their order of importance, in determining the potential of A. dorsale (or a similar predator) to restrict aphid populations.

The flow chart constructed on the basis of these simulations is shown in Figure 9.9; notice that for simplicity the complications of alternative prey and restriction of search area by low temperatures have been omitted. This does not make the flow chart less realistic because both of these parameters can be allowed for by altering voracity. The actual figures have been given where a question demands them, these would obviously vary for different predators but should not alter the order of the questions (see later).

The first five questions are based on simple reasoning; the predator must be able to find the aphids before it can eat them. Notice that there is a division between predators that can climb the wheat and find aphids at their feeding sites and those predators that are limited to the ground. This is a major division since the former predators can seek out aphids while the latter must wait for them to come down from the wheat. The controlling parameters will clearly be different for the two types of predator.

The subsequent five questions are all based on the output of the simulation model. Reference to Figure 9.7 and the relevant text show how the order and answers to the questions were arrived at. When all reproductive rates are considered (1.1 - 1.5) it is an increase in reproductive rate from 1.1 to 1.5 that produces the biggest change in outbreak area, but for reproductive rates of 1.2 - 1.5, % aphids available and voracity produce bigger changes. The first question then separates the reproductive rate of 1.1 from those of 1.2 to 1.5. The first graph in Figure 9.7 shows that if the reproductive rate is 1.1 then control covers nearly all the aphid densities (up to about 470 per m^2) provided that predator density is 2 per m^2.

Fig. 9.9 Flow chart to determine the potential of a predator such as A. dorsale to prevent cereal aphid outbreaks.



If reproductive rate is 1.2 or greater then the second graph of Figure 9.7 shows that control does not occur if aphid populations exceed 210 per m^2 (i.e. the next question). For reproductive rates of 1.2 - 1.5 then a "% aphids available" of less than 40 or a voracity of less than 16 reduce control potential (Fig. 9.7), with % aphids available having the biggest effect (the next two questions). Finally a predator density of less than 2 per m^2 can reduce control potential.

The order of the five questions produced by the simulation model shows that the potential of ground-based predators is determined principally by parameters of the aphid population. This poses important questions about the way in which research into predators of cereal aphids is conducted. In field studies for instance, an apparently reasonable first move would be to find the densities of the predators; in laboratory studies voracity is usually one of the first parameters to be measured. Both of these questions come at the bottom of the flow chart, i.e. last in importance.

The initial research to show that polyphagous predators do exist in numbers in cereal crops and that they do eat cereal aphids has now been done (see Vickerman & Wratten 1979; Carter et al. 1980 for reviews). This simulation study of A. dorsale has highlighted the areas where knowledge of both predator and prey is incomplete leading to uncertainty about the potential of ground-based predators to control cereal aphids:

The Carabidae are known to be distributed throughout fields of cereal crops(Thiele 1977) but little is known of whether or how they might respond to a patchy distribution of cereal aphids.

While some Carabidae have been caught in sweep nets (Vickerman & Sunderland 1975) nothing is known about the details of climbing behaviour for the majority of species. A. dorsale can climb wheat but does not climb high enough to encounter aphids. This may also be true for other Carabidae and is certainly true for the many Araneae which make their webs on the ground or lower parts of the wheat (Fraser pers. comm.). For these predators it becomes crucially important to know whether aphids regularly move from wheat plant to wheat plant via the ground

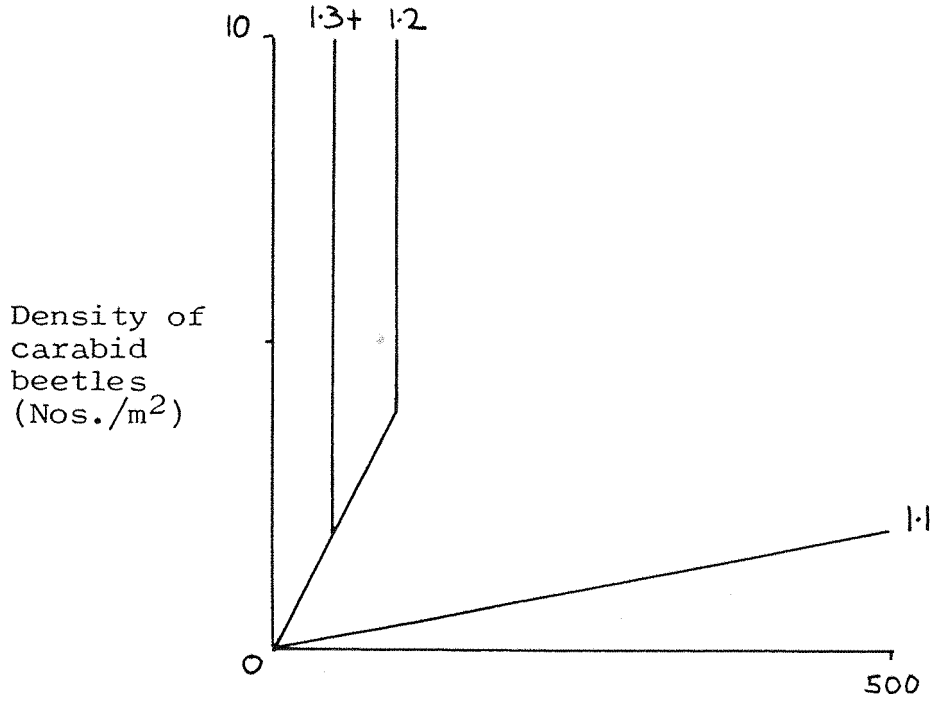
and if so what proportion of the total aphid population is involved. The extent of small-scale movement of aphids within a crop is unknown as are the causes of such movement.

If the simulation is altered to include all ground-based predators then both the predator voracity and density can be raised. The review of Thiele (1977) indicates that densities of single carabid species could be as high as 10 per m^2 and that the voracity of some species could reach several tens of aphids consumed per day. Other work (Sunderland & Vickerman 1980) indicates not only that carabids are unlikely to reach such high densities in England, but also that only a small proportion would be feeding on aphids during the important early phase of aphid population growth. To reflect both these opinions, carabid density was allowed to reach 10 per m^2 and voracity was set at 20 aphids eaten per day. The effect that these increases have on outbreak area is shown for a situation with minimum predation (5% aphids available) and with maximum predation (100% aphids available) in Figure 9.10 . The most important point is that reproductive rate is now less important than % aphids available in determining the outbreak area (compare these graphs with Fig. 9.5). With increased densities and voracities it becomes even more important to assess the percentage of aphids arriving on the ground. The analysis of this simulation was not taken any further, but, as the lower graph in Figure 9.10 indicates, if all ground predators are included the outbreak area is substantially reduced for all aphid reproductive rates.

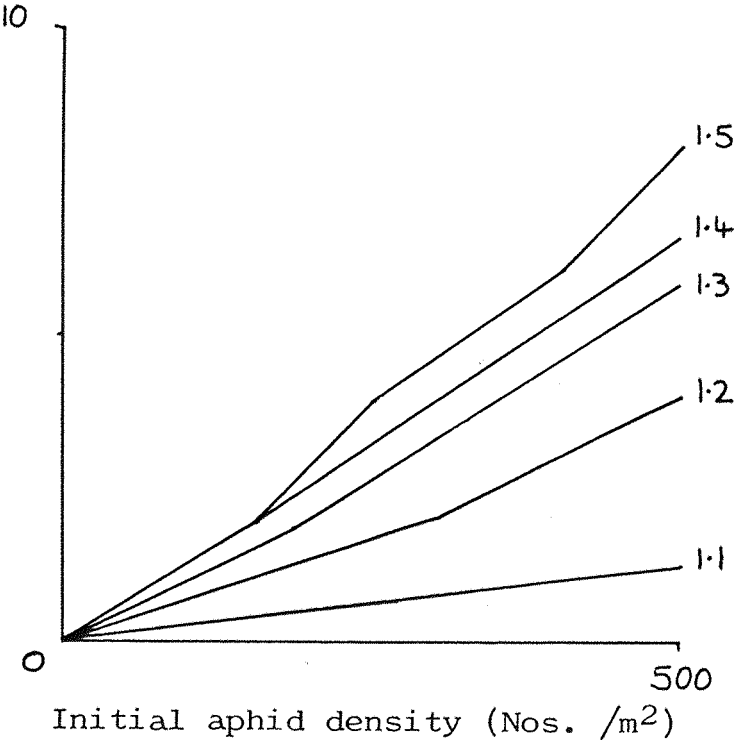
Finally, on the flow chart (Fig. 9.9) beside each question an indication is given as to whether the relevant parameter should be be measured in the field or the laboratory. The vast majority must clearly be measured in the field, with some requiring preliminary laboratory work to reveal underlying mechanisms. Only one parameter (predator voracity) can be measured in the laboratory(see Chapter 4.7; voracity vs. temperature) and even this requires supporting field measurements of temperature and alternative prey availability. This bias towards detailed fieldwork has not been reflected in many of the predator studies to date which have tended to be either synecological survey-type field studies or highly detailed laboratory studies. The

Fig. 9.10 The effect of reproductive rate on "outbreak area" when aphids are subject to minimum and maximum predation by the total carabid fauna.

Minimum predation (% aphids available = 5, voracity = 20)



Maximum predation (% aphids available = 100, voracity = 20)



(Figures beside lines are aphid reproductive rates)

former have indicated which actual species may be useful while the latter have shown what type of predator/predation is useful in biological control. Simulation shows that some detailed fieldwork is now needed to answer a few specific questions which may be the key to the role of ground-based predators in the control of cereal aphids.

C H A P T E R 1 0

CHAPTER 10

FINAL DISCUSSION

This discussion is divided into two parts, the first dealing with the autecological study of A. dorsale and its implications for such studies in the future and the second examining the future for polyphagous predators in integrated control in cereal crops.

10.1 The autecological study of A. dorsale

Polyphagous predators may be more useful in the early reduction of cereal aphid populations than specific predators for two principal reasons: they can exist in a cereal crop in the absence of aphids and are thus in a position to attack the aphid population in its vulnerable early growth stage. These predators may exhibit switching (sensu Murdoch 1969) between prey types, which can produce type III functional responses, an important density dependent mortality factor in certain predator-prey systems (Hassell 1978). A. dorsale was chosen for study because, although a polyphagous predator, cereal aphids could form a large part of its diet.

There are about 320 species of polyphagous predators in cereals (Sunderland pers. comm.), about 80% of which are Carabidae, Staphylinidae or Araneae. Of this 80% about 20% are Carabidae, 20% Staphylinidae and 40% Araneae, yet work to date has concentrated on the Carabidae only (Vickerman & Wratten 1979; Carter et al. 1980). There are some obvious practical reasons for this imbalance; Carabidae are easy to catch, easy to identify and are very robust in laboratory experimentation (see Chapter 3). A. dorsale was also chosen partly for these reasons, with the result that this study deals with one species of a taxon that forms only one fifth of the cereal field polyphagous predators. Extention of findings about the relationship between A. dorsale and cereal aphids to include other Carabidae may be acceptable, but does this hold for the Staphylinidae and Araneae? The following sections show that some of these findings are universal to all polyphagous predators in cereal crops.

