UNIVERSITY OF SOUTHAMPTON
Department of Biology

EFFECTS OF DENSITY AND AGE ON BODY CONDITION, REPRODUCTIVE PERFORMANCE, BEHAVIOUR AND SURVIVAL OF FALLOW DEER

by

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To Alison

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

BIOLOGY

DOCTOR OF PHILOSOPHY

EFFECTS OF DENSITY AND AGE ON BODY CONDITION, REPRODUCTIVE PERFORMANCE, BEHAVIOUR AND SURVIVAL OF FALLOW DEER

by

Jochen Langbein

This thesis investigates the effects of various population parameters, together with other factors such as climate and management intervention, on performance and behaviour of fallow deer, Dama dama. British deer parks were chosen for study as they provide a wide range of accurately measurable population densities, and animals within them can be observed and caught relatively easily in comparison to wild deer. The populations present fully mixed-sex herds which are entirely free-ranging within the boundaries of each park throughout the year, and thus offer a model system where population processes may be studied.

Live capture of fallow deer in 15 parks enabled collection of data on body weights and skeletal size in relation to age and sex on 3740 individuals, many of these being recaptured in a number of years. Intensive field observations focused on marked individuals in 9 populations, to determine fawning success, birth dates and weights, and variation in maternal and mating behaviour. Additional data on natural mortalities, culled carcases, food availability, climate and habitat characteristics were collected over the extended set of parks.

Wide variation occurred between parks in winter live weights, population means ranging from, for example 19.5 to 32.3 kg for male fawns, and 32.1 to 42.6 kg for yearling females. In contrast, such variation within sites between years rarely exceeded 10%. Within some populations changes in mean body weights between years could be explained directly by changes in stocking density, associations being strongest with density measured in the year of birth. Variation in body weights and skeletal sizes between populations showed density-independent associations with summer pasture productivity and winter climate; after accounting for these factors, density-dependent effects, acting through forage availability and supplementary feed obtained per deer in winter, were also apparent.

Reproductive rates of adult does (≥2 years old at rut) were very high in all the sites where age-specific data were collected. Fecundity of younger does (<2 years at rut) was consistently lower than that of adults, with differences greatest in parks offering most restricted resources. The winter body-weight threshold for yearlings, at which 50% produced fawns the next summer, was determined as 32 kg. Yearlings produced lighter offspring than adults, and mated and fawned an average of 11 days later. Near maximum reproduction was attained even in parks holding up to 6 deer/ha, as long as at high densities adequate supplementary feeding and shelter were offered.

Marked differences in mating behaviour occurred during the rut. Highly territorial systems ranging from single rutting stands to leks occurred in some parks, while non-territorial systems based on defense of mobile female groups by dominant males were observed in others. Variation in the systems observed is fully described, and was found to relate in particular to buck density, total number of bucks, and doe density. Individual male mating success was highly skewed in all systems. Costs and benefits of variation and timing of mating behaviour are discussed.

Juvenile mortality in summer, as well as other natural mortality was very low in the most parks and years. Higher mortality was associated with low body weights in years of cold late winter temperatures. Survival rates were highest where supplementary winter feeding was extensive and commenced before December.

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Scientific names of deer species cited in text

SUBFAMILY CERVINAE

Axis or Chital deer : *Axis axis*

Fallow deer : *Dama dama*

Red deer : *Cervus elaphus*

Sika deer : *Cervus nippon*

Wapiti : *Cervus canadensis*

SUBFAMILY ODOCOILINAE

Moose : *Alces alces*

Mule or Black-tailed deer : *Odocoileus hemionus*

Reindeer or caribou : *Rangifer tarandus*

Roe deer : *Capreolus capreolus*

White-tailed deer : *Odocoileus virginianus*

Chapter 1

INTRODUCTION

1.1 Introduction

This thesis investigates the effects of various population parameters, including density, age-structure and nutritional status, together with environmental factors, such as climate and management intervention, on population performance in fallow deer.

It is widely accepted today, that natural regulation of numbers (through variations in birth rate, mortality, immigration and emigration), is in most animal populations influenced by both density-dependent resource limitation (e.g. of food, nest sites) and density-independent factors such as weather conditions. Such a general statement would have been rather controversial only thirty years ago, when many ecologists were of the view that only one or other of the two types of factors is of importance in stabilising populations (Howard and Fiske 1911; Nicholson 1933; Andrewartha and Birch 1954). Today emphasis in population dynamics research has shifted away from merely proving the presence of density-dependent relationships; rather, "it is the magnitude of the density-dependent factors in relation to the whole environment that matters" (Andrewartha 1971), and understanding how these may act in regulating population increase or decline. Caughley (1977) stresses that answers to problems of this kind are unlikely to derive from simple approaches, and in order to obtain a deeper insight into a population it is important to study how age-specific survival and fecundity are influenced by the conditions in which the animals live.

Fallow are the most widespread of the six species of deer living wild or feral within Great Britain. In addition, fallow are possibly the most widely distributed species of deer in the world (Chapman and Chapman 1980), being established in the wild in 38 countries in the southern as well as northern hemisphere. Yet, surprisingly little work has been published addressing the population dynamics of this species. In contrast, a number of recent studies on other deer species, incorporating the more detailed, age-specific approach advocated by Caughley above, have contributed much to current understanding of population processes among mammals in general :

1.2 Previous demographic research on deer

As in many other mammals (Caughley 1970, Sinclair and Norton-Griffith 1982; and see reviews: Fowler 1981, 1987), the effects of density-dependent or independent factors in deer are usually most noticeable among juvenile age-classes (McCullough 1979; Albon 1983; Clutton-Brock et al. 1982, 1985b; Sauer and Boyce 1983; Skogland 1985). Hanks (1981) suggests that as a population declines in its rate of increase as a result of some form of environmental stress, a number of sequential events occur : firstly, juvenile mortality rate increases, followed by increases in the age at first reproduction, before adult fecundity declines, and finally adult mortality rates increase.

The particular sensitivity of juvenile mortality as an indicator of changing conditions is born out among deer by, for example, studies of overwinter survival of red deer on the Isle of Rhum (Clutton-Brock et al. 1982) and of reindeer in Norway (Skogland 1985), where mortality was shown to be density-dependent among juveniles, but density-independent among adult age-classes. As density increases differences in fecundity and survival between age-classes often become even more pronounced (Clutton-Brock et al. 1987b). Similar age-specific differences are also found in reaction to density-independent factors. Albon (1983) showed variation in survival of Scottish red deer calves at Glenfeshie to be related primarily to climatic conditions, while here variation in adult mortality was associated with changes in density. The accentuated effects seen among juvenile deer are likely to be associated with their lower fat reserves and small body size in relation to adults (Mitchell et al.1976; Albon 1983). In addition, high overwinter mortality of red deer calves on Rhum increases among late born cohorts, which are themselves associated with increased population density. Increases in juvenile mortality due to predation in whitetailed deer at high densities have also been attributed to changes in maternal behaviour, mothers in poor body condition having been observed to spent less time with their young (Langenau and Lerg 1976).

Puberty in a variety of mammals is known to be dependent on attainment of certain body size thresholds (cattle: Joubert 1954; rats: Widdowson et al. 1964; humans: Frisch and Revelle 1970; red deer: Mitchell and Brown 1974), and body size in deer has been shown to continue to exert effects on fecundity of adults (Hamilton and Blaxter 1980; Reimers 1983, Albon et al. 1986). Reduction in body size itself has long been known to be related to population density in many

Cervids (reindeer : Scheffer 1951; Klein 1964 mule deer: Julander et al. 1961; white-tailed deer : Severinghaus 1955), and hence where changes in fertility are associated with density these may result indirectly from differences in body weights. However, in some populations of Scottish red deer body size and fertility have been shown to be determined predominantly by density-independent factors (Albon 1983, Mitchell et al. 1986). It is clear in such cases that these influences of climate on survival and fecundity tend to become particularly pronounced under conditions of high population density (Klein 1968; Grubb 1974; Clutton-Brock et al. 1982, Reimers 1983); difficulties in separating effects of population density from those of climate may often arise as a result of such interactions between the factors.

Effects of changing environmental conditions on body size, reproductive success and survival, may differ not only between age classes within a species, but also between males and females. Mortality is higher among adult males than females in many polygynous mammals, and this imbalance is again most marked at high population densities or food limitation (Darling 1937, Robinette et al. 1957; Klein and Olson 1960; Clutton-Brock et al. 1982). At the same time climatic factors have shown to influence body weight and survival more among male than female red deer (Clutton-Brock and Albon 1983). Clutton-Brock et al. (1982) stress that differences in the ecology and behaviour between the sexes may have important implications on the population dynamics of polygynous species, and they point out that the performance of members of one sex may in fact be more closely related to the density of that same sex, than to the density of the species as a whole. Furthermore, while regulation of population density through changes in social behaviour and dispersal have mostly been demonstrated among small mammals (Krebs 1971, 1979; Gaines and McCleneghan 1980), based on their long-term studies of individually recognizable red deer, Clutton-Brock and Albon (1985b) suggest that social behaviour is also likely to be involved in population regulation of large ungulates.

The above studies have made much progress toward explaining the natural processes involved in the regulation of deer populations. They also serve, however, to show that the relative importance of the various regulatory factors changes not only between different age and sex classes, but also depending on the point within a species' geographic range (and hence climate) at which a particular population occurs.

1.3 The study species: Fallow deer, *Dama dama*.

The research on other species outlined above provides us with a wealth of hypotheses to test in relation to population dynamics of fallow deer populations experiencing differing conditions. The wide variation in the action of regulatory factors even between populations of a single species, however, suggests that differences between species will be even more pronounced. The extent to which the relationships shown for other deer species may apply to fallow will clearly depend on the degree of similarity in their ecological requirements and adaptation to particular environments. Therefore, while little is known to date about natural population regulation in fallow deer, it is useful here to review their basic biology and geographical range in relation to other deer species.

Taxonomically fallow are placed within the largest cervid Subfamily, the Cervinae or Eurasian deer, which also includes amongst others the red, sika, and axis deer.

Distribution

The widespread distribution of fallow deer throughout both hemispheres, is largely a result of introductions by man (Millais 1906). Fallow deer were widespread in Europe 100,000 years ago, but became extinct throughout most, if not all of Europe during the last glaciation (Chapman and Chapman 1975). Repopulation of Central Europe by fallow may have occurred from relic populations in Southern Europe or Asia Minor, although in the case of Britain reintroduction is thought to be due to the Romans or Normans. Within their native European range, free living fallow today extend between 61°N in southern Sweden and 39°N in Turkey (Whitehead 1972), and as such have a slightly narrower distribution than both red and roe deer within Europe. The great majority of wild fallow populations occur within warm temperate regions, where they experience a rainy climate, mild winters with average temperatures above 0°C but below 18°C in the coldest month, and above 10°C in the warmest month (Chapman and Chapman 1980).

The wide distribution of fallow in Britain has been aided much by releases from disbanded deer parks and escapes from others still in existence. Many wild fallow populations are clearly associated with the location of former as well as present day deer parks (Chapman and Chapman 1975), but their persistence and spread in the wild clearly shows them to be highly adaptable to a variety of differing habitats.

Body size and physical appearance

Fallow are medium-sized deer, adult females attaining heights of around 80 cm at the shoulder, and average body weights in different populations ranging from 35 - 50 kg (this study). Males are larger, averaging 90 cm at the shoulder with weights of 50 - 75 kg in winter, though in autumn individual animals may exceed 110 kg. Female fallow are already nearly fully grown at three years of age (Jackson 1973; Chapman and Chapman 1975), but males may continue to show significant growth up to 5-6 years (Mehlitz and Siefke 1973). Mature male fallow carry distinctive, broadly palmate antlers. Many coat colour varieties exist ranging from pure white, through common and menil, to melanistic. Of these the 'common' variety is thought to be typical of the species, showing a reddish-fawn summer pelage with white spots on the back and flanks, and less distinct spots on a grey-brown winter coat.

While their wide colour variation might suggest a high degree of genetic variability, electrophoretic studies have shown that fallow in fact have lower levels of heterozygosity than most other species of deer, including red, roe, reindeer and whitetailed deer (Pemberton and Smith 1989). On comparing fallow from a range of British parks, little biochemical polymorphism was detected, leading the authors also to the conclusion that British fallow, having originated from only a small number of reintroductions, are likely to have had a long history of inbreeding and hence now show little genetic variability (Pemberton 1983, - and Smith 1985).