There are three sections and they discuss the potential of A. dorsale for biological control, lessons learnt about the way to study polyphagous predators and the most important areas for future research into the role of such predators.

(i) The potential of A. dorsale for biological control

Early work on polyphagous predators in cereals showed that cereal aphids could form a substantial part of the A. dorsale diet (Sunderland 1975; Vickerman & Sunderland 1975); fieldwork in this project confirmed this (Chapter 7.3). Subsequent fieldwork suggested that A. dorsale may be the predominant carabid feeding on aphids (Edwards et al. 1979; Sunderland & Vickerman 1980). Laboratory work (Chapter 4.5) showed that A. dorsale had a type III functional response to all but the largest sizes of aphid and that it was capable of concentrating its search on an area where it had encountered prey. Work from the same Chapter showed that the beetle's voracity increased both with temperature and as it matured reproductively (both of these parameters could be expected to increase voracity as A. dorsale migrated into the field). Fieldwork (Chapter 7.2) showed that A. dorsale migrated rapidly into the field and that this migration occurred early enough for the beetle to arrive before aphid populations had started to increase.

A. dorsale seemed to have great potential for preventing aphid outbreaks. Detailed laboratory experiments (Chapter 5) failed to show however any response by A. dorsale to possible aphid-specific cues (kairomone, honeydew etc.). How was A. dorsale finding the aphids? Field sampling (Chapter 7.3) showed that a constant proportion of cereal aphids were on the ground, and encounters with these aphids may have been the cue that stimulated A. dorsale to climb the wheat and find aphid colonies. Laboratory experiments showed that aphids on the ground did not stimulate A. dorsale to climb and that the frequency of climbing was generally very low. This presented the problem of why a sizeable proportion of A. dorsale should contain aphid remains although aphids were at low field density (Sunderland & Vickerman 1980; see also Chapter 7.3) when the beetle was apparently foraging on the ground with an abundance of alternative prey.

Optimal foraging theory provided a non-specific mechanism which could lead A. dorsale to catch aphids rather than other prey. Bomb calorimetry data supported this by showing that aphids had a high

energy content per unit handling time (Chapter 6.2). Subsequent laboratory experiments showed, however, that A. dorsale was not optimally foraging, it did not choose aphids in preference to the less profitable alternative prey presented. Instead the beetle simply took the prey in the ratio predicted by taking into account the original prey ratio, individual prey capture rates and the difference in size between prey. A. dorsale behaved as a random forager and careful examination of optimal foraging theory showed that this is what would be predicted for such a predator.

Feeding trials (Chapter 6.7) showed that A. dorsale was much less successful at catching Collembola and Nematocera than aphids (these three prey types being the main constituents of the diet) and that capture efficiency for all the prey changed markedly with temperature. The differences between prey were potentially large enough to be the underlying cause of A. dorsale catching aphids, even though they were at low field densities and alternative prey were relatively abundant.

When changes of the three major prey types in the gut contents of A. dorsale were correlated with changes in the field abundances of the prey types (Chapters 7 and 8), the best correlations (though not significant) were obtained with prey samples taken from the ground zone only (of which cereal aphids could be a substantial proportion). The ground zone correlations only were significantly improved by correcting field abundances for the laboratory-measured capture efficiencies of the prey. This strongly corroborated the hypothesis that the success with which A. dorsale caught prey was the single biggest factor deciding the ratio in which prey were consumed and that A. dorsale was a ground-zone predator.

Field observations (Chapter 8) confirmed that A. dorsale did not respond to increased densities of aphids on the wheat with increased climbing activity. Prey sampling and gut analysis again showed that an increase in the density of aphids on the wheat (and hence an increase on the ground) was reflected by increased recordings of aphid remains in the gut contents.

In summary, A. dorsale was found to be a ground predator which made no choice of prey but instead caught them as they were encountered. The reason for the beetle catching an unexpectedly high proportion of aphids was that it was very inefficient at catching other prey types.

As A. dorsale does not climb its potential to control cereal aphid populations is decided by how many aphids come down onto the ground and what their fate is when they arrive there. For instance, if all aphids once on the ground would die there in the absence of predation, then ground predators such as A. dorsale form no part of the mortality factors acting on the aphid population. On the assumption that aphids on the ground can reclimb wheat plants and continue to reproduce it then becomes important to know the proportion of aphids reaching the ground.

A simulation model (Chapter 9) was constructed which showed the effect of varying this proportion on the potential of A. dorsale to control cereal aphid populations. The model showed that A. dorsale could prevent a cereal aphid outbreak in essentially two sets of conditions:

If aphid reproductive rate was very low then the A. dorsale population could prevent an outbreak even if the initial aphid population was large, the proportion of aphids reaching the ground small and the beetles' voracity low.

If reproductive rate increased even a small amount then the A. dorsale population could only prevent an outbreak if the initial aphid population was small, the proportion of aphids reaching the ground was large and the beetles' voracity high.

Field and laboratory studies have shown that the proportion of aphids reaching the ground (i.e. available for predation) is likely to be small and that low night temperatures and the presence of alternative prey will substantially reduce the voracity of A. dorsale (Chapter 9). Unless aphid reproductive rate is low A. dorsale has little potential to prevent aphid outbreaks.

The potential of A. dorsale is limited largely because it is a ground predator; many other polyphagous predators in cereal crops may

fall into this category. Aphids are highly aggregated on the crop plants and within and between fields and to find them by a method more sophisticated than random search requires a high level of adaptation by the predator. The combination of aphids only reaching high population levels sporadically and the often-abundant alternative prey on the ground in cereal crops makes it unrealistic to expect a general/ polyphagous predator to reach this degree of adaptation or spend much time searching on the crop plants.

The essential properties of cereal aphids as pests and possible predator adaptations to these are summarised in Table 10.1. Note that a "within-crop" predator is simply a predator that attacks the aphids while they are in the cereal crop; no consideration is given to predation of aphids while on their alternative hosts. To be effective a predator should possess at least one adaptation to each of the three pest quality categories. A. dorsale can be considered to show adaptation 3) to pest quality A), has none of the adaptations to pest quality B) and shows adaptation 2) to pest quality C). With one essential class of adaptation missing A. dorsale cannot be a true biological control agent nor will it be effective if it is the only polyphagous predator considered in an integrated control program.

A small-scale simulation of the control potential of the ground-based Carabidae as a whole (Fig. 9.10, Chapter 9) suggested that the increase in density and voracity that this represented considerably extended the range of parameters over which outbreaks were suppressed. In effect by considering all the Carabidae rather than just A. dorsale, the vital third adaptation to pest quality B) can now be included, i.e. adaptation 3), High density and voracity. However even if all the Carabidae were considered together there were some combinations of parameters in the simulation model that still led to aphid outbreaks. The implication is that polyphagous predators must be considered as part of an integrated control scheme and not as a means of biological control in their own right. The future of polyphagous predators in integrated control will be considered in the second half of this Chapter.

Table 10.1 The adaptations that an ideal "within-crop" predator should possess to prevent cereal aphid outbreaks.

Pest quality	Predator adaptation
(a) Only sporadically abundant from year to year and field to field.	(1) High search capacity: predator can find aphids even at very low field densities.
	(2) High mobility: predator less efficient within fields, but very efficient at locating fields with high densities of aphids.
	(3) Alternative prey: predator eats other prey but switches to aphids as soon as they arrive in the crop.
(b) Highly aggregated on crop plants.	(1) Search adaptation: predator has mechanism to lead directly to aphids on plants.
	(2) Long search time: predator makes undirected search of ground and crop plants but can search for extended periods of time.
	(3) High density/voracity: predator cannot climb wheat but consumes all aphids reaching the ground.
(c) Short generation time and high fecundity.	(1) Reproductive response: predator has short generation time and is very fecund so can attack aphid population at any stage.
	(2) Timing response: predator has long generation time/low fecundity but adaptations to cold weather and for rapid field colonisation allow it to attack aphid population at its vulnerable early growth stage.

(ii) The autecological study of a polyphagous predator as a natural enemy

The term natural enemy is used here to emphasise the point that the following comments refer to research where the aim is to establish the role of a predator/parasite in restricting the growth of a pest population. That is, an applied approach. Some of the points made clearly would not apply to pure research.

Assessing the control potential of a polyphagous predator can be considered to consist of two parts; finding the maximum sustainable voracity of the predator and then identifying and quantifying the constraints on this level of voracity that operate in the field. The two have quite different experimental requirements.

Assessment of maximum voracity requires only basic equipment (a simple arena with an excess of prey) although preparation may be more complicated, e.g. a temperature controlled room, predators at different states of reproductive maturity and so on. The aim is only to assess a maximum so the predator is presented with an excess of readily-available prey. The complicating effect of satiation/starvation producing very variable levels of hunger is eliminated by running the trials over several days.

Assessment of the constraints that would operate on voracity in the field needs more complicated equipment because the experiment requires an extra degree of realism. The functional response provides a good example of a laboratory technique which although often used on predators shows only a few of the requirements of this type of assessment.

Since Holling (1959) first defined his three functional responses, the type III (sigmoid) response has had an intuitive appeal for pest control because of its density dependent, and hence potentially regulating, component. But modelling work (Hassell 1978) has since shown that for many arthropod predator-prey systems the sigmoid response will not produce regulation and in addition Hassell suggests that the concept of regulation is not particularly useful in regularly disturbed environments such as annual crop systems. Despite this the functional response is still widely used as a first step in predator assessment.

The advantage of a functional response is that it gives the response of a predator to prey over a range of densities. The response can show that at above a certain prey density a predator eats proportionally less prey and so on. The disadvantage of a response obtained in a simple arena is that it may be a reflection of any one of several characteristics of the predator, e.g. satiation, aggregative behaviour and so on. This makes it difficult or impossible to extrapolate from the response to the behaviour of the predator in the field.

More complex arenas are more realistic but have the disadvantage that their complexity makes it impractical to conduct trials over a wide range of prey densities. A more simple high versus low prey density comparison has to be used. If this approach is to be used it is essential to use crop plants at a realistic growth stage with the prey in its natural distribution on the plant. Access to previous field sampling records is vital to determine reasonable prey densities and further field samples may be necessary to determine their distributions.

The use of the more complex arena has two main advantages: it allows the development of techniques for later use in the field (classification of climbing behaviour etc.) while pointing to the mechanisms by which the predator finds its prey. Secondly, for polyphagous predators, it shows the complexity of arena required for trials using both pest and alternative prey (as A. dorsale was a ground zone predator the arena could be simplified by excluding the crop plants). Laboratory methods can then be repeated in the field (Chapters 5 and 8) to provide confirmation of laboratory results or identify short comings in experimental design. Confirmation of laboratory results could be obtained less directly by using the correlation of predator gut contents with prey densities (Chapter 7.3). If prey are sampled from different parts of the crop (i.e. on the plants or on the ground), then the sample giving the best correlation with gut contents indicates where the predator was catching prey.