Reproduction

Reproduction is highly seasonal with the majority of females conceiving during the 'rut' in late autumn (October in the northern hemisphere). Usually only a single young is produced, after an average gestation period of 234 days (Asher 1986). In Germany Rieck (1955), in a survey including 107 fawns from various locations, noted 12% to be born in May, 72% in June, 16% in July. Parturition is thus later than for most seasonally breeding, temperate deer species, which may be one factor limiting their northern distribution. Does are polyoestrous with an average ovulation interval of 22.4 days (Asher 1986). Although most females tend to conceive during their first cycle, births have been recorded beyond September by a number of studies in Europe (Fisher 1983, Sterba and Klusak 1984; and in this study), and Asher (1986) showed 13% of does on New Zealand farms to conceive during their second cycle, and a further 5% during their third.

Males and females become sexually mature at around 16 months of age, and females will commonly conceive at that age. Males, however, do not exhibit the full range and seasonality of rutting behaviour before they are 4 years old (Sterba and Klusak 1984; Fisher 1983), and until then are mostly prevented from breeding by competition with older males. Conception rates of free-ranging fallow deer, as far as data are available from culled animals, range from 79-85% and 82-93% for yearling and adult does respectively (Baker 1973; Chapman and Chapman 1975; Sterba and Klusak 1984).

Diet and habitat use

Studies of the diet of wild fallow show them to be preferential grazers throughout the year (Jackson 1977; Matzner 1975; Caldwell 1983), with grasses contributing >50% of the forage intake in spring, summer and autumn. This is in accordance with Hoffmann's (1985) classification of cervids based on differences in gut structure, showing fallow to be better adapted to utilization of fibrous roughage than most other deer. Other forage commonly taken are herbs and broadleaf browse, while acorns, chestnuts, mast and other fruit form a major part of the diet in autumn and early winter. Even in winter Jackson (1977, in New Forest, England) found grasses still to contribute 20% of the diet.

In the wild state, fallow are particularly associated with mature deciduous woodland, with a well established understorey. Within their Europe range they have, however, also colonised coniferous forests, mixed woodlands and agricultural areas, as well as wet grasslands at Cote Donana in southern Spain. Fallow inhabiting forests often feed on rides or ground vegetation between the trees, but also leave the trees to forage on surrounding pastures or agricultural crops in the open (Chapman and Chapman 1975; Putman 1990); the same is true of the many populations in England established in agricultural areas, which are often associated with only small woodlands or scattered copses.

Social Behaviour

Fallow are traditionally regarded as a herding species, exhibiting territorial behaviour only during the mating season. Their social organisation is, however, very flexible and strongly influenced by the environment. While within most forest populations males and females are observed to occupy geographically distinct ranges for most of the year (Jackson 1974; Chapman and Chapman 1975), in more open agricultural areas with only small tracts of woodland, groups containing adults of both sexes tend to persist until late spring (Heidemann 1973; Schaal 1982; Langbein 1985; Thirgood 1990). Thirgood (1990) suggests that these differences arise in part due to variation in sex ratios and the overall numbers of adult males in the population, so that males tend to remain with female groups for much of the year when male numbers are low. Fallow group sizes are also highly variable between habitat types and between seasons, with largest groups forming in more open habitats and especially towards the end of winter. While large aggregations of >100 individuals are observed in the wild on preferred feeding areas, mean group sizes in woodlands have been assessed by various authors at < 5 throughout the year. At high stocking levels in deer parks fallow, nevertheless, consistently show a tendency to form larger herds than red deer kept at similar densities throughout the year (Putman and Langbein 1990).

During early summer group sizes tend to be at their smallest, as mature females become more solitary around parturition. Fallow fawns are able to follow their mothers within a few hours of birth, but for the first 3-4 weeks of life tend to 'hide' in cover on their own for much of the day and join the dam only for brief periods of the day. Dams may become 'dry' and wean their fawns as early as October, but suckling has been observed well into the following spring. Although males usually leave the maternal groups at around one year of age, female yearlings may stay associated with their mothers throughout their second year. However, the basic, recognizable social unit within female groups, appears to be the doe and her fawn (Chapman and Chapman 1975; Putman 1981, 1986), the organisation of the loose herds appearing to be one of passive leadership rather than a hierarchy arising out of well established dominance relationships; overt aggression between does is only rarely observed.

Aggression among males is largely confined to the mating season, when they compete fiercely (not infrequently receiving fatal injuries) for mating territories or access to females. Mating systems again show much variation between populations. Traditionally fallow bucks have been described as establishing widely dispersed, noncontiguous rutting 'stands', to which they attract females by calling or 'groaning' (Chapman and Chapman 1975). Recent studies have shown this to be just one of many different types of mating system exhibited by fallow deer. Thus Schaal (1985, 1987) describes non-territorial harem defence by fallow males during the rut in some populations, while at the other extreme he describes for the first time in this species the formation of true 'leks' by deer (Schaal 1986, 1987; and Chapter 5 - this study).

1.4 Aims and Approach of this study

This thesis describes research into the dynamics of a number of fallow deer populations, and the factors affecting demographic parameters over the four years 1985-89. As discussed above, in investigations of population dynamics of any species, it is often difficult to differentiate effects of density from density independent factors such as weather conditions, due to the interaction which may occur between these variables.

One approach to overcome this problem is to study one population over many years, as for example in the exemplary studies of red deer on the Scottish island of Rhum (reviews: Clutton-Brock et al. 1982, 1989). Even then, however, increases in population size may happen to coincide with an unforeseen amelioration in the climate over the duration of the study, and changes in population density over the course of the study may in any case be relatively small. Another way to separate the effects of density from the effects of climate, is by the parallel study of a number of separate populations of different density. This has the advantage that, if the populations are within a reasonably small geographic range, all are affected by similar climatic factors in any one year, and hence differences within years should relate primarily to density-dependent variables. Using a range of sites, however, also introduces additional confounding variables such as variation in habitat and soil types, pasture productivity and management practises. Further, in wild deer populations such a comparative approach is often hampered by the great difficulties which exist in the accurate assessment of densities in woodland environments (Anderson 1953; Ratcliffe 1987a,b). Even where wild animal numbers can be readily assessed, problems may also arise in definition of the home range of each 'population', which is necessary for calculation of its effective density. Not surprisingly therefore, many of the most successful population studies of deer have been carried out on small islands, with hence well defined boundaries to their range, or in open habitats where the animals are relatively easily seen so that age classes or even individuals could be distinguished.

In order to overcome the various problems posed above, the present investigation was based entirely within British parks, which support many well established populations of fallow deer at a wide range of densities. Here, total numbers in each population can be relatively easily counted, and densities may then be accurately assessed, as each population's home range is defined by a boundary fence or park wall. Most parks offer a relatively open habitat, thus also allowing easier observation of the animals than in the wild. Furthermore, due to their enclosure within the park the deer are also (mostly) possible to catch, allowing age-specific physical measurements to be made and marks to be attached to aid continued individual recognition. The 'artificial' enclosure of deer of course does pose the question of how applicable results of studies in parks will be to wild populations. The deer parks studied, however, extend over considerable areas (max 820 ha; mean 217 ha), without any interior fencing or sub-divisions. In contrast to farms therefore, the deer are 'free-ranging', in as far as they remain out on the park throughout the year, and all different age and sex classes of the population are able to associate freely at all times. Parks nevertheless, do generally offer a rather less diverse and more open type of habitat for fallow deer, than is 'typical' of their environment in the wild. Direct comparisons with wild deer must also consider that population densities in most deer parks exceed those found among any wild populations, although the associated food limitation is to a variable (but quantifiable) extent offset by artificial feeding during winter.

The approach of this study was based in particular on the establishment of a range of marked populations. Performance of these separate populations (and marked individuals) could then be monitored in parallel over a number of years. Differences in performance within parks between years, and between parks within years were then investigated in relation to differences in density and other ecological factors.

A large number of different deer parks were considered in setting up this study. While some of these were found to be unsuitable at a later stage, due to difficulties such as capture of the animals, other sites could not be fully included in the study until a later stage. Thus, although results presented in this thesis derive from a total of 18 different populations, field study was not equally intensive in all of these. Physical capture and marking high proportions of the deer was successful in 9 parks, and these hence form the 'core' study parks. In these core parks much detailed investigation was possible at the level of individual animals, each monitored for a number of years. For the remaining parks comparable data on overall population parameters, such as density, mortality, mean body weights and birth rates, were collected to allow investigation of relationships of these parameters with, for example, food supply or climate over a wider range of populations.

The **objectives** of the thesis may be summarised in terms of the following main questions :

1. Are there measurable differences in the performance of fallow deer in terms of their body size and growth, reproductive rates and survival a) between different park populations, and b) within populations between years ?

If significant variation is found between populations:

2. Are differences shown in all or confined among just some age classes ?

3. Are these differences related to
    a) density-dependent resource limitation ?
    b) population density directly, irrespective of food supply, and hence possibly due to social stress ?
    c) habitat characteristics such as shelter ?
    d) climatic conditions ?
    e) variation in management ?

4. How does age affect reproductive performance in fallow deer ?

5. Does variation in density between parks affect the social behaviour of the deer ?

6. Can the high degree of variability in fallow deer mating behaviour be explained in terms of differences in particular ecological conditions existing between populations ?

Thesis lay-out

Following a description of methodology and the study sites used (**Chapter** 2), the result of the investigation are presented in four major chapters: Body size and growth (**Chapter** 3), Female reproductive success and maternal behaviour (**Chapter** 4), Reproductive behaviour during the rut (**Chapter** 5), and Mortality (**Chapter** 6). Results are independently discussed in relation to previous research at the end of each chapter, while a concluding discussion is offered in (**Chapter** 7) to summarise the findings of all parts of the study, and to evaluate their implication for management, and for future studies of fallow deer.

Chapter Two

STUDY AREAS AND METHODS

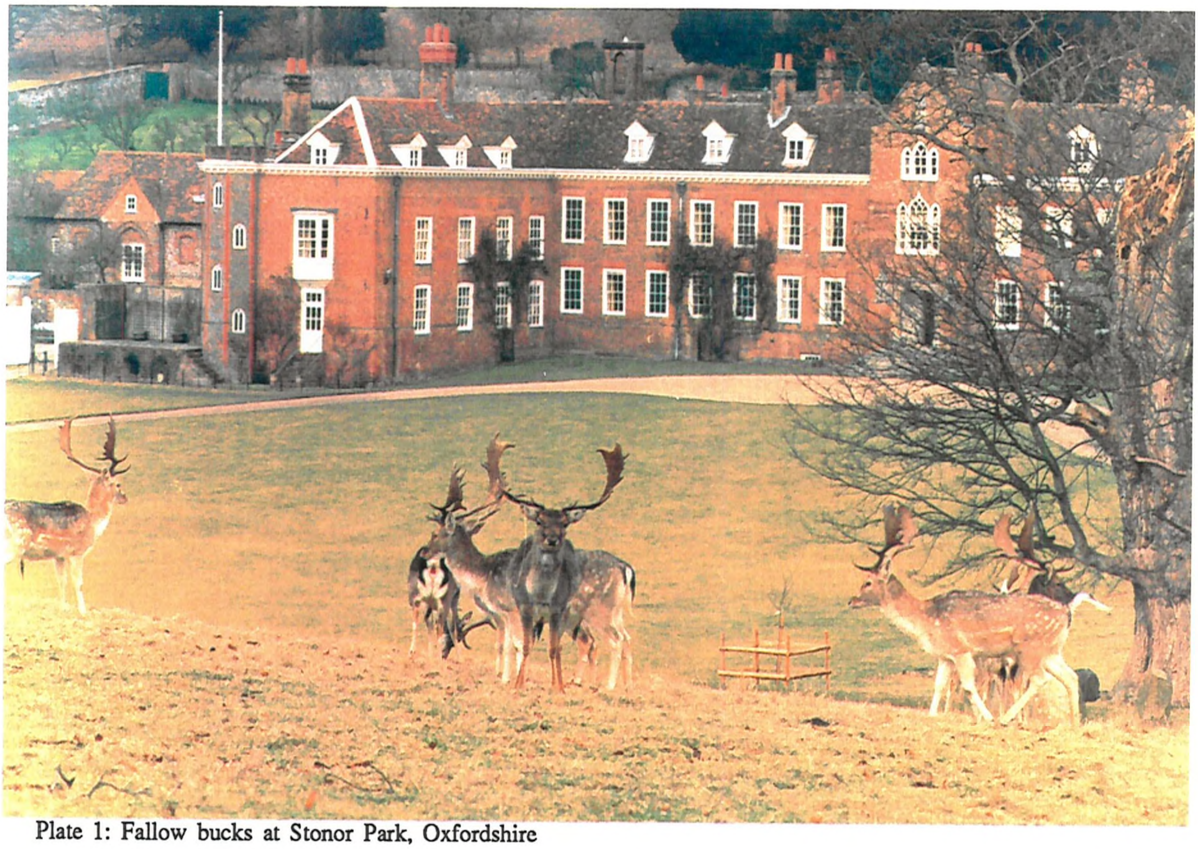


Plate 1: Fallow bucks at Stonor Park, Oxfordshire

2. STUDY AREAS AND METHODS

The aim of this chapter is to provide firstly a general description of the study sites and their deer populations, followed by an outline of the individual techniques and definitions used, to which I refer throughout this thesis.