If corroboration in the field is not possible the more complex laboratory arena can still give a more useful insight, in the applied sense, to the relationship between predator and pest than the detailed

and necessarily artificial functional response. Comparisons between the field study of Chapter 8 and the laboratory arena work of Chapter 5.6 showed that certain types of information could be safely extrapolated from the laboratory to the field. In general, relative statements such as "higher densities of aphids did not lead to any increase in frequency of climbing" could be extrapolated, while absolute statements such as "A. dorsale spent 50% of its time searching" could not. Essentially, predator behaviours could be quantified realistically in the laboratory, while daily time budgets of the behaviours could not.

Finally, the technique of small scale computer simulation proved invaluable for comparing the effects of parameters operating in the interaction between predator and prey. It was apparent from laboratory and fieldwork (Chapters 5 and 8) that as A. dorsale did not climb, the proportion of aphids arriving on the ground was important. The simulation showed how important (with respect to beetle voracity etc.) and with what degree of accuracy this proportion had to be measured. Simulation was used only at the end of this project with the result that this key issue of measuring the proportion of aphids arriving on the ground was only superficially studied. This is clearly a technique to be used mid-way through this type of project; the background work on the crop has already been done by other workers and by this stage many of the important parameters for the predator in question have been identified. Simulation can then be used to assess which parameters require further work and perhaps alter the emphasis of the research by showing their relative importance.

(iii) Future research on polyphagous predators

The earliest research on polyphagous predators in cereals was synecological. As nothing was known about them the research was almost of a survey form; how many species? how many feed on aphids? and so on. The initial research produced some results that could not be answered by the survey technique; how were some carabids able to find and eat aphids even though the aphids were at very low field densities? This autecological study was a response to the need for more detailed work to identify the underlying causes of unusual results produced by the surveys. The study has pointed to three areas for

future work, the first two of which once again require a synecological approach:

Can polyphagous predators aggregate to patches of high aphid density in cereal fields?

Can polyphagous predators find cereal aphids at their feeding sites on the cereal crop plants?

What are the daily small scale movements of apterous aphids in a cereal crop?

The three questions lead on from one another to show whether polyphagous predators can find aphids within a field, then whether they can find the aphids on the crop plants, and if they can't, how many aphids make themselves available for predation because of their small scale movements between ground and crop plants.

The reasons for making the first two studies synecological are both pragmatic and in the interests of partially-guided research:

Some of the work would probably be done within the three year grant/Phd system. Within this time it is probably not possible to study both the aggregation and the detailed prey finding/climbing behaviour of one predator species because both would require the use of very labour-intensive techniques. More efficient use of the time could be made by studying one or other of the questions but using the techniques to study several species.

Much research is necessarily on an individual and essentially uncoordinated basis but in subjects that have a strong applied bias some directing of effort is required to ensure that problems are answered within a reasonable time period. The approach of an academic for instance might be "Are polyphagous insects capable of optimally foraging by exploiting the patchy distribution of prey in their environment? "; and she/he may choose a carabid beetle as the predator, aphids as the prey and a cereal field as the environment. The academic would have coincidentally answered the aggregation question for just

one carabid species. The applied biologist would be more interested in asking "Of the carabid species that feed on cereal aphids, how many are capable of aggregating to patches of aphids in the field?". The latter approach sacrifices a deeper understanding of the mechanisms involved for a more complete picture of aggregation in the Carabidae as a whole. A detailed autecological study of the aggregative prey-finding behaviour of a carabid should only become necessary if the more general synecological study of aggregation produced results that could not be explained and hence required further, more detailed, study.

A similar argument applies to the climbing behaviour of polyphagous predators. The Carabidae have been credited with being "good plant climbers" (see Sunderland and Vickerman 1980) with the implication that they are good aphid predators as a result. This study has shown that climbing ability need not be linked to aphid predation and that careful behavioural observation is required to quantify "climbing" ability. A survey is required of which polyphagous predators can climb and as a result feed on aphids on the plant.

If the survey of climbing ability of polyphagous predators showed that large numbers or even whole taxa did not climb then it would be important to assess the movement of aphids within a cereal crop. If for instance either almost no aphids ever reached the ground or those that did died of causes other than predation (desiccation, etc.) then the role of ground-zone predators in the control of aphid population growth would be nil. Work on the aphids should include detailed laboratory studies to reveal the underlying causes of their small scale movements, followed by accurate field sampling and/or observation of aphids to confirm or reassess laboratory findings.

The first of the three studies (aggregation) is already under way (K.D. Bryan, Southampton University) but the other two have only been touched on in related studies. Both are vital because they may decide the role of polyphagous predators in cereals without the need to consider complications such as alternative prey, amount of time spent searching the field and so on. Applied biology requires the asking of precise, dichotomising questions; the ability of polyphagous predators to climb and the movement of aphids within the crop are examples of this.

10.2 The future of polyphagous predators in integrated control of cereal aphids

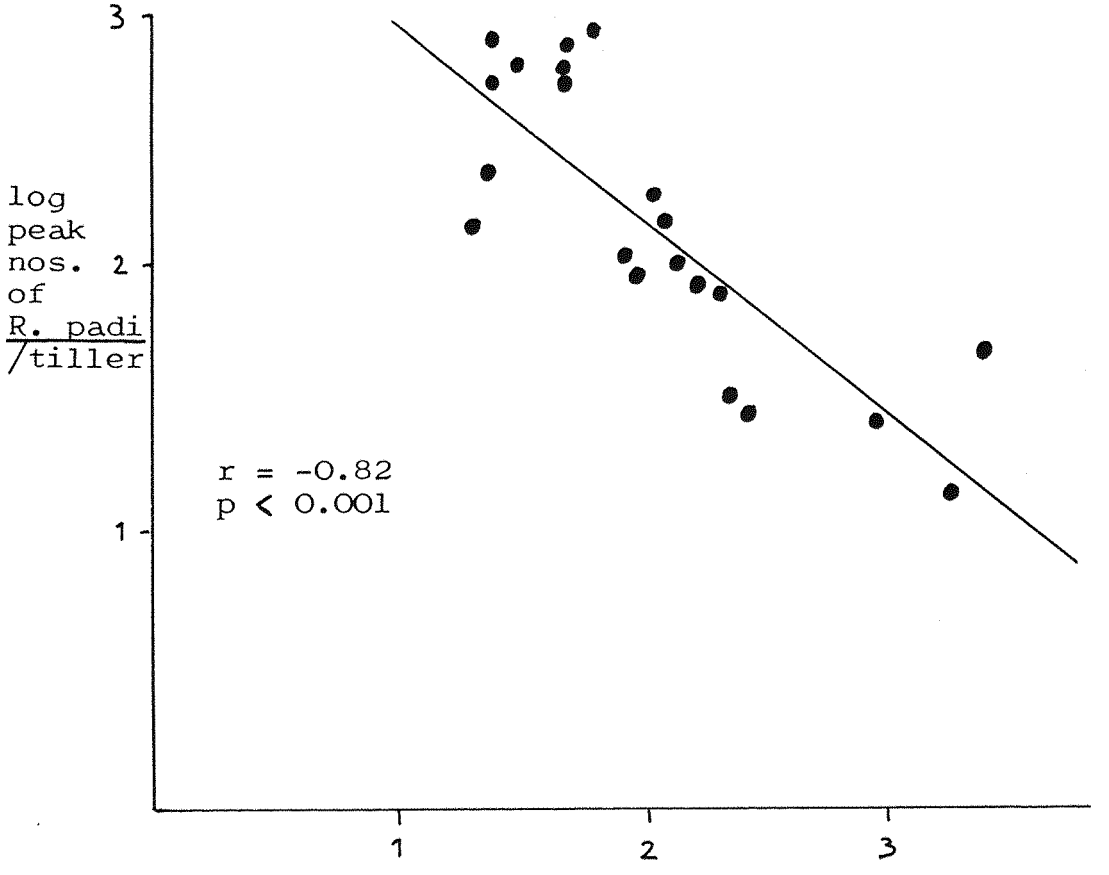
The output of the simulation model used here (Chapter 9) and other simulation work (Carter unpubl.) shows it to be unlikely that any one polyphagous predator species could prevent cereal aphid outbreaks. Slight increases in aphid reproductive rate or a slight delay in the predator attacking the aphids would lead to rapid increases in the aphid population. Even if polyphagous predators as a whole are used in the simulation (Carter unpubl.) they cannot prevent aphid outbreaks under all sets of conditions. They must therefore be considered as part of an integrated control system in which spraying of aphicides occurs only in years when the aphid population is beyond the control of the polyphagous predators.

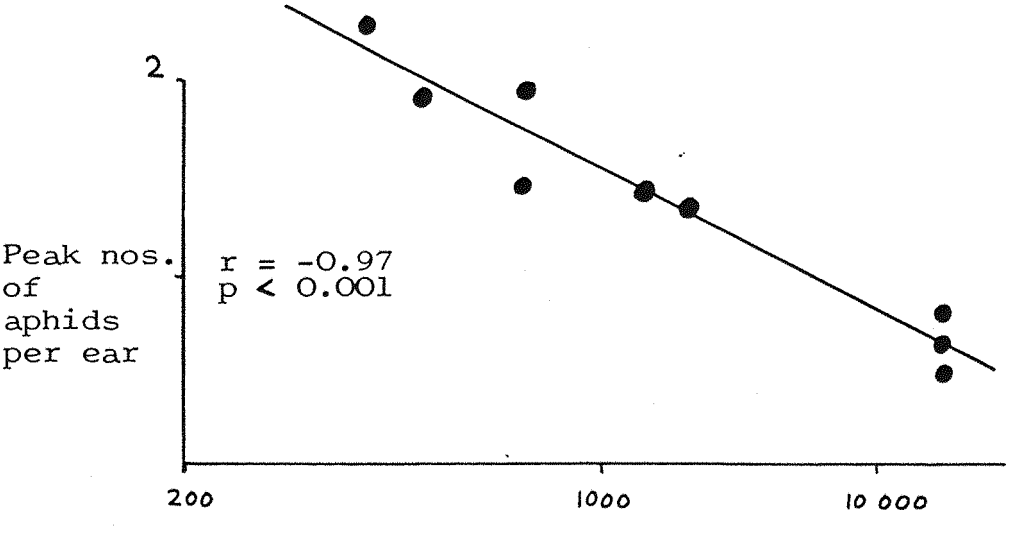
(i) The current potential of polyphagous predators for integrated control

The simulation model emphasised that the density and voracity of the polyphagous predator population was important in determining the degree of control over the aphid population. It should be possible to show this in the field by making use of the natural variation in polyphagous predators between fields. There should be a negative correlation between aphid density and polyphagous predator density. The negative, though indirect, correlations between numbers of aphids and the proportion of predatory arthropods in fields found by Potts & Vickerman (1974) may be an example. Barrier experiments where polyphagous predators were excluded have also shown this correlation for carabid beetles (Edwards *et al.* 1979). More recently a between-fields survey in Sweden showed a significant negative correlation between peak numbers of cereal aphids of the species *R. padi* and numbers of polyphagous predators caught (Chiverton unpubl.). This work strongly implies that polyphagous predators are imposing a significant mortality on aphid populations in the field.

In the two latter relationships referred to above, the range of numbers of polyphagous predators was very large (Fig. 10.1). The work of Sunderland & Vickerman (1980) provides an explanation for this. They showed that even when aphid densities were high the proportion of

Fig. 10.1 The relationship between numbers of polyphagous predators and the cereal aphid Rhopalosiphum padi (Chiverton unpubl.), and secondly between numbers of Carabidae and cereal aphids (Edwards et al. 1979).





individuals containing aphid remains in many carabid species was very low (less than 5%). Many of the carabids were taking alternative prey and this in effect reduces their voracity so that a higher density of the beetles is required to reduce aphid numbers significantly.

Studies on the phenology of the Carabidae in cereal crops (Jones 1979; Brown unpubl.) show that the necessary farm practices of rolling, harvesting, burning and ploughing fields occur at times when their field activity is at a minimum. As many of the resting stages of the carabid life cycle occur at some depth in the soil or in field boundaries, (Thiele 1977) these practices are unlikely to be a significant source of mortality.

The application of sprays to combat weeds, fungi and pests is a much larger source of mortality in carabid populations (Thiele 1977; see also Chapter 7.4). Applications of broad-spectrum pesticides can cause severe reductions in carabid populations (Vickerman & Sunderland 1977). The depletion in numbers may be within one season only or may be carried over into the following year (Vickerman unpubl.). In addition there has been no work on the sub-lethal effects of these pesticides on the predatory potential of the Carabidae. Increasing use of pesticides could lead to "target-pest resurgence" (van den Bosch & Messenger 1973) with aphid outbreaks occurring with increasing frequency as pesticides deplete the natural enemy population.

In summary, where the Carabidae (and other polyphagous predators) occur naturally in high numbers they seem to depress aphid numbers. Normal agricultural practices probably do not affect this relationship. The use of pesticides, however, can produce high mortality in predator populations reducing the number of areas where aphid populations will be "naturally controlled". The consequences of this for the future of control of aphids in cereals are discussed in the following section.

(ii) The future potential of polyphagous predators for integrated control

The previous section made the point that some fields seem naturally to contain a high enough density of polyphagous predators to restrict

the growth of aphid populations. Two points arise from this observation:

The cereal ecosystem is not like an orchard or a glasshouse where interactions between predator and prey may continue without major physical disturbance until the predator successfully controls the pest. In the cereal system the number of polyphagous predators at the start of a season must be sufficient to effect control; these predators mostly breed in an annual cycle making a reproductive response to aphids impossible.

The scale of cereal growing makes artificial boosting of polyphagous predators on a yearly basis impossible, but in any case the differences between fields that produce the natural range of predator densities may make introduction of extra predators into some fields worthless.

There would seem to be two approaches to enhancing the effect of polyphagous predators in cereal fields. Either enhance the effect of the predators already present in the field or increase the actual number of predators in the field. The former could be a short term project but the latter certainly requires a long research and initiation period.

(a) Enhancement of the potential of the resident predator population

The efficiency of polyphagous predators as consumers of cereal aphids can be reduced both by the presence of alternative prey and by the predators' lack of climbing ability:

Reduction of alternative prey alone may be not only impossible but also undesirable. Spraying to remove alternative prey would almost certainly affect the aphid and predator populations as well, making it more economic to spray specifically against aphids in the first place. Removal of alternative prey would also seriously deplete the overall density of prey in the field. This could lead to many predators starving or leaving the field for areas of higher prey density.

Lack of climbing ability may be compensated for by knocking aphids off the cereal plants onto the ground. A chemical irritant, aphid alarm pheromone or sub-lethal dose of a knock-down aphicide may be the easiest and least environmentally-damaging way to achieve this. There would be at least two advantages over conventional pesticides; as the spray application need only dislodge the aphids it should be less toxic to the polyphagous predator population, aphid mortality may be supplemented by other factors such as desiccation once the aphids are on the ground.

(b) Increasing the size of the resident predator population

If the size of the resident predator population is determined by the abundance of prey in a field then it may not be feasible to increase the predator population. Undersowing of crops can lead to lower aphid populations (Vickerman 1978), and this may be an effect of higher densities of alternative prey encouraged by the ground-zone vegetation, which in turn encourages more predators. Undersowing is a yearly commitment and due to changing agricultural practices (i.e. farms grow cereals only and so don't need to undersow) is not now widely adopted by farmers (Vickerman pers. comm.), making assessment of its potential to enhance polyphagous predator populations difficult.

The use of "organic" fertilisers (originating from livestock) on land (as opposed to artificially manufactured fertilisers) has also been linked to increased predator populations (Jepson unpubl.; Dritschilo & Erwin 1982). Once again it is the change in agricultural practices by farmers (i.e. a polarisation towards livestock or cereal production) that makes this impractical as a yearly commitment. In addition the current lack of understanding of the cause of the relationship limits the potential of the method.

Manipulation of field boundaries may provide a better-understood and more acceptable way of increasing the number of polyphagous predators in a field. Studies on the species of polyphagous predators overwintering in field boundaries have shown that they are the ones identified by Vickerman & Sunderland (1980) as having the most potential to control cereal aphids (Sotherton unpubl.). In addition, the favoured field boundaries, although varying slightly between predator species, can be

as structurally simple as raised grass strips between fields. The cost of constructing such simple boundaries may not be prohibitive, particularly as they would form a permanent and self-renewing predator reservoir. It is interesting to note that polyphagous predators were found to be less important in East Anglia (McLean 1980) than in other parts of the country (see references in previous section). Field sizes in East Anglia are generally larger than in other parts of the country and hence have less boundary area (and hence predator over-wintering sites) per unit area of field (see also Chapter 7.2).

In summary, enhancement of the potential of resident predator populations could be achieved relatively easily by the expedient of inducing aphids to leave/fall off the wheat to the ground, where they will be more available to the predator population. This method requires however that the resident polyphagous predator population is large enough to suppress the aphid population. Increasing the size of the resident predator population is likely to be more difficult because it requires a substantial input from the farmer. This must be either in terms of less "efficient" cereal growing (i.e. use of undersowing and organic fertiliser and retaining field boundaries) or in terms of capital expenditure on providing overwintering sites for polyphagous predators. Aspects of minimum expenditure versus long term integrated control are discussed next.

(iii) Long or short term economics

The methods proposed for enhancing the effect of polyphagous predators require the farmer either to decrease the efficiency of his cereal fields (e.g. by using organic fertiliser/undersowing) or to expend capital on making alterations to his land (field boundaries) and using different sprays (aphid "knock-downs"). An examination of the profits and costs of cereal growing (Watt pers. comm.) shows why farmers may opt for prophylactic spraying of pesticides rather than enhancement of natural enemies.

The expected gross profit from a hectare of high quality wheat is £500.

The fixed costs (labour, machinery maintenance, interest charges etc.) of growing the hectare of wheat are £250.

The cost of a spray application of insecticide over the hectare of wheat is £15.

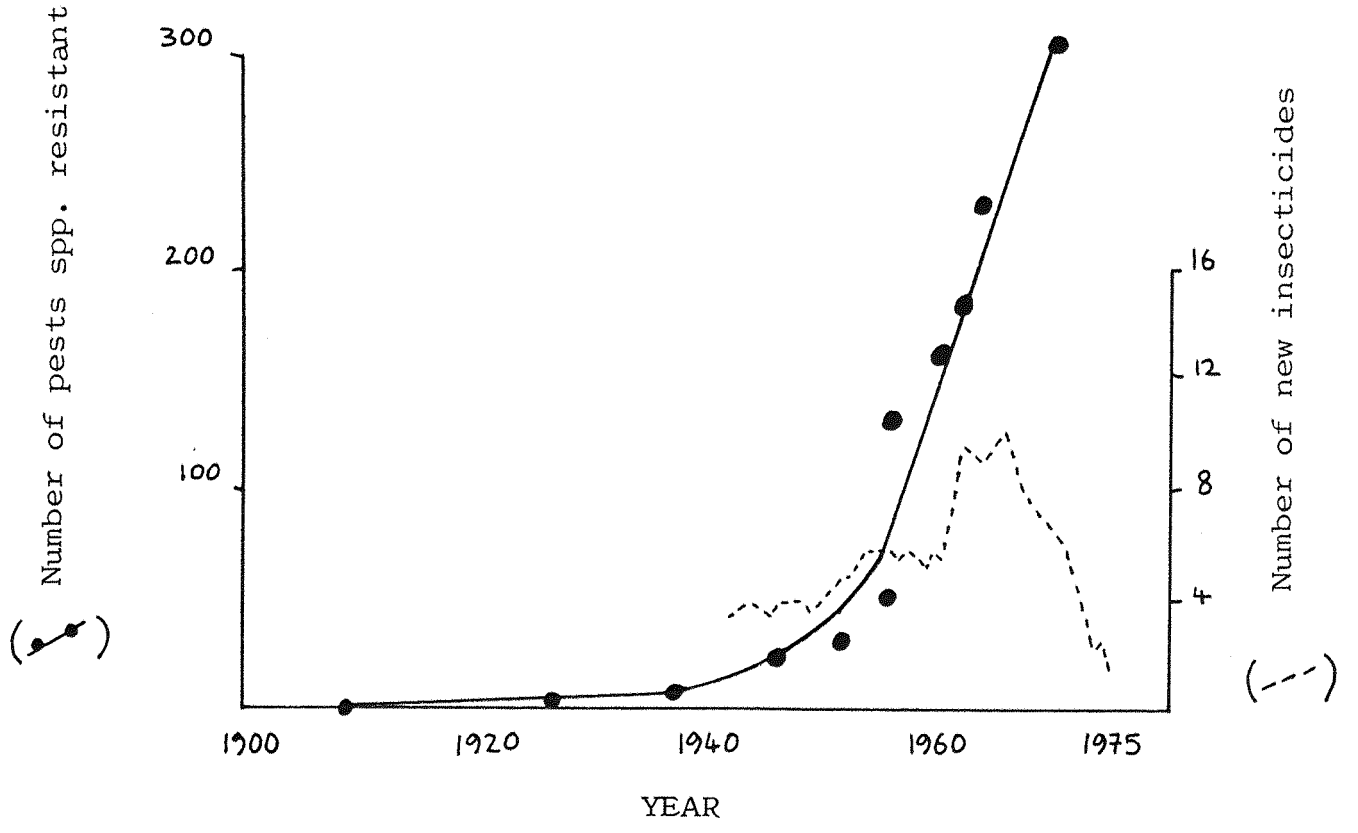
As insecticides are currently very effective against aphids the farmer, for a £15 outlay, is guaranteed his £500 gross profit from the wheat, which after all costs have been deducted becomes £235 net profit. With this ratio of cost of spray to net profit it would be impossible to convince a farmer on economic grounds that it is worthwhile spending several hundred or several thousand pounds on altering his farm to encourage polyphagous predators which in any case cannot be guaranteed to control aphid populations every year.

These are the short-term economics of cereal growing calculated on the basis of the current situation of cheap pesticides which are 100% effective in preventing cereal aphid outbreaks. This situation is likely to change; the cost of pesticides will increase although it seems improbable that they will reach levels where polyphagous predator enhancement becomes a comparable short-term economic option. The potential development of resistance to pesticides by aphids is much more likely to make enhancement of polyphagous predators a serious proposition.