The data presented in the thesis derive from a total of 18 different emparked populations of fallow deer distributed throughout England and Wales. Field studies were not, however, made at the same level of intensity at all these sites; the majority of analyses are in fact based on results of intensive field studies made between 1985-89 in 9 parks, where live capture of 50-100% of individuals in each population could be achieved.

2.1 The study parks and their deer populations

2.1.1 Historical perspective

Fallow deer have been kept in parks in Britain for well over a thousand years, with 36 enclosures already being recorded in the Domesday Book. Such parks have existed in this country ever since. They became particularly popular during the early Middle Ages when they were mostly of less than 100 hectares in size, and were used mainly for hunting, wild fallow deer at that time being the property of the Crown. Close to 2,000 different deer parks are known to have existed during the Middle Ages, although not necessarily all at one time (Cantor 1983). During the later Middle Ages rather larger 'amenity' parks, often covering more than a thousand hectares each, began to be established; fallow deer remained the main species, but now kept for ornament and for their meat, rather than for hunting. Perhaps the largest land area was given over to deer parks during the sixteenth century prompting Harrisson (1577; in Cantor 1987) to write: *"The twentieth part of the realm is employed upon Deer and Conies already ...... the owners still desirous to enlarge those grounds do not let daily to take in more."* Even a hundred years ago still over 390 fallow deer parks were recorded by Whitaker (1892), which were estimated to have held a total of 71,000 deer. While the exact number of parks in existence today is unknown, it now seems to lie rather lower at around 150 to 250 (Hingston 1988, Cantor 1989), but fallow deer as ever continue to be the most popular species kept in at least 135 parks, as well as being kept on an increasing number of deer farms.

Of the 18 parks included in this study, 16 have been established, and grazed by deer, for over two hundred years; of the two exceptions one was emparked 20 years ago, and the other 7 years ago by reenclosing an area of a former deer park disbanded during the nineteenth century.

2.1.2 Study site Codes

For commercial reasons, the owners of a number of the study parks requested that the name of their park should be omitted from any publication of results. For this reason, as well as for the sake of simplicity of presentation, all study sites have been allocated an individual code letter which is used consistently throughout this thesis. Capital code letters 'A' to 'K' are used to denote the 11 study-sites where large samples of deer were caught and handled, and these have been ranked alphabetically according to increasing average adult female body weights which were recorded for the populations during the study. Additional parks, where no or only limited live capture was carried out, have been allocated lowercase code letters 'q' to 'w', alphabetical rank for these being allocated arbitrarily.

2.1.3 Habitat and population parameters of study sites

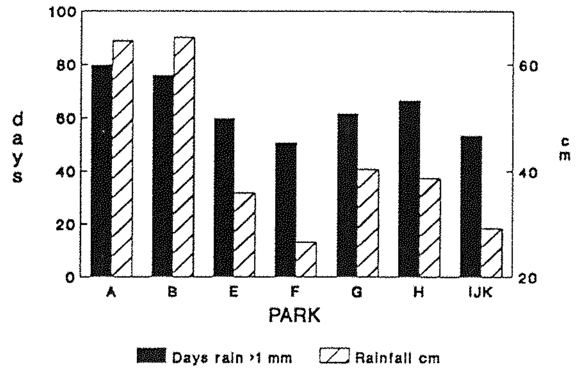
All the parks used during this study were located in England and Wales between latitudes of 50° 30' and 53° 30'. With the exception of parks 'A' (298 m) and 'H' (185 m), they all occurred at mean altitudes of less than 100 metres above sea-level. Figure 2.1 provides a summary of the climatic conditions recorded near each of the main study sites during the study period.

The range of population sizes, densities and other general characteristics offered by the study sites is illustrated in Table 2.1 and Figure 2.2. Full definitions and methods of assessment of the various parameters shown, are provided in later sections (2.2 to 2.13) of this chapter.

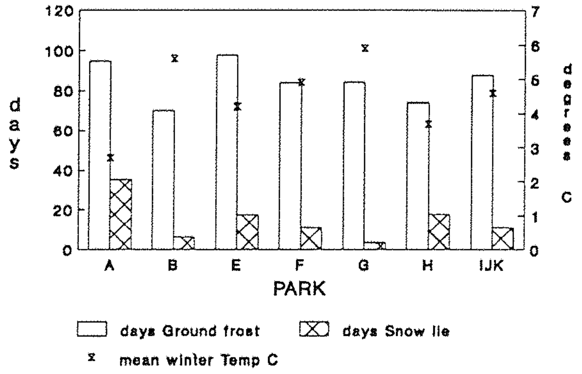
In all the parks a high proportion of the area consisted of mature permanent pasture, usually with widely dispersed mature trees, although closed canopy woodland also contributed up to 45% to the total park area in some cases (Table 2.1).

Figure 2.1 : Climatic conditions at the main study sites

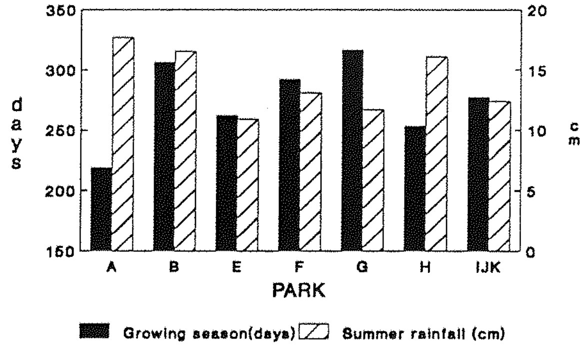
(mean values over the 4 years of study)



a) WINTER RAINFALL (Nov-Mar)



b) MEAN WINTER TEMPERATURE GROUNDFROST, AND SNOW LIE



c) ANNUAL GROWING SEASON DURATION AND SUMMER RAINFALL (May-Jun)

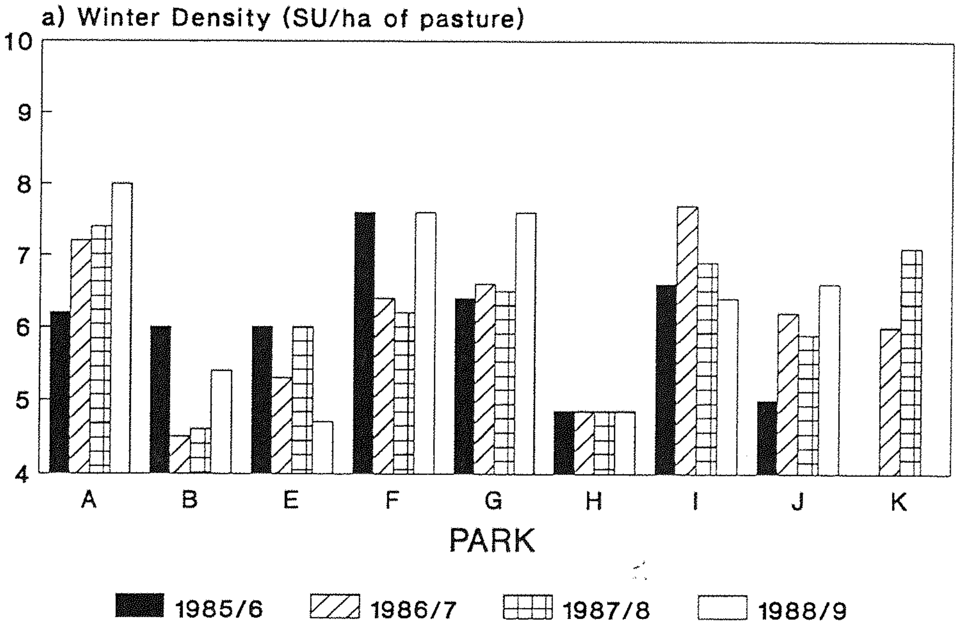
(for calculation of growing season and other variables see 2.8)

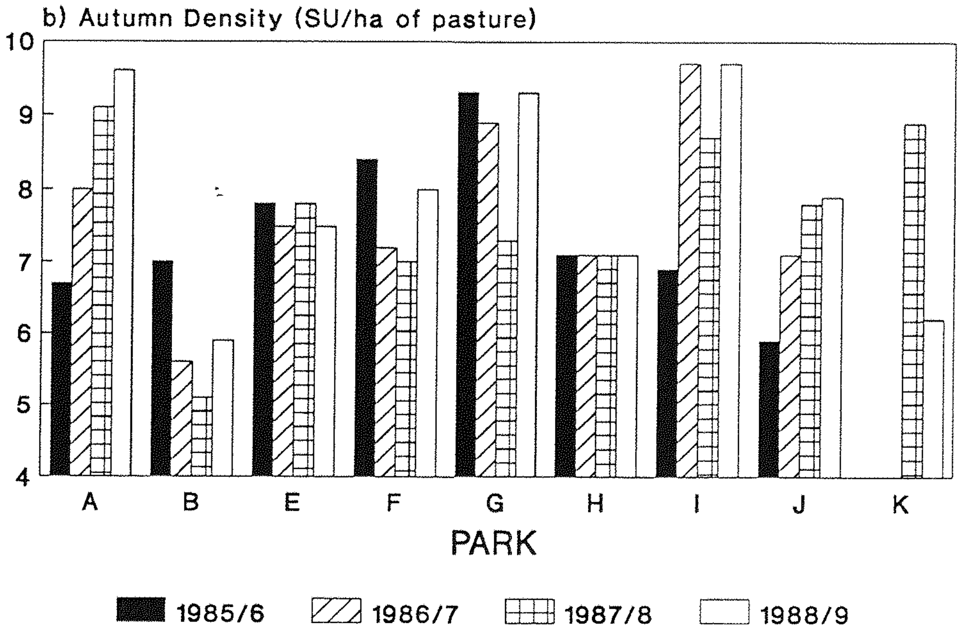
Table 2.1 : Overview of park and population parameters.

Population parameters shown relate to numbers overwinter averaged over the study period (1985/6 -1988/9).
(livestock other than fallow are given in stock units (SU), each unit taken as equivalent to one fallow deer - see text).

	Area (hectares)			%	Mean Overwinter stock (SU)			Density per ha of:	
Park code	Total area	'good' pasture	wood-land	public access	Fallow deer	Other deer	Non-deer livestock	total area (SSD)	pasture area (GAD)
A	17.5	6.3	7.0	80	46	0	0	2.6	7.2
B	285.0	119.7	40.0	100	605	8	0	2.2	5.1
C	16.0	16.0	0.0	0	65	0	0	4.0	4.0
D	141.0	91.7	18.6	80	879	0	0	6.2	9.6
E	251.0	168.2	2.4	100	911	0	20	3.7	5.5
F	5.7	4.8	0.0	5	34	0	0	5.9	7.0
G	71.0	54.7	3.0	10	373	0	0	5.3	6.8
H	40.0	40.0	0.0	0	42	152	0	4.9	4.9
I	28.0	15.1	12.6	0	69	2	35	3.8	6.9
J	87.0	42.6	29.6	20	252	0	0	2.9	5.9
K	14.2	11.2	0.6	0	63	0	0	4.5	5.6
q	165.9	83.0	50.0	5	221	613	0	5.0	10.1
r	350.0	269.5	24.2	72	447	330	92	2.5	3.2
s	121.4	106.0	2.0	100	183	284	0	3.8	4.4
t	820.0	467.4	148.0	100	393	686	0	1.3	2.3
u	70.0	39.9	7.0	0	243	0	0	3.5	6.1
v	385.0	238.7	12.5	100	191	340	0	1.4	2.2
w	389.0	287.9	7.5	100	213	0	90	0.8	1.1
x	69.0	66.2	1.2	16	124	304	104	7.7	8.0
Min :	5.7	4.8	0	0	34	0	0	0.8	1.1
Max :	820.0	467.4	148	100	911	686	104	7.7	10.1

Figure 2.2 :
Variation in grazing density (GAD) assessed a) overwinter, and b) in autumn, in each of the nine main study parks (calculated as stock units per hectare of good pasture area, see section 2.11).


a) Winter Density (SU/ha of pasture)


b) Autumn Density (SU/ha of pasture)

Overwinter fallow deer population sizes, based on average values over the four winters of study in each population (1985/6 - 1988/9), ranged from just 34 to 911 deer, on areas extending from 5.7 to 820 ha. Resulting winter densities, including any other livestock ranged from 0.8 to 7.7 stock units (see section 2.6) per hectare of the total park area (SSD), or up to 10.1 per ha if calculated in relation to the area of available good pasture in each park (GAD). Densities were highest in autumn (after new fawns were born but before the annual cull), reaching levels of up to 12.7/ha (GAD) at that time. The range of variation in densities between parks, as well as within parks between years, is further illustrated in Figure 2.2 for the 9 most intensively studied sites.