Southwood (1979) graphically illustrated the problem of pest resistance by comparing year by year the increasing number of resistant pests with the decreasing number of new pesticides (Fig. 10.2). So far, cereal aphids have not developed resistance (Stribley et al. 1983), but prophylactic application of pesticides makes it very probable that this will occur (van den Bosch & Messenger 1973; de Bach 1974). Probably because of the non-specific toxicity of most pesticides, once a pest has developed resistance to one chemical it also has resistance to several others (Huffaker & Messenger 1976). This has resulted in well over 200 examples of resistance to pesticides with some pest species almost impossible to control with any chemical. Were this to happen with cereal aphids, polyphagous predators would become an economic, if not the only, option for control.

An integrated control system based on pesticide applications only in years when polyphagous predators could not provide effective control would avoid the problem of resistance. As aphid outbreaks are still

Fig. 10.2 The change in the number of new pesticides produced and the number of pest species showing resistance to pesticides during this century (after Southwood 1979).



sporadic (Vickerman & Wratten 1979), the aphid population should not be under sufficient selective pressure to develop resistance to pesticides. The farmer will profit because his spraying costs will be reduced; in some crops spraying regularly actually increases pest outbreaks (van den Bosch & Messenger 1973). If integrated control is to be feasible then forecasting of cereal aphid outbreak years (i.e. years when polyphagous predators will be ineffective) must be 100% efficient. Applied research has shown that polyphagous predators have a role to play in aphid control; it must now provide an accurate forecasting system to make the polyphagous predator part of a truly economic option.

REFERENCES

REFERENCES

AKRE, B.G. & JOHNSON, D.M. (1979). Switching and sigmoid functional response curves by damsel fly naiads with alternative prey available. J. Anim. Ecol. 48, 703-720.

ALCOCK, J. (1975). Animal Behaviour. Sinauer Assoc. Inc., U.S.A.

ALLEN, R.A. (1979). The occurrence and importance of ground beetles in agricultural and surrounding habitats. Carabid beetles: their evolution, natural history and classification. (Ed. by T.R. Erwin, G.E. Ball, D.R. Whitehead & A.L. Halpern.), pp. 485-505. Dr. W. Junk. Hague.

AUCLAIR, J.L. (1958). Honeydew excretion in the pea aphid, Acyrthosiphon pisum. J. Ins. Physiol. 2, 330-337.

BAARS, M.A. (1979). Patterns of movement of radioactive carabid beetles. Oecologia. 44, 125-140.

BAILEY, N.T.J. (1964). Statistical methods in biology. English Universities Press.

BANKS, C.J. (1957). The behaviour of individual coccinellid larva on plants. Anim. Behav. 5, 12-24.

BARLOW, N.D. & DIXON, A.F.G. (1980). Simulation of lime aphid population dynamics. PUDOC, Amsterdam.

BARNES, R.D. (1974). Invertebrate zoology. Third edition. W.B. Saunders Co. U.S.A.

BASEDOWN, T., BORG, A., DE CLERCQ, R., NIJVELDT, W. & SCHERNEY, F. (1976). Studies on the occurrence of Carabidae in European wheat fields. Entomophaga. 21, 59-72.

BAUER, T. (1977). The relevance of the brightness to visual acuity, predation, and activity of visually hunting ground-beetles. Oecologia. 30, 63-73.

BEDDINGTON, J.R., FREE, C.A. & LAWTON, J.H. (1978). Modelling biological control: on the characteristics of successful natural enemies. Nature 273, 513-519.

BIBBY, C.J. & GREEN, R.E. (1980). Foraging behaviour of migrant pied flycatchers on temporary territories. J. Anim. Ecol. 49, 507-521.

BLACKMAN, R. (1974). Aphids. Ginn & Co. Ltd. London.

BOSSERT, W.H. & WILSON, E.O. (1963). The analysis of olfactory communication among animals. J. Theoret. Biol. 5, 443-469.

BRADSHAW, J.W.S. (1981). The physicochemical transmission of two components of a multiple chemical signal in the African weaver ant. Anim. Behav. 29, 581-585.

BRIGGS, J.B. (1961). A comparison of pitfall trapping and soil sampling in assessing populations of two species of ground beetles. Rep. E. Mall. Res. Sta. 1960, pp. 108-112.

BROWN, W.L., EISNER, T. & WHITTAKER, R.H. (1970). Allomones and kairomones: transpecific chemical messages. Bioscience 20, 21-22.

CARTER, N., LEATHER, S., McLEAN, I. & WATT, A. (1978). Cereal aphid research at East Anglia. Unpublished report: p.8.

CARTER, N., McLEAN, I.F.G., WATT, A.D., & DIXON, A.F.G. (1980). Cereal aphids: a case study and review. Appl. Biol. 5, 271-348.

CHINERY, M. (1973). A field guide to the insects of Britain and Northern Europe. Houghton Mifflin Co., Boston.

COCK, M.J.W. (1977). Searching behaviour of polyphagous predators. Unpubl. Ph.D. Thesis, University of London.

COCK, M.J.W. (1978). The assessment of preference. J. Anim. Ecol. 47, 805-816.

CODY, M.L. (1974). Optimisation in ecology. Science. 183, 1156-1164.

COLLINGBOURNE, R.H. (1976). Radiation and sunshine. The climate of the British Isles. (Ed. by T.J. Chandler & S. Gregory), pp. 74-95. Longman Group Ltd., New York.

COMINS, H.N. & HASSELL, M.P. (1979). The dynamics of optimally foraging predators and parasitoids. J. Anim. Ecol. 48, 335-351.

COOK, R.M. & HUBBARD, S.F. (1977). Adaptive searching strategies in insect parasites. J. Anim. Ecol. 46, 115-125.

COOK, R.M. & COCKRELL, B.J. (1978). Predator ingestion rate and its bearing on feeding time and the theory of optimal diets. J. Anim. Ecol. 47, 529-547.

CORNELL, H. (1976). Search strategies and the adaptive significance of switching in some general predators. Am. Nat. 110, 317-320.

CORNIC, J.F. (1973). Etude du regime alimentaire de trois especes de Carabiques et de ses variations en verger de pommiers. Ann. Soc. ent. Fr. 9, 69-87.

COWIE, R.J. & KREBS, J.R. (1979). Optimal foraging in patchy environments. Population Dynamics. (Ed. by R.M. Anderson, B.D. Turner & L.R. Taylor), pp. 183-206. Blackwell Scientific Publications, Oxford.

COX, C.B., HEALEY, I.A. & MOORE, P.D. (1976). Biogeography an ecological and evolutionary approach. Blackwell Scientific Publications, Oxford.

CROWSON, R.A. (1981). The biology of the Coleoptera. Academic Press. London.

DAVIES, M.J. (1953). The contents of the crops of some British carabid beetles. Entomol. Mon. Mag. 89, 18-23.

DAVIES, N.B. (1977). Prey selection and social behaviour in wagtails. J. Anim. Ecol. 46, 37-57.

DAWSON, N. (1965). A comparative study of the ecology of eight species of fenland Carabidae. J. Anim. Ecol. 34, 299-314.

DEAN, G.J.W. (1973). Distribution of aphids in spring cereals. J. Appl. Ecol. 10, 447-462.

DEAN, G.J.W. (1973b). Bionomics of aphids reared on cereals and some Gramineae. Ann. Appl. Biol. 73, 127-135.

DEAN, G.J.W. (1974). Effect of temperature on the cereal aphids Metopolophium dirhodum, Rhopalosiphum padi and Macrosiphum avenae. Bull. Ent. Res. 63, 401-409.

DE BACH, P. (1951). The necessity for an ecological approach to pest control on citrus in California. J. Econ. Ent. 44, 443-447.

DE BACH, P. (1974). Biological control by natural enemies. Cambridge University Press, London.

DICKER, G.H.L. (1951). Agonum dorsale: an unusual egg-laying habit and some biological notes. Entomol. Month. Mag. 87, 33-34.

DIXON, A.F.G. (1973). Biology of aphids. Edward Arnold, London.

DREISIG, H. (1981). The rate of predation and its temperature dependence in a tiger beetle, Cincindela hybrida. Oikes 36, 196-202.

DRITSCHILO, W. & ERWIN, T.L. (1982). Responses in abundance and diversity of cornfield carabid communities to differences in farm practices. Ecology, 63, 900-904.

DUNNING, R.A., BAKER, A.N. & WINDLEY, R.F. (1975). Carabids in sugar beet crops and their possible role as aphid predators. Ann. Appl. Biol. 80, 125-128.

EDWARDS, C.A. & FLETCHER, K.E. (1971). A comparison of extraction methods for terrestrial arthropods. Methods of study and quantitative soil ecology: population, production and energy flow (Ed. by J. Phillipson), pp. 150-185. I.B.P. handbook No. 18, Blackwell Scientific Publications, U.K.

EDWARDS, C.A., PARSONS, N., GEORGE, K.S. & HEILBROON, T. (1978). Carabids as predators of cereal aphids. Report Rothamsted Experimental Station for 1977, 101.

EDWARDS, C.A., SUNDERLAND, K.D. & GEORGE, K.S. (1979). Studies on polyphagous predators of cereal aphids. J. Appl. Ecol. 16, 811-823.

EHLER, L.E. & van den BOSCH, R. (1974). An analysis of the natural biological control of Trichoplusia ni (Lepidoptera: Noctuidae) on cotton in California. Can. Ent. 106, 1067-1073.

ELNER, R.W. & HUGHES, R.N. (1978). Energy maximization in the diet of the shore crab. J. Anim. Ecol. 47, 103-116.

EMLEN, J.M. (1966). The role of time and energy in food preference. Amer. Nat. 100, 611-617.

ERICHSEN, J.T., KREBS, J.R. & HOUSTON, A.I. (1980). Optimal foraging and cryptic prey. J. Anim. Ecol. 49, 271-276.

ERWIN, T.L., BALL, G.E. & WHITEHEAD, D.R. (Eds.) (1979). Carabid beetles: their evolution, natural history and classification. Junk, the Hague.

ESTABROOK, G.F. & DUNHAM, A.E. (1976). Optimal diet as a function of absolute abundance, relative abundance and relative value of available prey. Amer. Nat. 110, 401-413.

EVANS, G. (1975). The Life of Beetles. Allen & Uniwin Ltd. London.

GEORGE, K.S. & GAIR, R. (1979). Crop loss assessment on winter wheat attacked by the grain aphid, Sitobion avenae. Pl. Path. 28, 143-149.

GILBERT, N., GUTIERREZ, A.P., FRAZER, B.D. & JONES, R.E. (1976). Ecological relationships. W.H. Freeman & Co., Great Britain.

GREENSLADE, P.J.M. (1963). Daily rhythms of locomotor activity in some Carabidae. Entomol. exp. et appl. 6, 171-180.

GREENSLADE, P.J.M. (1964). Pitfall trapping as a method for studying populations of Carabidae. J. Anim. Ecol. 33, 301-309.

GOSS-CUSTARD, J.D. (1977). Optimal foraging and the size selection of worms by redshank. Anim. Behav. 25, 10-29.

GRIFFITHS, D. (1975). Prey availability and the food of predators. Ecology 56, 1209-1214.