While fluctuations in densities did occur within sites during the study period, all the populations were subject to an annual cull, which was aimed at keeping deer numbers at approximately the same level from year to year. A higher proportion of females than males were kept at all sites. Sex ratios [excluding fawns] in autumn lay between 1 - 3.5 females per male (≥1 year) throughout the study in all sites, with the exception of park 'K' (>6.2 :1, in all years), and in 1986 in park 'B'(6.3:1).

Methods of data collection

An overview of all the methods employed in data collection is provided in Table 2.2, broadly distinguishing between animal-based and habitat-based techniques; a summary of the type of data and the range of study sites for which this was collected is also given.

A. Animal based techniques

2.2 Winter Live capture

Data on live weights, morphometric measurements, age, and reproductive condition were collected at live capture operations carried out in each study park during winter. All live capture data presented in this study (with exception of that for fawns caught soon after birth) relate to deer caught during winter, catches all having taken place between 18 November and 6 March in any one year. The great majority of estates used as study sites had no permanent facilities for the capture of deer, nor indeed had most herds been caught previous to this study. The various methods

Table 2.2 : Outline of methods used and data collected for different parks
[figures indicate section in text]

METHODS	DATA COLLECTED	STUDY SITES included
Live capture [2.2]	live weight linear body measures age class udder condition ear tags	(A to K)
Summer fawn searches [2.3]	birth weight/ sex birth dates natality	(A,B,H,I,J,K,t,w)
Cull data & natural mortalities [2.4]	carcase weights age-determination jaw length pregnancy	(all sites)
Direct observation [2.5] Summer	fawning success parturition dates maternal behaviour	(A,B,E,H,G,I,J,K)
Autumn	mating behaviour	(A,B,E,G,I,J,t,v,w)
Censuses [2.6]	population size age & sex structure	(all sites)
Past herd records [2.7]	cull numbers & weights population sizes fawning rate feeding levels	(some info. all sites)
Meteorological data [2.8]	mean monthly rainfall snow lie groundfrost temperatures grass 'growing season'	(all sites)
General habitat assessment [2.9]	areas of good pasture rough grazing woodland cover	(all sites)
Pasture assessment [2.9]	standing crop	(A,B,E-K,t,v,w)
	qualitative analyses	"
	productivity enclosures	(A,B,E,F,G,H,I,J)
Density and Food availability [2.10 & 2.11] Seasonal density-calculation per unit :	i.of total park area (SSD) ii.area of good pasture (GAD)	(all sites)
[2.12 & 2.13] Forage production	pasture production per deer (kg)	
Supplementary feed per deer	energy, protein per day overwinter	

which may be used to capture free-ranging deer are reviewed fully by Dansie (1984), Smith (1979) and Harrington (1990). The main approach used during this study was based on physical restraint of the deer without use of narcotising agents, by long-netting or use of purpose-built catching pens. The exact procedures adopted varied depending on the habitat offered by each study site, but may be summarised as follows :

Netting

An area of 1 to 3 hectares providing the maximum amount of woodland cover available was selected within each site. Whenever possible these 'catching areas' were located close to the boundary fence of the park, or positioned along a route which was known to be used by the deer to withdraw into cover when disturbed. In the weeks before the first catch-up in any site wooden fence posts to a height of 2.5m were erected around the boundary of the catching areas. They were spaced approximately at intervals of 5 m (or more if trees are also available in between posts). On the day of the catch, a strong, 2.5 m high nylon 'holding' net was erected taught around the entire periphery (ca. 300 to 600 m) of the catching area. In order to deter deer inside the catching area from jumping into the 'holding-net' this was then either covered with 2 m high hessian sheeting, or hessian laid flat on the ground beneath it. Once the entire catching area has been enclosed a gap of around 30 to 50 m is reopened as a 'gate' to allow the deer to enter the catching area. Using volunteers as beaters the deer were then 'collected' from different regions of the park, and moved slowly in the direction of the gate into the catching area. In most cases the majority of the herd bunch up quickly to form a single group when the beaters walk the park, and if the drive is successful a high proportion enter the catching area together. Once the deer were enclosed, soft, 20 cm^2 mesh nylon netting (2m high x 50m lengths) was hung loosely on trees or sticks erected within the catching area. The deer, which at that stage tended to withdraw into any available cover, were then driven into these nets in small groups for capture. As soon as a deer was caught up in a net it was restrained on the ground and blindfolded with a mask made especially for this purpose (Plate 2). Such blindfolding noticeably calms the deer. The animal was then extracted from the net, and positioned, legs folded beneath it, onto a small 'trawl' net (approx. 1m x 0.6m), which is used to envelop the deer. Once tied up (Plate 2), the animal could be carried out of the catching area for any inspection and measurements that were required, before being released again or alternatively transferred away from the park for culling or live sale.

Catching pens

The above method was used to catch deer in all but two sites where permanent catching facilities were available. Such facilities comprised of a fenced raceway which can be used to channel the deer into a small, high-boarded wooden building. Within this the deer can be restrained in small pens, or led into livestock crushes. Further descriptions of permanent catching facilities suitable for catching fallow deer are given by Asher (1986) and Kerckerinck (1987).

The following data were collected whenever possible for all deer caught:

2.2.1 Live weight

Animals were weighed on a portable electronic platform balance (Plate 2) fabricated specifically for this project by Griffith Elder Ltd.. The balance (1.2 m x 0.6 m x 0.15 m) consists of a metal frame covered with a wooden platform, and is supported on three feet (0.1 m dia) each incorporating a load cell. The system, which is connected to a digital read out, may be powered by a 12-Volt battery or mains electricity. Measurements are recorded to the nearest 0.2kg, with a maximum load of 500 kg; any weight such as a livestock crush placed on top of the balance can be tared before weighing the deer.

In parks where permanent catching facilities have been constructed, weights were taken with the animal restrained in a crush or box on top of the balance. Animals taken in net catches were weighed while restrained in the trawl net; in such cases 0.5 kg was subtracted from the weight recorded.

2.2.2 Head length

Head length of live deer were measured to the nearest millimetre, using callipers pressed gently against the snout and posterior end of the skull (Plate 3).

2.2.3 Canon bone length

The canon bone represents the fused metatarsals of toes three and four. Its length in live deer was measured to the nearest millimetre using callipers, assessed as the distance between the digits and wrist (or "knee"), when the leg is flexed (Plate 4).

Plate 2
Doe on electronic weighing platform

Plate 3
measuring the head of a yearling male

Plate 4
measuring the canon bone of a mature doe

2.2.4 Incisor height

The height by which permanent central incisor teeth (I1) protruded above the gum line was measured to the nearest 0.5 mm, using vernier callipers.

2.2.5 Age

Live fawns (usually 5-8 months of age at the winter catches) of either sex could confidently be recognised as such based on their body size in relation to the length of the head, as well as by the presence of deciduous or not yet fully erupted permanent incisiform teeth. Male fawns are further distinguished from older males due to the lack of antlers.

Yearling males (usually 17-20 months old at catches) could be readily distinguished by the presence of simple spiked antlers. Yearling females, which had not already been tagged fawns, were distinguished from older females by the form and wear pattern of their incisors and condition of the udder. The second pair of permanent incisors in fallow usually erupt at between 11 - 14 months of age (Chapman and Chapman 1975), and the first pair around 4 months earlier. The spade-shaped and clean appearance of incisors, which have experienced little wear at that stage, was used as one criteria to indicate yearlings. The udder of does which have never lactated (i.e. including 1 year old animals) are recognized as such by hair-covered nipples and undeveloped udders. Head-length of yearlings were also noted to mostly fall 1-3 cm short of sizes achieved by adults in the same park. The common availability of animals marked as fawns the previous year, allowed regular cross-checking of criteria against known-aged yearling females at the same site.

Animals of two-years or older were recorded as 'adults' unless their exact age in years was known due to previous capture as juveniles. Ages of adult males could be estimated to some extent by the size and shape of antlers, but because of great variation in antler sizes achieved by bucks within as well as between sites, antlers were not used to allocate adult males to any narrower age-category. Incisor height (see above) of all adult animals was measured to investigate the possibility of using the patterns of wear on these teeth in age-determination at a later date (see Appendix-I).

2.2.6 Lactation

Udders of adult does were checked for the presence of milk. If any milk could be extracted from the nipples the doe was scored as '*milk*'. If no milk could be extracted during the catch-up, but the shape and appearance showed signs of recent use (i.e previous autumn), the doe was scored as *'n-milk'*. If no milk could be extracted, and the appearance and flaccid shape of the udder indicated that the animal was unlikely to have been in milk during the previous summer/ autumn, the doe was scored as *'yeld'*.

2.2.7 Ear-tags

Animals to be released back to the park were fitted with individually numbered, plastic ear-tags (Plate 5). Tags used were mostly 'Jumbo' tags manufactured by Dalton Ltd., measuring 15mm x 40mm. Tags attached were colour-coded to indicate the animals year of birth, a new colour being introduced for fawns born during each year of study. Ear-tags could be read in the field at considerable distances using a telescope (x 20-60 zoom).

2.3 Summer searches for newborn fawns

Searches for newly born fawns were carried out throughout June and July in selected study sites at intervals of 1 to 7 days, either by myself or occasionally with a small number of helpers. Searches concentrated on areas of good cover such as nettles and bracken, in which young fawns tend to 'hide'. Any fawn found was approached slowly and, if possible, a net (fisherman's landing net type, 1m diameter) was placed over it to prevent it from running off.

Fawns caught were weighed to the nearest 0.1kg using a spring balance (max. 10kg), and then fitted with a numbered ear-tag (see 2.1.7 above), before release back to the park (Plate 5). A record was made of the sex of each fawn as well as its approximate age in days; ages were judged relative to known aged fawns (i.e. ones found on a number of occasions during fawn searches). Fawns less than one day old could be readily distinguished from older ones by remains of wet umbilical cord, as well as by their ill-coordinated movements. Fawns at one to two days old showed little inclination to run off when approached and mostly remained quiet during ear-tagging; fawns only a few days older usually attempted to flee (& often succeeded), and on handling or application of ear-tags often emitted screams. The weights recorded for fawns judged to be less than 3 days old at handling were taken as their *'birth-weights'*, while any recorded for fawns judged to have been older than 3 days were discarded from any later analysis using 'birth-weights'.

Plate 5:
Weighing and tagging newly born fawn.

Plate 6:
Doe giving birth. (Matching does with their fawns was rarely this straightforward!

Plate 7 :
A pasture exclosure in July.

Fawns were released, usually within <5 mins, at the point of capture. No rejection of tagged fawns by their mothers was recorded throughout the study, with the great majority being observed later in the summer and at the winter catches. Mortality was in fact lower among tagged than untagged fawns, probably explained by the fact that a high proportion of neonatal mortality occurs during the first day or so of parturition.

The same records as those above were also made of any dead neonates found during searches.

2.4 Cull and mortality data

Park rangers at all study sites were issued with record sheets on which they were asked to record the date, weight, age, sex, and for females presence/absence of a foetus, for any animals they culled or found dead during the year. Rangers were also asked to retain the lower jaw bones of all animals other than fawns and yearlings. Any dead deer found during my own fieldwork in the parks were dealt with in the same manner.

As a consequence of the fact that live catching operations were organised in support of this research, most of the main study parks culled none or only very few females over the duration of this project, taking advantage of the opportunity to sell surplus females alive instead. Only a small number of adult males were culled in any year, and hence data accumulated on culled animals related mostly to yearling male animals.