GRUM, L. (1975). Mortality patterns in carabid populations. Ekologia Polska 23, 649-665.

HASSELL, M.P. (1978). The dynamics of arthropod predator-prey systems. Princeton University Press, Princeton.

HASSELL, M.P. (1982). What is searching efficiency? Ann. Appl. Biol. (In press).

HASSELL, M.P., LAWTON, J.H. & BEDDINGTON, J.R. (1976). The components of arthropod predation, I. The prey death rate. J. Anim. Ecol. 45, 135-164.

HASSELL, M.P., LAWTON, J.H. & BEDDINGTON, J.R. (1977). Sigmoid functional responses by invertebrate predators and parasitoids. J. Anim. Ecol. 46, 249-262.

HASSELL, M.P. & MAY, R.M. (1973). Stability in insect-host parasite models. J. Anim. Ecol. 42, 693-736.

HASSELL, M.P. & MAY, R.M. (1974). Aggregation in predators and insect parasites and its effect on stability. J. Anim. Ecol. 43, 567-594.

HASSELL, M.P. & VARLEY, G.C. (1969). New inductive population model for insect parasites and its bearing on biological control. Nature, 233, 1133-1136.

HENGEVELD, R. (1980). Qualitative and quantitative aspects of the food of ground beetles: a review. Neth. J. Zool. 30, 555-563.

HINDE, R.A. (1970). Animal behaviour. McGraw-Hill, Kogakusha Ltd., Japan.

HOLLING, C.S. (1959). The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Can. Ent. 91, 293-320.

HUBBARD, S.F. & COOK, R.M. (1978). Optimal foraging by parasitoid wasps. J. Anim. Ecol. 47, 593-604.

HUFFAKER, C.B. & MESSENGER, P.S. (Eds.) (1976). Theory and practice of biological control. Academic Press, New York.

HUGHES, R.N. (1979). Optimal diets under the energy maximization premise: the effects of recognition time and learning. Amer. Nat. 113, 209-221.

HUGHES, R.N. & ELNER, R.W. (1979). Tactics of a predator, Carcinus maenas, and morphological responses of the prey, Nucella lapillus. J. Anim. Ecol. 48, 65-78.

HUSSEY, N.W. & BRAVENBOER, I. (1971). Control of pests in glasshouse culture by the introduction of natural enemies. Biological control (Ed. by C.B. Huffaker), pp. 195-216. Plenum Press, New York.

IMMS, A.D. (1973). Insect natural history. Collins, U.K.

JONES, M.E. (1976). Topographic climates: soils, slopes and vegetation. The climate of the British Isles (Ed. by T.J. Chandler & S. Gregory), pp. 288-306. Longman Group Ltd., New York.

JONES, M.G. (1979). The abundance and reproductive activity of common Carabidae in a winter wheat crop. Ecol. Ent. 4, 31-43.

KREBS, J.R. (1978). Optimal foraging: decision rules for predators. Behavioural Ecology an evolutionary approach. (Ed. by J.R. Krebs & N.B. Davies), pp. 23-63. Blackwell Scientific Publications, Oxford.

KREBS, J.R., ERICHSEN, J.T., WEBBER, M.I. & CHARNOV, E.L. (1977). Optimal prey selection in the Great Tit. Anim. Behav. 25, 30-38.

KREBS, J.R., KACELNIK, A. & TAYLOR, P. (1978). Test of optimal sampling by foraging great tits. Nature 275, 27-31.

KRECKWITZ, Von H. (1980). Experiments in the breeding biology and the seasonal behaviour of the carabid beetle Agonum dorsale in temperature and moisture gradients. Zool. Jb. Syst. 107, 183-234.

KVAMME, T. (1977). On the distribution and habitat choice of A. dorsale in Norway. Norw. J. Entomol. 24, 31-32.

LARGE, E.C. (1954). Growth stages in cereals. Illustrations of the Feekes scale. Pl. Path. 3, 128-129.

LAROCHELLE, A. & LARIVIERE, M. (1978). A case of gregariousness in Carabidae. Cordulia. 4, 149-150.

LAWTON, J.H., BEDDINGTON, J.R. & BONSER, R. (1974). Switching in invertebrate predators. Ecological Stability. (Ed. by M.B. Usher & M.H. Williamson), pp. 141-158. Chapman & Hall, London.

LEWIS, T. & TAYLOR, L.R. (1967). Introduction to experimental ecology. Academic Press, London.

LINDROTH, C.H. (1974). Handbooks for the identification of British insects: Coleoptera, Carabidae. Royal Entomological Society, London.

LLEWELLYN, M. (1972). The effects of the lime aphid on the growth of lime. J. appl. Ecol. 9, 261-282.

LUFF, M.L. (1968). Some effects of Formalin on the numbers of Coleoptera caught in pitfall traps. Ent. Mon. Mag. 104, 115-116.

LUFF, M.L. (1974). Adult and larval feeding habits of Pterostichus madidus. J. Nat. Hist. 8, 403-9.

LUFF, M.L. (1978). Diel activity patterns of some field Carabidae. Ecol. Ent. 3, 53-62.

McARDLE, B.H. & LAWTON, J.H. (1979). Effects of prey-size and predator-instar on the predation of Daphnia by Notonecta. Ecol. Ent. 4, 267-275.

McLEAN, I.F.G. (1980). The ecology of the natural enemies of cereal aphids. Ph.D. thesis, University of East Anglia.

MANLY, B.F.J., MILLER, P. & COOK, L.M. (1972). Analysis of a selective predation experiment. Amer. Nat. 106, 719-36.

MARGOLIS, J. & KENRICK, K.G. (1968). Polyacrylamide gel electrophoresis in a continuous molecular sieve gradient. Anal. Biochem. 25, 347-362.

MARGOLIS, J. & WRIGLEY, C.W. (1975). Improvement of pore gradient electrophoresis by increasing the degree of cross-linking at high acrylamide concentrations. J. Chromat. 106: 204-209.

MITCHELL, B. (1963). Ecology of two carabid beetles, Bembidion lampros and Trechus quadristriatus. II. Studies on populations of adults in the field, with special reference to the technique of pitfall trapping. J. Anim. Ecol. 32, 377-392.

MITTLER, T.E. (1953). Amino-acids in phloem sap and their excretion by aphids. Nature 172, 207.

MOORE, N.W., HOOPER, M.D. & DAVIS, B.N.K. (1967). Hedges, I. Introduction and reconnaissance studies. J. Appl. Ecol. 4, 201-220.

MURDIE, G. & HASSELL, M.P. (1973). Food distribution, searching success and predator-prey models. In The mathematical theory of the dynamics of biological populations. (Ed. by R.W. Hiorns) pp. 87-101. Academic Press, London.

MURDOCH, W.W. (1966). Aspects of the population dynamics of some marsh Carabidae. J. Anim. Ecol. 35, 127-156.

MURDOCH, W.W. (1969). Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Mon. 39, 335-354.

MURDOCH, W.W. & OATEN, A. (1975). Predation and population stability. Adv. Ecol. Res. 9, 1 - 125.

MURRAY, R.A. & SOLOMON, M.G. (1978). A rapid technique for analysing diets of invertebrate predators by electrophoresis. Ann. Appl Biol. 90, 7-10.

NEUDECKER, C. (1974). Das praeferenzverhalten von Agonum assimile in temperatur -, Feuchtigkeits - und helligkeits - gradienten. Zool. Jahrb. abt. Syst. Oekol. Geogr. Tiere. 101, 609-627.

NICHOLSON, A.J. (1933). The balance of animal populations. J. Anim. Ecol. 2, 132-178.

NIE, N.H., HULL, C.H., JENKINS, J.G., STEINBRENNER, K., & BENT, D.H. (1975). Statistical package for the social sciences. 2nd edition. McGraw-Hill book Co.

OLDROYD, H. (1970). Collecting, preserving and studying insects. Hutchinson, London.

PAUER, R. (1975). On the dispersal of Carabidae in the agrarian landscape, with special reference to the boundaries between different field crops. Z. Agnew. Zool. 62, 457-489.

PENNEY, M.M. (1966). Studies on certain aspects of the ecology of Nebria brevicollis. J. Anim. Ecol. 35, 505-512.

PHILLIPSON, J. (1964). A miniature bomb calorimeter for small biological samples. Oikos, 15, 130-139.

PLOTKIN, H.C. (1979). Learning in a carabid beetle. Anim. Behav. 27, 567-575.

POLLARD, E. (1968). Hedges III. The effect of removal of the bottom flora of hawthorn hedgerow on the Carabidae of the hedge bottom. J. Appli. Ecol. 5, 125-139.

POTTS, G.R. & VICKERMAN, G.P. (1974). Studies on the cereal ecosystem. Adv. Ecol. Res. 8, 107-197.

POTTS, G.R. & VICKERMAN, G.P. (1975). Arable ecosystems and the use of agrochemicals. The ecology of resource degradation and renewal. (Ed. by M.J. Chadwick & G.T. Goodman) pp. 17-29. Blackwell Scientific Publications, Oxford.

PRIOR, R.N.B. (1975). Key for the field identification of apterous and alate cereal aphids with photographic illustrations. Ministry of Agriculture, Fisheries and Food publication, U.K.

PULLIAM, H.R. (1975). Diet optimization with nutrient constraints. Amer. Nat. 109, 765-768.

PYKE, G.H. (1978). Optimal foraging in bumblebees and coevolution with their plants. Oecologia 36, 281-293.

ROGERS, D.J. (1972). Random search and insect population models. J. Anim. Ecol. 41, 369-383.

ROSENBERG, N.J. (1974). Microclimate: the biological environment. Wiley & Sons, New York.

SCHMIDT-NIELSEN, K. (1975). Animal physiology, adaption and environment. Cambridge University Press.

SCOPES, N.E.A., RANDALL, R.E. & BIGGERSTAFF, S.M. (1975). Constant temperature, ventilated perspex cage for rearing phytophagous insects. Laboratory Practice, January 1975, p. 34.

SHAW, C.R. & PRASAD, R. (1970). Starch gel electrophoresis of enzymes - a compilation of recipes. Biochem. Gen. 4, 297-330.

SHIYOMI, M. (1967). A model of the plant-to-plant movement of aphids. 1. Description of the model. Res. Popul. Ecol. 9, 53-61.

SIEGEL, S. (1956). Non-parametric statistics for the behavioural sciences. McGraw-Hill Kogakusha, Ltd., Tokyo.

SKUHRAVY, V. (1959). Die nahrung der feld caribiden. Acta. Soc. Entomol. csl. 56, 1-18.

SMIT, H. (1957). Onderzoek naar het voedsel von Calathus erratus en Calathus ambiguus aan de hand van hun mogen inhouden. Entomol. Ber. Amst. 17, 199-209.

SNEDECOR, G.W. & COCHRAN, W.G. (1967). Statistical Methods. Iowa State University Press, U.S.A.

SOKAL, R.R. & ROHLF, F.J. (1969). Biometry. W.H. Freeman & Co. U.S.A.

SOUTHWOOD, T.R.E. (1977). The relevance of population dynamic theory to pest status. Origins of pest, parasite, disease and weed problems (Ed. by J.M. Cherrett & G.R. Sagar) pps. 35-54. Blackwell Scientific Publications, Oxford.