2.4.1 Carcase weight

The following alternative measures were recorded on spring balances to the nearest 0.5 kg :

i. entire-weight - total weight *less* readily bleedable blood.
ii. hog-dressed weight - total weight *less* viscera, head, and lower limbs.
iii. skinned-weight - total weight *less* viscera, head, lower limbs, and skin.

Weights recorded were mostly either of type (ii) or (iii) depending on the requirements of the game-dealers used by the estates, with (i) only being recorded as an additional measure at a minority of sites.

2.4.2 Age-determination

The age in years of dead animals was estimated based mainly on inspection of the eruption and wear pattern of the pre-molar and molar teeth in the lower jaw, by comparison to: a) a series of jaw bones collected during the course of this study from fallow deer whose ages were known due to having been tagged as fawns, and b) the guide provided by Chapman and Chapman (1975) to tooth eruption and wear patterns in fallow deer.

The patterns of tooth replacement and stage of eruption of the various teeth can be used in addition to wear pattern for animals up to six years old. In fallow the crowns of all molar teeth above the age of six years are usually clear of the alveolus, and ageing thereafter using wear patterns alone was thought to be unreliable. The age of any animals estimated to have been over 6 years old by the above method was therefore reassessed by cutting a longitudinal section through the crown and root of the first molar (M1); the age in years was then determined as the number of distinct layers visible in the cementum on viewing the sectioned tooth under a binocular microscope (Mitchell 1963, Fancy 1980).

2.4.3 Jaw length

Length of the lower jaw (or *mandibulare* bone) was measured using callipers, as 'the distance between the alveolus of the first incisiform tooth and the proximal end of the processus angularis'.

2.4.4 Incisor height

Incisor heights of culled animals were measured as the distance between the cemento-enamel-junction (the point at which the crown joins with the root of the tooth) and the top of the crown (see Appendix I).

2.5 Direct observation

2.5.1 General methods

Despite a certain level of habituation to human activity, the deer in most of the main study sites could not be directly approached closer than within 50 to 100 metres without causing them to flee. In order to get as undisturbed and as close a view as possible, direct observations of the deer were therefore mostly made from within permanent or temporary hides constructed at each site, or from within a stationary car. Although such stationary observation often resulted in some 'fruitless' hours when no deer were in view, recording of all the required information (see below) was much easier when the deer were observed unaware of my presence.

A telescope (Opticron with x20-60 zoom) and binoculars (9 x 63) were used to assist individual recognition of deer in the field. With a telescope the numbers on ear-tags could be read at over 100 m, although such visibility was reduced down to around 50 metres during rainy conditions, or due to glare off tags due to bright sunshine. Individual recognition of additional animals not yet fitted with ear-tags was based on natural markings. Adult male fallow possess highly variable antlers; drawings made of these during direct observation in the field in each year were used, together with other physical characteristics such as fur colour, to distinguish between individuals. For un-tagged females, the pattern of white spots on the fur of both hind flanks was drawn to provide individual 'finger-prints'. The white spots on common or menil coloured fallow can be seen particularly clearly whilst the animals are in the summer coat, although the pattern also stays consistent throughout the year, as well as from one year to the next (Rand, in Putman 1986).

2.5.2 Fawning success and parturition date

The primary aim of direct observation in the summer months was to assess the fawning success and parturition date of all known aged females in 8 different study populations. Fieldwork required to fulfil that aim was considerably more time-consuming than initially anticipated, and took precedence over any other observational fieldwork during summer.

Visits were made at least every 5-10 days to each of eight parks from the end of May to August during each year of study. As is the case in red deer (Blaxter et al. 1974), udders of pregnant fallow does, were noted not to fill visibly with milk until a day or so within parturition, after which they quickly swelled in size.

Additionally, the udders of any does which lost their fawns early in the summer regressed again within a very short period. During each visit any doe positively identified by its ear-tag, was allocated a condition score from I. to V. to indicate its current pregnancy status, based on the degree of abdominal distension and condition of the udder :

I. = parturition has already taken place; swollen 'milky' udder is clearly visible.
II. = heavily pregnant, parturition likely within few days.
III. = visibly pregnant but parturition possibly not yet imminent.
IV. = doe in average or heavy body condition; may or may not be pregnant.
V. = animal very thin around lower abdomen and thought unlikely to be pregnant.

The change in the condition score (rather than the score itself) allocated when the animal was observed during any future visit was used to estimate its parturition date. Thus for example an animal which was scored as heavily pregnant (II) on the first visit, but in-milk (I) at the next visit 5 days later, could be taken to have produced in the intervening period. Does allocated condition scores of 'IV 'or 'V' throughout the whole summer were recorded as not having produced that year, while only scores of 'I' were taken as conclusive evidence of having given birth during that summer.

Parturition dates could in some cases also be determined by matching does, during observation of suckling bouts (and see Plate 6), with any fawns which had been tagged soon after birth (see 2.2).

Observations made during the first summer of study, while the above scoring system was still being developed, have been excluded from statistical analyses presented in this thesis.

2.5.3 Suckling behaviour and sexing of offspring

Whenever possible during other field observation in summer and autumn, observations of suckling by fawns were recorded opportunistically, and timed using a stop-watch. Duration of any suckling bouts which were interrupted but restarted within 10 minutes were summed, and scored as a single bout. The identity and age of the mother and, if known, the identity, age and sex of the fawn were recorded for each bout. The sex of fawns only a few weeks old was often difficult to assess by observations made from a long distance away. However, fawns often stand with their tail in an upright position while suckling, making this a very suitable time at which to determine their sex.

2.5.4 Direct observation during the rut

Observations were made during the peak of the mating season or 'rut' in a total of 9 different parks. The short time-span of the rut necessitated that my fieldwork input concentrated on a different sub-set of 3-8 parks within this sample in each year of study. Parks were visited for a period of 1-2 days in rotation returning to each site every fourth to sixth day throughout October and early November, giving a total of up to 10 observation days per site; only parks visited on at least three days in any one year were included in statistical analyses of differences in rutting behaviour between sites (see Chapter 5).

Two main types of behavioural data were collected for each study population. Firstly, a census of the study park was made 1-4 times daily and the identity, location, activity, group size and composition of each deer encountered was recorded. Male reproductive activity and social interactions, categorized as either male-female: displaying, following, herding, nudging, mounting, ejaculation; or male-male : displaying, fighting, chasing, were recorded opportunistically during censuses. Secondly, continuous watches were made on individually recognized mature bucks for periods of up to 10 h, during which all reproductive activity and social interactions were recorded. Whenever more than one buck was within the field of view, focal animal watches were interrupted every 10 min to record the position and activity of other adult males. Successful matings seen at any time were recorded, together with the identity and age-class of the buck and doe involved, and when possible, the duration of intense courtship between them (first attempted mount to ejaculation) was timed with a stop-watch.

2.6 Censuses

Throughout the study, censuses were carried out at least twice a year at all study sites, once in late autumn and once in early spring, to count total numbers of fallow deer present, broken down into age and sex classes as far as possible. Methods of census varied according to the size of the park and amount of cover available.

In 8 of the main study sites counting could be carried out by myself during surveys of the park, by choosing times of the day when the majority of animals assembled at the locations used to provide supplementary feed, or when, mostly around dawn and dusk, the deer came out onto pastures in large group sizes. For censuses of some of the largest sites, parks were divided into small sections each simultaneously patrolled by pairs of observers, whose records were then pooled.

In addition to field censuses, total population capture could be achieved during some winters in three sites, and even incomplete capture provided at least minimum estimates for particular age/sex categories.

Numbers of other livestock present on the park were also regularly assessed. To account for differences in the body size and metabolic requirements between differing species of livestock, the total livestock including deer present on the park has been expressed here in terms of Stock Units (SU). The following relationship was assumed, based on published figures which report the average winter energy requirements of an adult female as 11 MJ metabolisable energy per day for fallow deer, and 22 MJ for red deer (Ueckermann 1971; Suttie 1983; and for domestic ruminants see MAFF 1975).

1 SU = 1 fallow deer = 1 sika deer = 1 sheep = 0.5 red deer = 0.25 cattle.

(*Note* - the above adjustment was only necessary in a limited number of instances, as the great majority of data presented in this thesis come from those parks where fallow deer were the only or clearly predominant livestock species present. - see Table 2.1.)

2.7 Past herd records

Most deer park owners could make available some past records made concerning their deer herds. The details of such records varied widely between sites, but could provide useful runs of data for comparative purposes in some cases. Where records provided sufficient detail and were thought to be reliable, data abstracted included the numbers culled in each year, weights of carcases sold, mortalities, basic census information, and amounts of supplementary feed provided. When censuses as well as cull figures were recorded in the past, other parameters such as the population fawning success could also be estimated.

B. Assessment of other environmental variables

2.8 Climate

Meteorological data were based on records from the nearest weather station to each park occurring at a similar altitude, published monthly by the Meteorological Office (HMSO). Parameters extracted for the period between 1984-1989 comprised :

Mean monthly temperatures °C (Nov, Dec, Jan, Feb, Mar, May, June)
Total precipitation mm overwinter (November to March inclusive)
Total precipitation mm May to June
Number of days precipitation exceeded 1mm overwinter
Number of days precipitation exceeded 1mm in May to June
Number of days overwinter with snow-lie at 0900 hrs
Number of days overwinter with groundfrost at 0900 hrs

The length of the *pasture growing-season* at each park was calculated from mean monthly temperatures above as "the period when the annual curve of mean monthly screen temperature exceeds 5.6 °C" (Gloyne 1968).

2.9 Vegetational characteristics

The following parameters were determined from large scale (> 1: 10000) estate maps, confirmed and expanded by ground surveys:

Total park area: area enclosed by the perimeter fence minus any areas inaccessible to the deer such as large lakes or fenced off exclosures within the park.

Area of *closed canopy woodland* : area of deciduous plus evergreen woodland but excluding areas of 'parkland' with only widely spaced standard trees.

Area of *'good' grazing* : grass swards of 'fine' grasses (containing common forage species such as *Festuca rubra, Lolium perenne, Agrostis capillaris*) kept short by grazing and in addition, in some cases, by mechanical cutting or chain-harrowing during spring or summer.

Area of *'rough' grazing* : coarse grass swards, usually with a high proportion of *Deschampsia flexuosa*, often tussocky in structure, and of relatively high sward height (> 30 cm) throughout the year.

Standing crop of available pasture

Samples of the above ground standing crop of vegetation present in different pasture areas within each site were taken in November, January, and March in each year of study. On each occasion between 4 and 8 areas were selected at random from throughout the pasture area and sampled using a wire quadrat (0.5m x 0.5m); vegetation within each quadrat was cut close to the ground using a pair of sheep shears, and all grass cut was collected for analysis in the laboratory. The dry weight of each grass sample was determined after oven drying at 80 °C. Further qualitative analyses to determine the digestibility, calorific value, and nitrogen content of grass samples were carried out by technical staff of the University, but were not completed during this study. Methodology and results of qualitative analyses will therefore be published elsewhere (Putman and Langbein 1990).

Summer pasture productivity

Productivity of pastures was measured in two to four small exclosures per park, installed at the end of March on good grazing swards (see 2.8). Each exclosure, measuring a minimum of 1m x 1m x 1m, was constructed from 4 posts surrounded by wire mesh (Plate 7). A standing crop sample was taken of the pasture <u>outside</u> each exclosure when first installed. Four months later a 1 x 1 m square of the vegetation inside the exclosures was cut close to the ground using sheep-shears. Any cut grass was collected and oven dried at 80 °C before weighing. Total spring/summer production in each enclosure was calculated as : *(dry weight [g/m^2] in exclosure end-July) - (weight outside exclosure end-March)*

Values of all enclosures in each park were averaged to obtain an overall value of productivity/m^2 for its good pasture area. Pasture production exclosures were installed in seven parks. Cuts of vegetation inside some exclosures were also taken during October, although at a number of sites they had become too damaged to be of further use by the autumn.

C. Assessment of densities and food availability

Values obtained from censuses (2.6) and habitat assessment (2.8) were used to calculate a number of population variables defined as follows :

2.10 Simple Stocking Density (SSD)

Simple stocking density was calculated as the number of stock units per hectare of the total park area.

SSD was assessed seasonally to provide three separate variables in each year of study using values for:

i. stock units present in spring

ii. stock units present in autumn (ie. after fawning but before most annual culling)

iii. mean stock units present overwinter between November and March (to take into account differences between parks in any sudden off-take of animals (e.g. extensive live sales or culling) during the winter)

2.11 Grazing Area Density (GAD)

Grazing area density was calculated as the number of stock units per hectare of 'good' grazing area in the park.

GAD was assessed seasonally to provide three separate variables in each year of study as in the case of SSD above.

2.12 Forage production per deer

A relative measure of the growing season production of the good grazing areas at each park, per deer, was calculated as :

(area of good grazing x production m2 [Apr-July]) ÷ (nos. of stock units present)

2.13 Supplementary feed

All estates were asked to provide records of the total quantity, type, and timing of supplementary feed provided for the deer during the winter months. The types of feed given varied widely between parks and years from hay only, hay plus silage or root crops, corn and concentrated compound feeds. For all those estates who could reliably inform me of the total amounts of each type provided, the percentage dry matter, metabolisable energy, and digestible crude protein content provided were assessed using standard food composition tables (MAFF 1975). Having divided the total amounts of feed given by the number of stock units using this supply, this was further divided into a standard of 135 feed days in order to obtain a comparable figure of the average daily contribution of supplementary feed to the metabolism of the deer at each site during winter.

Chapter Three

BODY SIZE AND CONDITION

Plate 8 :

a)

b)

Adult bucks (4 - 6 years old) in (a) average summer condition and (b) poor summer condition. Note the overgrazed sward in b.

3.1 INTRODUCTION

The initial aim of this chapter will be to illustrate the wide range in body weights, skeletal size, and growth rates of fallow deer observed within British deer parks. We will then go on to investigate the causes underlying the observed variation in terms of the ecological conditions (e.g. population density, climate, habitat types) and management experienced (e.g. supplementary feeding, pasture husbandry) by the different herds over the duration of the study.

Of the limited amount of published information available to date describing physical variation of fallow deer, the great majority originates from studies in Central-European forests (Mehlitz and Siefke 1973; Ueckermann and Hansen 1983; Petrak 1987; Sterba & Klusak 1984), and in common with most British studies on this subject (Chapman & Chapman 1975, Jackson 1974), figures quoted are based entirely on carcase materials obtained from a selective cull. Dansie (1977), and Pemberton and Dansie (1983) provide some published detail on live weights of fallow deer, with data based on measurements of a number of park populations; the only other information so far available on live measurements and growth rates, however, is restricted to studies of farmed stock, such animals necessarily being raised under more controlled conditions, mostly within single sex enclosures (e.g. Asher 1985, 1986; Vigh-Larsen 1988). Having accumulated during the course of this study what is probably the largest data set yet available on measurements of live fallow deer across a range of populations, the variation found within this will first be considered in some detail for its own interest.

In investigation of factors responsible for observed variation in body weights, size and growth, special attention has been paid to the effects of population density, forage availability and various management factors, as well as the influence of climatic conditions. As discussed in Chapter 1, deer parks were chosen for this study primarily because they provide us with fenced areas within which total populations can be relatively easily counted; the population home ranges are defined by a perimeter fence and thus densities can be accurately assessed. Park herds are nevertheless very dynamic with regard to density within and between years, depending not only on variation of birth and mortality rates, but also the amount and timing of any off-take (i.e. animals removed from the herd by culling or live sale). Culling of deer in the study parks could take place at any time between August and May, and even live sales ranged from mid-November to early March. As herds are often reduced by around 30% at the annual cull or sale, the variation in this figure, as well as its timing and speed with which it is achieved, can have pronounced effects on the effective over-wintering density experienced by the herds from year to year.

In its simplest form **population-density** may be calculated as the number of animals per unit of the total park area accessible to them, which in this account I refer to as the Simple Stocking Density (**SSD** - see Chapter 2). However, where density-dependent effects on condition or body size have previously been demonstrated for large herbivores, food resource limitation has most often been implicated as the pathway by which such effects are thought to act (e.g. Lowe 1969; Jewell et al. 1974; Sinclair 1977; Skogland 1985; Ratcliffe 1987). Fallow, more so than most other deer species, are anatomically adapted to a 'grazing' feeding style (Hoffmann, 1985), borne out by Jackson's (1977) findings that over half their diet from Spring through to Autumn is made up of grasses. As calculation of SSD uses the entire area of a park, not all of which is necessarily of significance in terms of food to the deer, this figure may not reflect differences in food limitation accurately. The study parks vary considerably in the proportion of their areas made up of good pasture (Table 2.1), and thus a second measure of density (**GAD** - Grazing Area Density) will also be considered here, calculated as stock numbers per unit of pasture area (see section 2.11); this measure hence relates more directly to the main feeding areas. Measurements made of the relative productivity of pastures in the different study parks are then used to further refine estimates of the amounts of grass available per animal.

All the study parks provided at least some supplementary feedstuffs for the deer during the winter period; the amounts of food supplements provided (expressed in terms of metabolisable energy, protein etc. *per animal*) thus constitute another set of density-dependent factors, to be considered in relation to their effects on body size and growth rates.

A number of density-independent factors may also be of importance in relation to body size and condition. Verme (1977) showed that the birth-weight of white-tailed deer fawns vary depending on the severity of the preceding winter, and similarly Albon et al. (1987) note positive correlations of red deer birth weights with spring temperatures. Among adults, cold winter weather may lead to increased weight losses by putting greater demands on thermoregulation (Beddington 1973, Moen 1973, Watts 1980, Clutton-Brock and Albon 1983). Albon (1983) shows further indirect effects of climate in summer on winter weight losses of Scottish red deer, thought to be mediated by changes in production of heather, *Calluna vulgaris and Erica spp.*. As the sites used during the present study are dispersed widely throughout England and Wales and occur at a range of altitudes, temporal as well as spatial climatic variations between sites must be taken into account. Habitat variables such as the presence or absence of shelter (rather than total amount available), soil types and drainage, and degree of public access might also be expected to act independently of density, if at all, on deer performance.

Rising population density, or independent factors such as climate are unlikely to affect all categories of animals equally (Begon 1984, Clutton-Brock et al. 1983, 1987b), and they will therefore be investigated for a range of age/sex classes.

The majority of the data under discussion in this Chapter were obtained by means of live-capture and handling of a large proportion of the animals in each study herd during every winter, while additional measurements taken from culled material are also considered to allow a wider perspective of seasonal weight variation. Live- rather than cull-records form the major part of animal based data collected during the present study, because **individual** growth and performance between years, as well as the condition of the population as a whole, are of interest here. Parallel study of several populations for a number of years enables comparisons not only between animals from different parks within a particular year, but also within any one park across years. In contrast to many previous population studies on ungulates, this comparative approach allows concurrent assessment of the influences of density-dependent factors at several sites, as well as those of climatic variation between years.

During the four winters between January 1986 to March 1989 we were able to catch and handle **3740** different individual fallow deer. Of these 323 animals were recaptured two to four times each in successive winters, providing in total over of 4100 sets of winter live-handling data obtained from 15 different park locations. In addition, 115 fawns were weighed and/or tagged in summer within a few days of birth, yielding valuable information in relation to birth weights and early growth rates. The full details of records made at each handling are described in section 2.2 above. In this chapter we shall in the main be concerned with only some of these measures, namely body weight and the skeletal measurements, that is the lengths of the head and of the canon bone.

Huot (1988), on reviewing the methods available to wildlife biologists for assessing the physical condition of ungulates or the quality of their habitats, based on examination of the animals (see also Hanks 1981, Franzmann 1986), concludes that "no one method seems clearly better than the others or reliable enough to be used alone".

Body weight in relation to age is one of the simplest and most frequently used parameters for determining the physical condition and growth of large herbivores and the quality of their habitat (Klein 1970; Huot 1988). Klein (1968) demonstrated the usefulness of weight as an index of physical condition for reindeer, and Kie et al. (1983) concluded that for management purposes body weight is a reliable index of physical condition in white-tailed deer. For moose, Franzmann et al. (1978) consider seasonal variation and influences of rumen content to be too great for bled weights to detect differences between populations. Hessleton and Sauer (1973), however, demonstrated that for white-tailed deer bled and eviscerated weights are also so closely correlated that within a given season either may be used. While the possibility remains, that individual variation in rumen fill will introduce additional heterogeneity , data presented by Jackson (1974) in fact suggests that this will tend to dampen relative variations in live weight rather than to exaggerate them. During the present study all live weights were assessed in winter, and on the same day (usually within 1-3 hours) for all animals sampled within any one population. Hence at least that part of the variance in rumen fill which is due to seasonal and possibly also diurnal variation in feeding patterns, is likely to be much reduced here.

Morphometric data have also been widely applied in previous studies of ungulate physical condition and growth. Such measures, as for example mandible length, when used as an indices of skeletal development have the advantage that they resist the seasonal variations which may affect body weight and fat reserves (Mitchell et al. 1976; Skogland 1983; Suttie and Mitchell 1983). Skogland (1983) suggests that, for reindeer of any age, mandible length is a good index of habitat quality . Hind foot length is also commonly measured, although this parameter is sometimes considered to be independent of food supply with variation linked to heredity by Klein (1964). In addition to comparing skeletal measures directly between populations, morphometric data can be useful in adjusting body weight measures for skeletal size, or to obtain simple ratios of body weight with respect to linear measures to improve comparability of measures across populations

(McEwan and Wood 1966; White 1968; Goudreault 1982). The relative 'fleshiness' of animals assessed by plotting body weight on skeletal measures (Albon 1983; Ratcliffe 1987) can provide similar indication of relative condition. Skeletal parameters chosen during this study were in part governed by the possibility of obtaining reproducible measurements from live animals under the conditions of a catch-up; the highly variable thickness of tissue covering bones such as for example the mandible, rule this out as a reliable measure on live deer. Instead records were made whenever possible of the total length of the head, and length of the canon bone in the hind limb, in addition to weighing all animals caught.

RESULTS

3.2 BODY WEIGHT

As the first physical measure we will commence with an evaluation of results on live body weights recorded at the annual catching operations. Table 3.1a & 3.1b show the mean live weight determined for each of three age classes of female and male fallow deer caught in 11 parks[1] during up to four successive winters. The three age classes distinguished at this stage are fawns (ca. 5-8mths of age at the catch), yearlings (ca. 17-20 mths), and adults (> 2 years)[2], with any animals which were not classified into one of these groups at the catch being omitted from the table.

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[1] Study parks where live capture was possible have been allocated an uppercase code letter (A to K) based on the mean adult female body weight recorded over the duration of the study, and are referred to by this same code throughout this thesis. 4 further parks provided either only very small live-capture samples or age/sex classifications which were not directly comparable to the remainder, and have been omitted from the main analyses.

Parks denoted in the text by lowercase code letters (q to w) are ones where physical measures of deer were only available from culled animals.

[2] In order to attempt a split of this adult category, the possibility of ageing live deer caught for the first time as adults, by measurement of their incisor teeth was investigated (Appendix [I]). Progressive wear of incisors with age could be readily detected, but individual variation in rates of wear, both between and within populations, was too great for regressions obtained to allow confident prediction of age to the nearest year. The adult age-class was therefore not further divided except when true individual ages were known as a result of tagging as juveniles (see 3.4 : Growth).