SOUTHWOOD, T.R.E. (1978). Ecological methods. Chapman & Hall, London.

SOUTHWOOD, T.R.E. (1979). Pesticide usage, prodigal or precise. Proceedings of the 1979 British crop protection conference - Pests and diseases III, 603-619.

SOUTHWOOD, T.R.E. & COMINS, H.N. (1976). A synoptic population model. J. Anim. Ecol. 45, 949-966.

STEEL, R.G.D. & TORRIE, J.H. (1980). Principles and procedures of statistics. McGraw-Hill Kogakusha, Ltd., Tokyo.

STENSETH, N.C. & HANSSON, L. (1979). Optimal food selection: a graphical model. Amer. Nat. 113, 373-389.

STERNLICHT, M. (1973). Parasitic wasps attracted by the sex pheromones of their coccid hosts. Entomophaga 18, 339-343.

STORK, N.E. (1980). A scanning electron microscope study of tarsal setae in the Coleoptera. Zool. J. Linn. Soc. 68, 173-306.

STRIBLEY, M.F., MOORES, G.D., DEVONSHIRE, A.L. & SAWACKI, R.M. (1983). Application of the F.A.O.-recommended method for detecting insecticide resistance in Aphis fabae (Scop.), Sitobion avenae (F.) Metopolophium dirhodum (Walk.) and Rhopalosiphum padi (L.). Bull. ent. Res. 73, In Press.

STUBBS, M. (1980). Another look at prey detection by coccinellids. Ecol. Ent. 5, 179-182.

SUNDERLAND, K.D. (1975). The diet of some predatory arthropods in cereal crops. J. Appl. Ecol. 12, 507-15.

SUNDERLAND, K.D. & VICKERMAN, G.P. (1980). Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. J. Appl. Ecol. 17, 389-396.

SWIECIMSKI, J. (1957). The role of site and memory in food capture by predatory beetles of the species Cincindela hybrida. Pol. Pismo. Ent. 26, 205-232.

THIELE, H.U. (1977). Carabid beetles in their environments. Springer-Verlag, Berlin.

TISCHLER, W. (1958). Synokologische untersuchungen an der fauna der felder und feldgeholze (Ein beitrag zur okologie der kulturlandschaft) Z. Morphol. Oekol. Tiere. 47, 54-114.

van den BOSCH, R., LEIGH, T.F. FALCON, L.A. STERN, V.M., GONZALES, D., & HAGEN, K.S. (1971). The developing program of integrated control of cotton pests in California. Biological Control (Ed. C.B. Huffaker) pps. 377-394. Plenum Press, New York.

van den BOSCH, R. & MESSENGER, P.S. (1973). Biological control. International textbook Co. Ltd., England.

VICKERMAN, G.P. (1978). The arthropod fauna of undersown grass and cereal fields. Scient. Proc. R. Dubl. Soc., Series A. 6, 155-165.

VICKERMAN, G.P. & SUNDERLAND, K.D. (1975). Arthropods in cereal crops: nocturnal activity, vertical distribution and aphid predation. J. Appl. Ecol. 12, 755-766.

VICKERMAN, G.P. & SUNDERLAND, K.D. (1977). Some effects of dimethoate on arthropods in winter wheat. J. Appl. Ecol. 14, 767-777.

VICKERMAN, G.P. & WRATTEN, S.D. (1979). The biology and pest status of cereal aphids in Europe: a review. Bull. ent. Res. 69, 1-32.

WAAGE, J.K. (1977). Behavioural aspects of foraging in the parasitoid, Nemeritis canescens. Unpubl. Ph.D Thesis, University of London.

WAAGE, J.K. (1979). Foraging for patchily-distributed hosts by the parasitoid, Nemeritis canescens. J. Anim. Ecol. 48, 353-371.

WEAVER, N. (1978). Chemical control of behaviour-intraspecific. Biochemistry of Insects. (Ed. by M. Rockstein). pp. 360-389, Academic Press, London.

WERNER, E.E. & HALL, D.J. (1974). Optimal foraging and the size selection of prey by the Bluegill Sunfish. Ecology 55, 1216-1232.

WIESER, W. (Editor) (1973). Effects of Temperature on Ectothermic Organisms. Springer-Verlag, Berlin.

WILSON, D.S. (1978). Prudent predation: a field study involving three species of tiger beetles. Oikos 31, 128-136.

WILSON, E.O. (1975). Sociobiology the new synthesis. Harvard University Press, Cambridge, Massachusetts.

WILSON, E.O., BOSSERT, W.H. & REGNIER, F.E. (1969). A general method for estimating threshold concentrations of odorant molecules. J. Insect. Physiol. 15, 597-610.

WYATT, I.J. (1972). Progress towards biological control under glass. Biology in pest and disease control. (Ed. by D. Price Jones & M.E. Solomon) pp. 294-301. Blackwell Scientific Publications, Oxford.

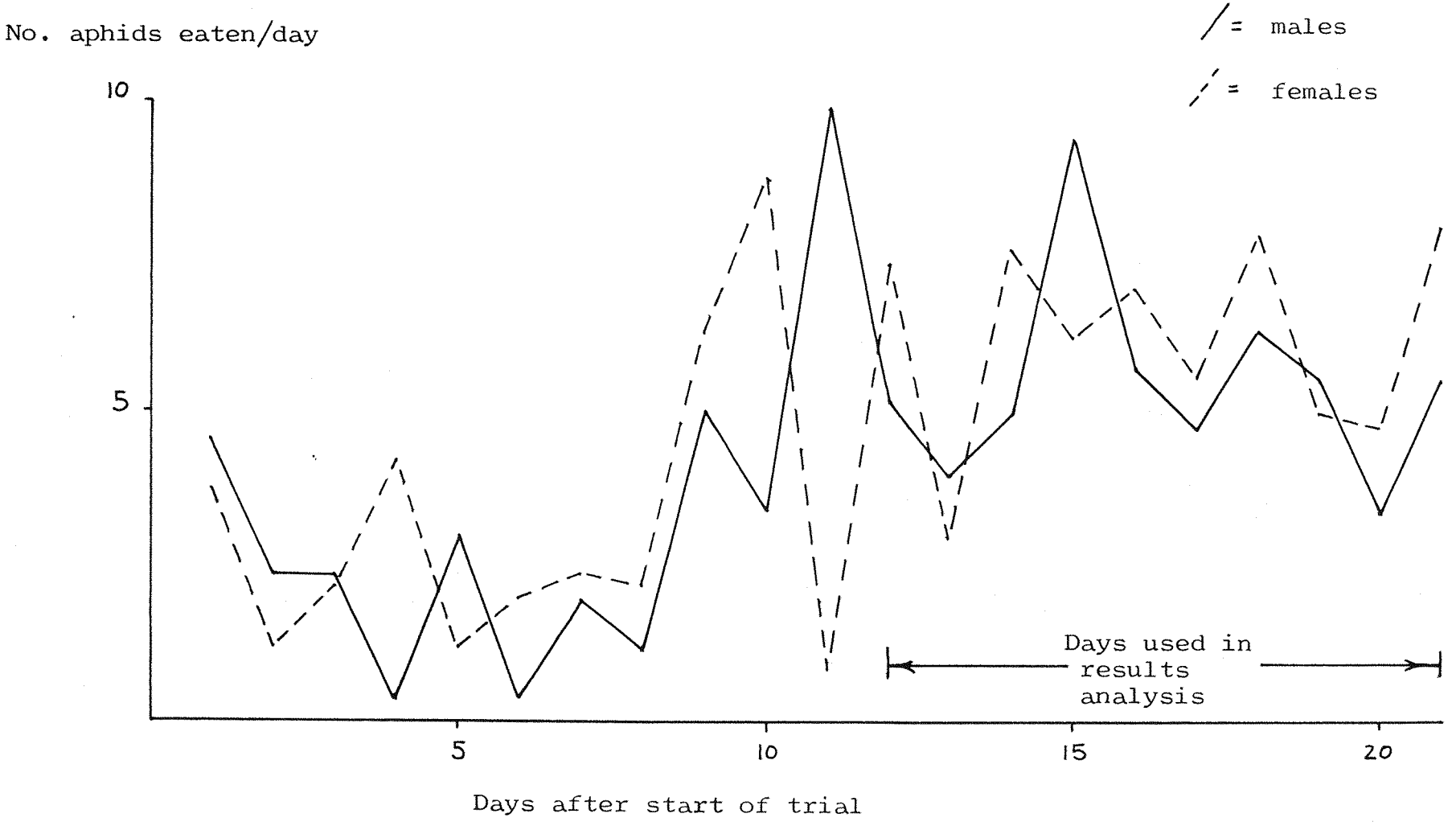
A P P E N D I C E S

APPENDIX I

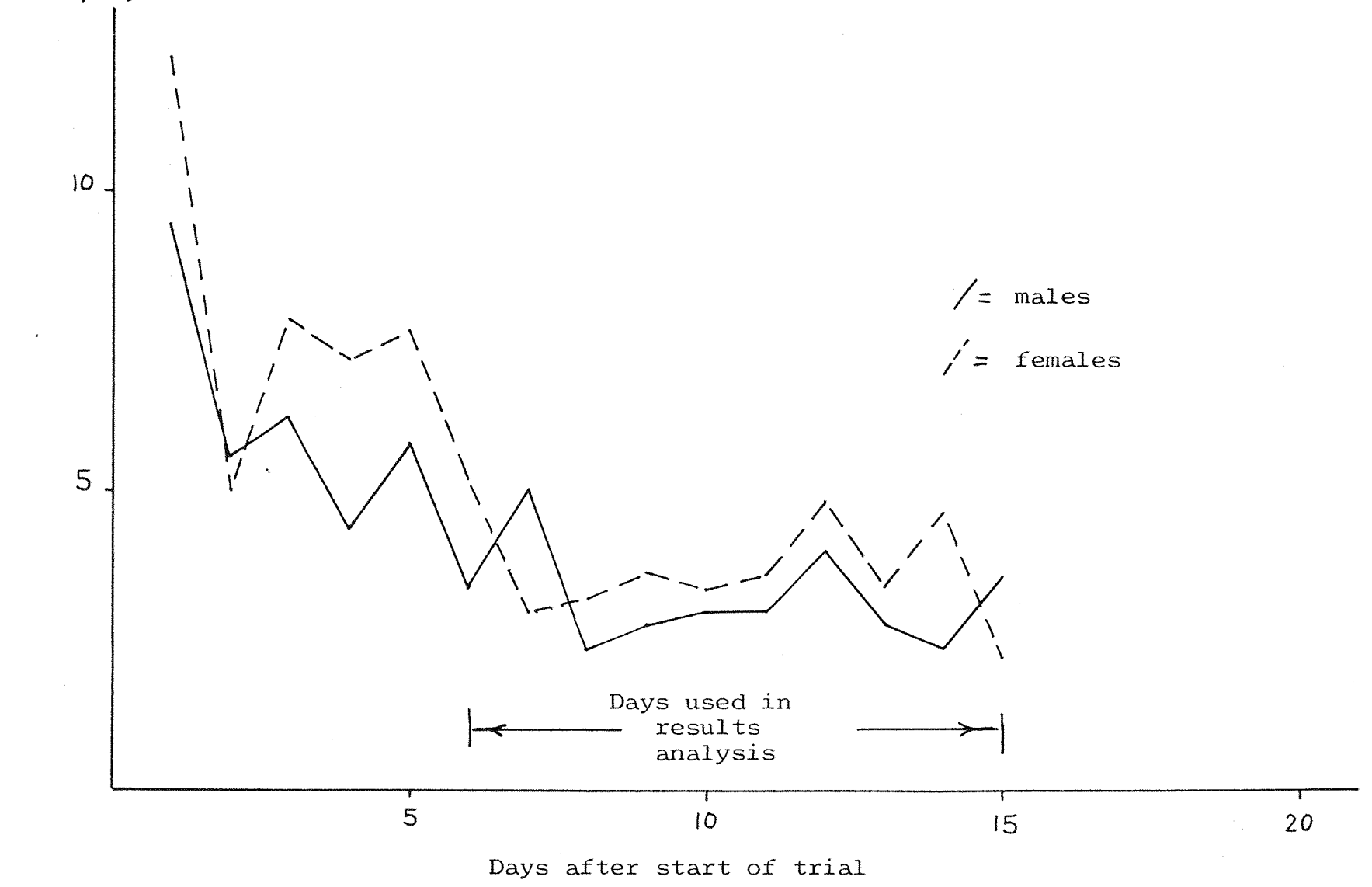
(See Chapter 4.8)

Figs. I - III; Graphs to show the numbers of aphids eaten per day by three groups of A. dorsale differing in their reproductive maturity.