Table 3.1 a :

Average live body weights (kg) of Female fallow deer in 11 British parks during winter. (Catch-up period: Early=18Nov-17Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar; n= number weighed, sd=st.deviation)

		FEMALES > 2 YEARS			FEMALE YEARLINGS			FEMALE FAWNS			Catch-up
PARK	YEAR	weight	n	sd	weight	n	sd	weight	n	sd	Period
A	85/6	36.3	3	0.76	-	-	-	20.5	1	-	M
A	86/7	38.7	3	4.01	33.8	2	0.35	-	-	-	E
A	87/8	37.5	8	3.93	32.4	2	4.45	19.3	8	2.68	E
A	88/9	37.6	8	1.78	32.1	5	3.22	17.7	2	0.57	E
B	86/7	37.5	86	2.93	35.1	39	2.64	23.4	39	2.93	M
B	87/8	38.2	31	2.21	33.7	8	1.25	23.6	11	3.02	L
B	88/9	38.3	44	2.74	35.3	15	2.00	21.5	27	3.08	L
C	87/8	40.4	24	1.70	35.4	16	2.78	21.7	15	2.00	L
D	88/9	40.6	154	3.39	36.5	54	2.03	23.2	63	3.48	M
E	85/6	42.6	82	3.50	37.1	44	3.03	24.1	29	3.33	M
E	86/7	42.4	70	3.49	34.7	34	2.21	22.9	59	2.19	E
E	87/8	40.2	130	3.99	34.6	30	2.81	24.4	44	2.87	M
E	88/9	39.9	69	3.41	35.8	59	3.46	23.9	107	2.45	E
F	85/6	42.3	2	-	37.1	1	-	-	-	-	E
F	86/7	39.5	18	3.27	-	-	-	26.0	1	-	L
F	87/8	42.2	20	2.02	38.1	-	-	20.8	3	5.25	M
F	88/9	44.0	17	2.75	36.3	2	0.57	26.8	6	1.92	L
G	86/7	42.5	52	3.33	35.4	22	2.00	24.2	24	1.89	L
G	88/9	41.9	77	3.27	35.8	10	1.69	25.3	33	2.16	L
H	85/6	43.5	4	5.26	38.0	1	-	26.0	2	2.82	L
H	88/9	41.4	11	2.79	37.9	4	2.90	22.5	1	-	L
I	85/6	40.3	17	4.24	34.3	3	2.47	23.6	11	2.41	L
I	86/7	44.2	29	3.37	36.9	10	2.17	24.1	14	2.07	E
I	87/8	46.0	13	3.19	35.8	4	1.17	26.5	3	1.44	E
I	88/9	42.5	30	3.47	37.6	16	2.27	24.1	14	2.88	E
J	86/7	43.7	31	3.19	40.8	17	4.06	25.3	12	1.89	L
J	87/8	45.1	41	3.27	41.7	12	2.14	28.9	20	2.00	E
J	88/9	44.1	56	2.48	39.0	19	2.09	27.0	20	2.09	M
K	87/8	43.9	38	2.96	37.7	13	1.75	26.3	19	0.91	L
K	88/9	48.9	23	3.03	42.6	17	1.36	27.4	11	1.80	E

One-way Analysis-of-variance across parks within years :

86/7	***	***	*
87/8	***	***	***
88/9	***	***	***

(p< 0.0001 ***, p< 0.001 **, p< 0.01*, 1985/6 insufficient sample size)

Table 3.1 b :

Average live body weights (kg) of Male fallow deer in 11 British parks during winter. (Catch-up period: Early=18Nov-17Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar; n= number weighed, sd=st.deviation)

PARK CODE	YEAR	MALE FAWNS weight	n	sd	MALE YEARLINGS weight	n	sd	MALES > 2 YEARS weight	n	sd	Catch-up Period
A	85/6	22.7	3	0.58	39.5	1	-	-	-	-	M
A	86/7	20.5	2	0.71	-	-	-	59.3	2	8.83	E
A	87/8	23.0	6	3.36	39.9	2	1.98	54.0	5	5.92	E
A	88/9	19.5	6	1.92	-	-	-	52.0	3	3.40	E
B	86/7	24.5	31	2.53	40.9	9	3.14	60.6	14	4.05	M
B	87/8	24.7	14	1.62	40.3	5	1.30	51.9	13	5.26	L
B	88/9	25.5	14	3.01	42.4	13	2.10	55.2	7	8.79	L
C	87/8	25.0	10	2.05	40.2	3	1.53	62.5	7	9.54	L
D	88/9	25.9	66	3.10	43.9	20	2.10	57.8	22	7.30	M
E	85/6	28.0	19	2.86	42.7	16	3.54	60.3	23	8.02	M
E	86/7	25.7	57	2.57	41.3	28	3.55	60.3	50	7.24	E
E	87/8	28.2	59	2.89	41.8	21	2.76	58.4	76	7.73	M
E	88/9	26.4	103	2.76	45.4	39	2.49	65.3	100	5.18	E
F	85/6	29.4	1	-	49.4	1	-	65.7	1	-	E
F	86/7	-	-	-	46.3	2	1.06	-	-	-	L
F	87/8	31.0	4	1.47	-	-	-	68.6	2	4.10	M
F	88/9	29.3	5	2.67	48.3	3	1.21	69.3	1	-	L
G	86/7	26.2	14	3.05	42.3	13	-	-	-	-	L
G	88/9	27.8	15	2.81	46.3	3	0.70	70.8	3	8.90	L
H	85/6	30.0	1	-	-	-	-	-	-	-	L
H	88/9	26.8	4	2.69	46.5	1	-	56.5	1	-	L
I	85/6	26.6	5	2.04	47.2	3	6.02	64.8	9	8.12	L
I	86/7	26.3	14	2.61	45.7	9	4.00	68.9	12	8.67	E
I	87/8	28.3	5	1.80	46.2	5	3.16	66.0	8	8.10	E
I	88/9	27.1	15	2.67	50.5	11	3.17	74.4	14	8.70	E
J	86/7	29.8	14	1.56	46.0	12	3.99	64.4	17	6.46	L
J	87/8	32.0	17	2.32	51.1	14	1.99	72.5	17	5.84	E
J	88/9	30.8	20	2.45	49.1	11	4.53	71.7	8	5.89	M
K	87/8	30.8	15	1.98	48.7	1	-	71.9	1	-	L
K	88/9	32.3	11	1.88	55.9	4	2.59	66.5	1	-	E

One-way Analysis-of-variance across parks within years :

86/7	***	**	**
87/8	***	***	***
88/9	***	***	***

(p< 0.0001 ***, p< 0.001 **, p< 0.01*, 1985/6 insufficient sample size)

In addition to live body-weight measurements data were also collected on weights of carcases shot during autumn and winter in a range of park sites, including some where live-capture was not possible. While we shall concentrate here on the evaluation of live data, as these are not subject to biases introduced by the selectiveness of culling, cull data are valuable in interpretation of much of this material and will be introduced for comparisons where appropriate.

3.2.1 Variation of body weights between sites within years

Wide variation between parks is already apparent on gross inspection of Tables 3.1a & b, whereas variation within parks between the different years of study appears to be of a much smaller scale and limited to just a few sites. Within any one year the parks with the heaviest deer often showed mean weights more than 30% higher for each age class than those parks with the lightest mean weights. Greatest differences were recorded amongst fawns: for example, male fawns in 1988 averaged 32 kg in 'Park K' and only 19.5 kg in 'Park A'; a difference here of 66% despite both samples having been caught in the same month (November) and showing near identical standard deviations (Table 3.1b). These differences may perhaps be most easily thought about in terms of the live weight of the adult fallow males, which (not dissimilar to humans) average overall around 70kg in winter, while herd averages in specific populations ranged from just 52kg up to 75kg (ca.8st & 12st). Plate-8 illustrates one buck in no more than average mid-summer condition, and another from a park where the deer are in very poor condition and the sward is clearly overgrazed even at that time of the year.

Before evaluating further these observed differences in body weights between parks in terms of ecological differences between sites, it is important to know which of the differences shown in Table 3.1 are in fact statistically significant rather than having occurred by chance. During the first winter season (1985/86) catching operations were rather less successful than in the later years, with good proportions of the herds only being caught in two of our main future study parks. Analysis of between-park variation in weights was therefore restricted to within each of the three following winters: 1986/87, 1987/88, and 1988/89.

One-way analyses of variance[1] showed variation in body weights between the study parks sampled to be very highly significant (p<0.0001) within all age/sex classes during 1987/88 and 1988/89, as well as for the rather smaller sample of parks during 1986/87, when merely for male yearlings (p<0.001), adult bucks (p<0.001), and female fawns (p<0.01) slightly reduced significance levels applied (Table 3.1).

Results of Tukey's multiple comparison tests between parks illustrate that the above results are not just due to a few widely differing park samples in each year. If we consider each age/sex class in turn sample sizes sufficed for comparisons of weights within years of a total of 359 inter-park pairs, of which over half in fact showed significant differences in means mostly at the 99% level of confidence or better (154 at p<0.01, 29 at p<0.05). For the sake of clarity we will limit ourselves here to a detailed discussion of the results applying to 'adult does' (Table 3.2).

'Adult does' (females 2 years or older) provided the largest sample sizes at most of our catches and hence usually allow inclusion of our most extensive set of parks for statistical analyses. Table 3.2 shows for which pairs of parks differences in adult female body weights were significant and those between which no such differences were apparent. For example, park 'B' had significantly lower weights than park 'I' in each of the three years, while differences between parks 'I' and 'J' were never significant.

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[1] *Statistical procedure* :
By virtue of differences in the sizes of the study herds the number of animals handled in different parks necessarily range quite widely, and catching-up of complete herds was also only rarely possible. Once split into the six age and sex classes distinguished (fawns, yearling, and adults for both sexes), sample sizes in each winter still remained reasonably large in most cases, though falling below five in a few instances. Average figures for any age/sex class within a park were not accepted as useful for statistical analyses unless based on at least 5 individual weights, with the exception of those parks where a lower figure represented more than 40% of the parks population for that age-class; in such a case a mean calculated from <u>at least</u> 3 individuals was taken as a valid figure for that site.

One-way analyses of variance (ANOVA) were first carried out to test for overall differences in mean body weights within a winter across sites, considering each age/sex class in turn. Tukey-Kramer's test (Sokal & Rolff 1981) was then used to elucidate which pairs of parks differed significantly from one another on body weight means. A 'multiple-comparison' procedure of this type was thought more suitable here than the commonly used Student's t-test, because the large number of necessary inter-park comparisons would increase the risk of obtaining spurious significant results for 't' in at least some cases (Snedecor 1967), whereas multiple comparison tests offer protection against this.

Table3.2 : Comparisons of body weights attained by adult females in different deer parks, as sampled by winter live-capture.
(Tukey's multiple comparison tests : # = p<0.001, * =p<0.05; ○ indicates comparisons of pairs of parks where catches held during the same catching period(cp), where E= 18 Nov-17 Dec, M= 1Jan-26Jan, L= 5Feb-6Mar).

a. (WINTER 1988/89)

cp	weight	PARK	A	B	E	D	H	G	I	F	J	K
E	37.6	A	\									
L	38.3	B		\								
E	39.9	E	○		\							
M	40.6	D		*		\						
L	41.4	H		○			\					
L	41.9	G	*	(#)	*		○	\				
E	42.5	I	(*)	#	(*)				\			
L	44.0	F	#	(#)	#	*	○	○		\		
M	44.1	J	#	#	#	(#)		*			\	
E	49.0	K	(#)	#	(#)	#	#	(#)	(#)	#		\

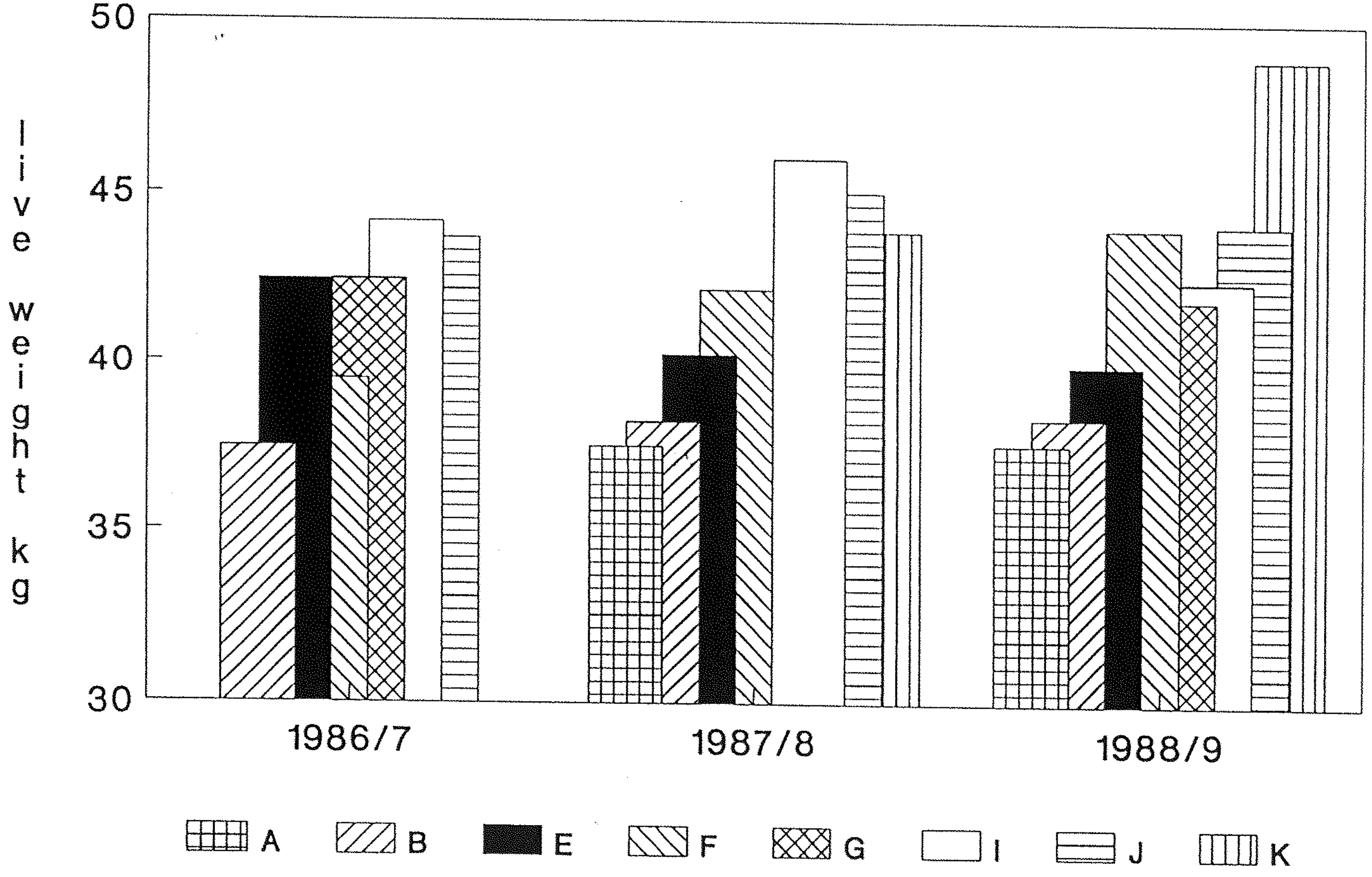
b. (WINTER 1987/88)