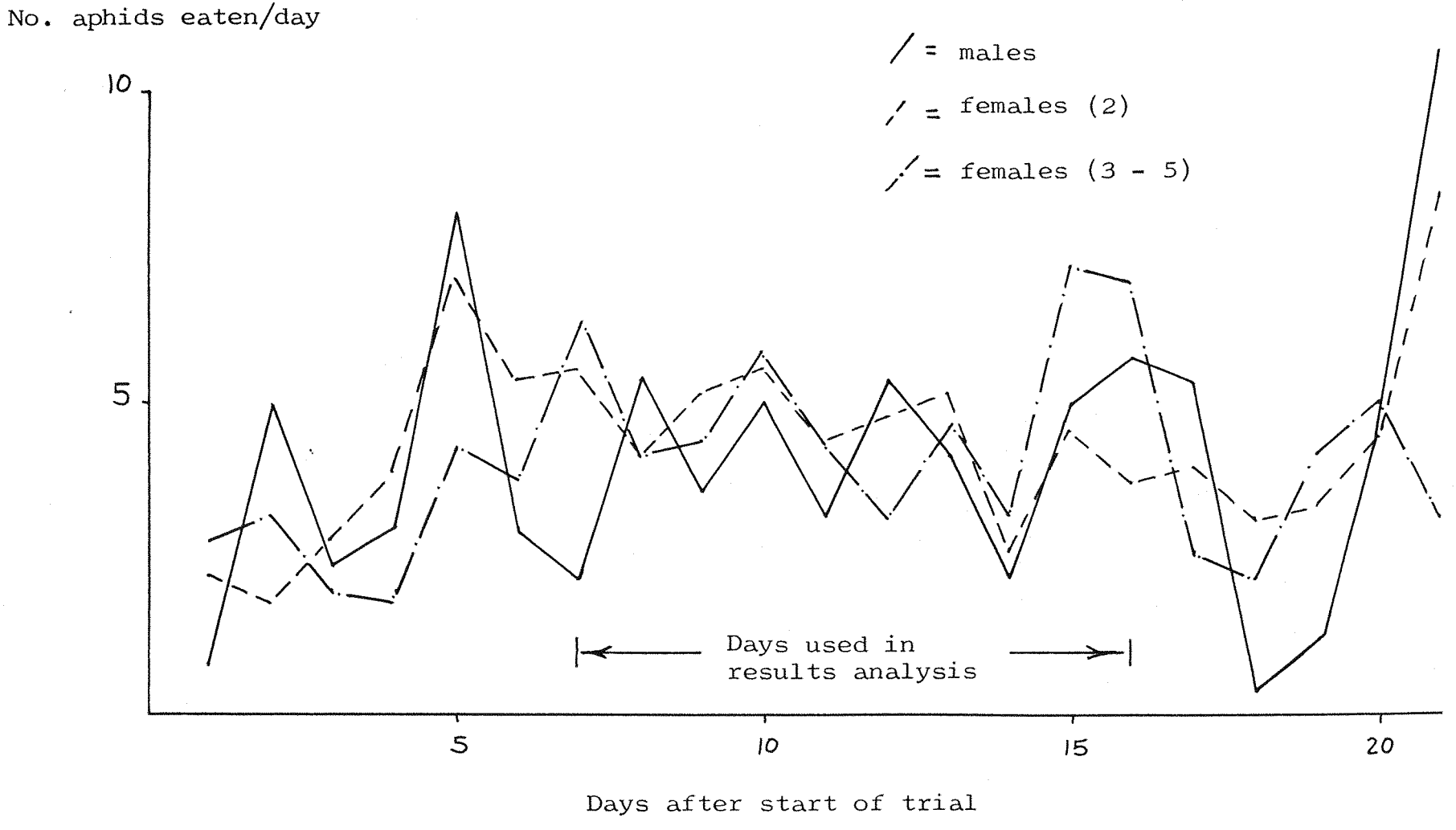
Appendix I/Fig. 1 The change in numbers of aphid prey eaten per day throughout the trial period by reproductively-immature A. dorsale collected from the field (see Chapter 4.8).



Appendix I/Fig. 2 The change in numbers of aphid prey eaten per day throughout the trial period by laboratory-maintained reproductively-immature A. dorsale. (see Chapter 4.8).



Appendix I/Fig. 3 The change in numbers of aphid prey eaten per day throughout the trial period by laboratory-maintained reproductively-mature A. dorsale (see Chapter 4.8).



APPENDIX 2

(See Chapter 9)

Program listing of the simulation model. Table I: detailed output from the simulation model.

Program listing of simulation model used in Chapter 9 to assess the impact of A. dorsale on a cereal aphid population.

```
10  DIM N (100)
20  PRINT "Set minimum and maximum aphid densities and increment size"
30  INPUT N1,N2,N3
40  PRINT "Set minimum and maximum predator densities and increment size"
50  INPUT B1,B2,B3
60  PRINT "Set aphid rate of increase per day"
70  INPUT R
80  PRINT "Set predator consumption"
90  INPUT A
100 PRINT "Set the percentage of aphids available for predation"
110 INPUT F1
120 F=F1/100
130 PRINT "Set number of days for simulation"
140 INPUT D
142 PRINT "Full daily printout (F) or final population summary (S) ?"
143 INPUT A$
144 IF A$="S" GOTO 150
145 PRINT "Day Predator density Starting aphid density Aphid density
    Log (aphids+1)"
146 GOTO 160
150 PRINT "Day Predator density Starting aphid density Final aphid density"
160 FOR K=N1 TO N2 STEP N3
170 FOR J=B1 TO B2 STEP B3
180 N(1)=K
190 FOR I=2 TO D
200 GOSUB 270
205 REM - APHID POPULATION GROWTH SECTION
210 N(I)=N(I)*R
211 L=LOG(N(I)+1)
212 IF A$="S" GOTO 220
213 PRINT I,J,K,N(I),L
220 NEXT I
225 IF A$="F" GOTO 240
230 PRINT D,J,K,N(D)
240 NEXT J
250 NEXT K
260 END
265 REM - PREDATION SUBROUTINE
270 G=N(I-1)*F
280 M=(J*A)
290 IF M<G THEN 310
300 M=G
310 N(I)=N(I-1)-M
320 RETURN
```

Table I. The relative decrease in outbreak area caused by changes in reproductive rate, % aphids available or voracity as successive reproductive rates are excluded from the analysis.

Parameter producing change in outbreak area	Description of Boundary Lines	Decrease in outbreak area (as proportion of graph area)
	FOR R = 1.1 → 1.5	
Reproductive rate	1.1, 5%, 16 & 1.5, 5%, 16	0.602
% aphids available	1.1, 5%, 16 & 1.1, 10%+, 16	0.014
	1.2, 5%, 16 & 1.2, 20%+, 16	0.143
	1.3, 5%, 16 & 1.3, 30%+, 16	0.133
	1.4, 5%, 16 & 1.4, 30%+, 16	0.104
	1.5, 5%, 16 & 1.5, 40%+, 16	0.084
Voracity	1.1, 10%+, 8 & 1.1, 10%+, 16	0.167
	1.2, 20%+, 8 & 1.2, 20%+, 16	0.098
	1.3, 30%+, 8 & 1.3, 30%+, 16	0.069
	1.4, 30%+, 8 & 1.4, 30%+, 16	0.053
	1.5, 40%+, 8 & 1.5, 40%+, 16	0.051
	FOR R = 1.2 → 1.5	
Reproductive rate	1.2, 20%+, 16 & 1.5, 40%+, 16	0.290
% aphids available	1.2, 5, 16 & 1.2, 20%+, 16	0.333
	1.3, 5, 16 & 1.3, 30%+, 16	0.310
	1.4, 5, 16 & 1.4, 30%+, 16	0.243
	1.5, 5, 16 & 1.5, 40%+, 16	0.195
Voracity	1.2, 20%+, 8 & 1.2, 20%+, 16	0.229
	1.3, 30%+, 8 & 1.3, 30%+, 16	0.162
	1.4, 30%+, 8 & 1.4, 30%+, 16	0.124
	1.5, 40%+, 8 & 1.5, 40%+, 16	0.119

Table I. contd...

FOR R = 1.3 → 1.5

Reproductive rate	1.3, 30%,16 & 1.5, 40%+,16	0.171
% aphids available	1.3, 5, 16 & 1.3, 30%+,16	0.464
	1.4, 5, 16 & 1.4, 30%+,16	0.364
	1.5, 5, 16 & 1.5, 40%+,16	0.293
Voracity	1.3, 30%+,8 & 1.3, 30%+,16	0.243
	1.4, 30%+,8 & 1.4, 30%+,16	0.186
	1.5, 40%+,8 & 1.5, 40%+,16	0.179

FOR R = 1.4 → 1.5

Reproductive rate	1.4, 30%+,16 & 1.5, 40%+,16	0.083
% aphids available	1.4, 5, 16 & 1.4, 30%+,16	0.425
	1.5, 5, 16 & 1.5, 40%+,16	0.342
Voracity	1.4, 30%+, 8 & 1.4, 30%+,16	0.217
	1.5, 40%+, 8 & 1.5, 40%+,16	0.208

FOR R = 1.5

% aphids available	1.5, 5, 16 & 1.5, 40%+,16	0.410
Voracity	1.5, 40%+, 8 & 1.5, 40%+,16	0.250

The following published papers were included in the bound thesis. These have not been digitised due to copyright restrictions, but the links are provided.

https://doi.org/10.1111/j.1744-7348.1982.tb00809.x