cp	weight	PARK	A	B	E	C	F	K	J	I
E	37.5	A	\							
L	38.2	B		\						
M	40.2	E			\					
L	40.4	C		○		\				
M	42.2	F	*	*	○		\			
L	43.9	K	#	(#)	#	(*)		\		
E	45.1	J	(#)	#	#	#			\	
E	46.0	I	(#)	#	#	#			○	\

c. (WINTER 1986/87)

cp	weight	PARK	B	F	E	G	J	I
M	37.5	B	\					
L	39.5	F		\				
E	42.4	E	#	*	\			
L	42.5	G	#	(*)		\		
L	43.7	J	#	(#)		○	\	
E	44.2	I	#	#	○			\

Figure 3.1a: Average winter live weights of Adult Females (› 2 years old) in 8 fallow deer parks (A to K) from 1985-8.



(for sample sizes and standard deviations see Table 3.1)

Figure 3.1b: Average winter live weights of Male Fawns in 8 fallow deer park.

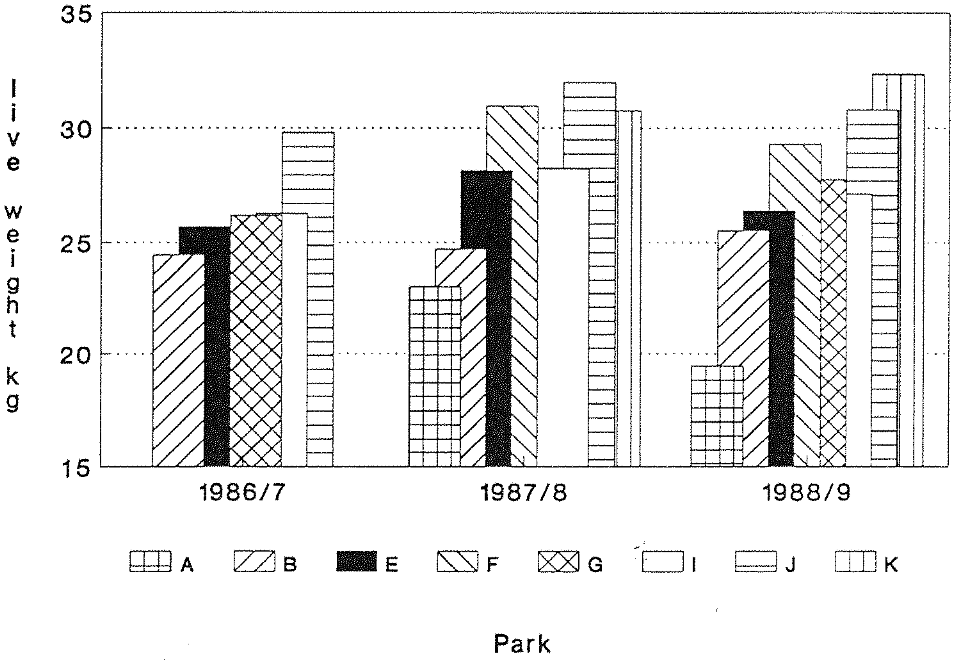
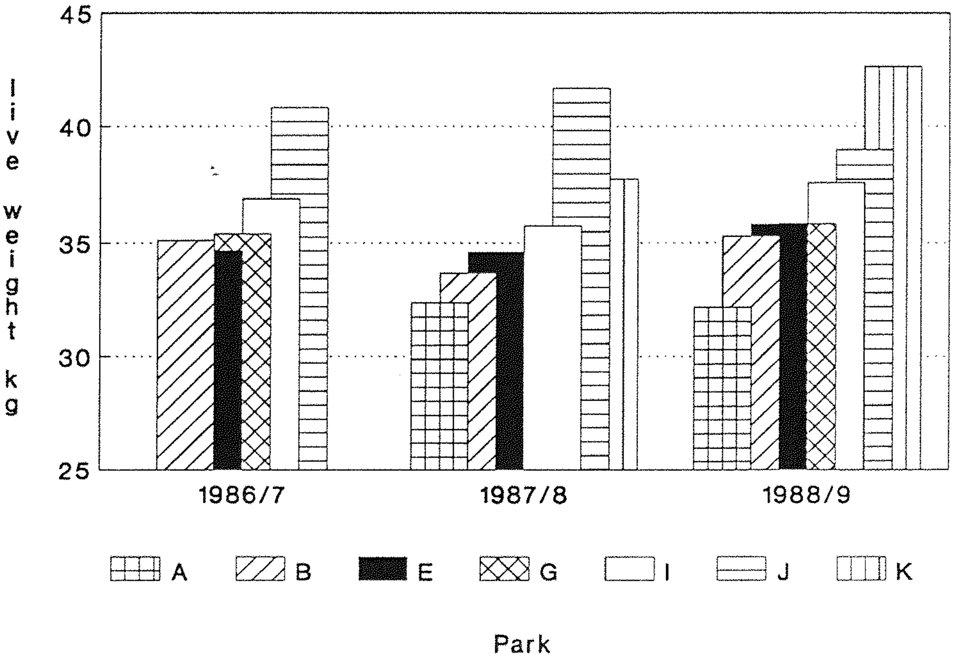


Figure 3.1c : Average winter live weight of female Yearling fallow in 7 parks



(for sample sizes and standard deviations see Table 3.1)

<u>Table 3.3</u>: **Carcase weights of adult does (>2 years old) shot in different months of the year.** Data are shown for parks 'B' and 'J' from this study, together with comparable data from the literature [weights in kg, (×) sample size].

SITE/YEAR	SEP/OCT	NOV/DEC	JANUARY	FEBRUARY
Park 'B':				
1981/82	-	19.0 (21)	17.4 (6)	17.0 (20)
1983/84	23.0 (11)	22.7 (25)	21.9 (11)	22.1 (16)
Park 'J':				
1981/82	-	25.9 (28)	23.8 (7)	22.5 (12)
1982/83	28.6 (14)	25.8 (33)	24.7 (18)	23.2 (20)
1983/84	-	23.6 (34)	24.0 (10)	-
New Forest : (S. England)				
1970/71	-	25.9 (10)	24.7 (12)	20.9 (7)
1971/72	-	24.2 (36)	25.1 (37)	24.0 (16)
1972/73	-	21.8 (66)	22.1 (21)	20.1 (14)
Nedlitz & Serrahn: (NE. Germany)				
1958-70	32.5 (33)	31.7 (59)	32.6 (24)	(no later data)
GARTOW : (N. Germany)				
1974-76	31.1 (13)	30.9 (99)	31.3 (51)	(no later data)

New Forest data from Jackson,1974; Nedlitz & Serrahn data from Mehlitz & Siefke,1973; Gartow data from Ueckermann and Hansen 1983.

(Weights from this study and the New Forest are for 'hog-dressed' carcases (entire weight minus viscera, head and lower limbs). Weights from northern Germany are 'german-gralloch' weights, and <u>include</u> head and lower limbs)

The mean weights of adult does in those sites where catches were held in at least two years are illustrated in Figure 3.1a for each winter. With the exception of park 'F', the relative position of the parks did not change dramatically between study years; generally three main groups of parks may be distinguished : that is 'Light'(A and B), 'Medium'(E, G, and possibly F), and 'Heavy-weight'(I, J, and K) sites. Parks within each of these groups showed very few statistically significant differences in mean weights, while differences between parks of separate groups were common (Table 3.2).

Effects of month of capture on between park variation

Another important question, which needs to be addressed before seeking to explain observed variation in body weight in relation to various ecological factors, is whether the observed between-park variation may be due simply to weight losses occurring in all populations over our 3.5 month winter 'catching-season'. Thus it could be argued that animals from one park caught early in the winter will appear heavier than those from another park caught at the end of winter, merely because the latter animals have had longer to lose condition over the winter. In fact strong evidence to the contrary comes from three main sources : a). highly significant differences in weights even between parks caught within the same months, b.) low rate of change of carcase weights of animals within a park shot over a range of dates, and c.) low degree of variability in live weights within parks across years even if caught-up in different months in successive years.

a.) In Tables 3.1 & 3.2 the time of year when each catch-up took place is indicated, classified within one of three 30 day periods during winter (**Early** 18Nov.-17Dec, **Middle** 1-26Jan, **Late** 5Feb-6Mar). During each year of study at least 2 to 4 parks were sampled within each one of these periods, so that many of our tests shown in Table 3.2 in fact compare pairs of parks in which catch-ups occurred within one to 4 weeks of one another, and in practise often within only a few days. If the heterogeneity of body weight means demonstrated above had arisen due to weight losses over the winter, one should expect most of our significant results to occur between 'Early' and 'Late' catches. In fact, in pair-wise comparisons between parks caught in different months, the animals caught later showed heavier mean weights nearly as often as lighter ones, than those from the earlier caught park (Table 3.2). Based on Tukey's test for 'adult does', out of a total of 25 valid comparisons of parks caught within the same month 15 were significant; this is in fact a somewhat higher proportion of significant results than were obtained in comparisons of parks caught in differing catching months.

b.) Data of animals culled over a range of dates can provide further information on weight losses during the catching period. As a consequence of the fact that live catching operations were organised in support of the research most of our main study parks, the owners culled none or only very few females over the duration of this project, taking advantage of the opportunity to sell these alive instead. Some rangers also carried out much of the male cull at the catch-ups, with the result that only a limited amount of cull material over a spread of dates is available from our main sites for the last three years. Therefore, in order to investigate seasonal weight changes within parks, cull records from some earlier years were examined, in addition to any culled during this study.

Table 3.3 shows fluctuations noted in carcase weights over the duration of the cull in a number of separate years for adult-does from parks 'B' and 'J', together with some data from previous studies (Jackson 1974; Mehlitz and Siefke 1973, Ueckermann and Hansen 1983). Mean carcase weights have been calculated for periods equivalent to our Early, Middle, and Late winter catching-season periods used above, and also for those culled earlier in the autumn. In park 'J' differences between Nov/Dec : January were not significant (Student's t-test) for any of the three years for which such analysis were possible; this result is also supported by data from Jackson (1974), Mehlitz and Siefke (1973) and Ueckermann and Hansen (1983), who each report no significant reduction in weight from Nov/Dec to January (Table 3.3). Only for park 'B' in 1983/4 could a significant difference be shown between Nov/Dec and January carcase weights of does ($p< 0.05$). Differences are, however, apparent between carcase weight means in Nov/Dec : February for both our parks, as well as in Jackson's studies for free-living New Forest deer in 1970/71 and 72/73 where comparisons between January and February were also significant. Nonetheless, in the intermediate year (1971/72) Jackson found no significant weight losses between any of the cull months despite large numbers of animals being sampled, showing that such weight losses are not inevitable in every year even in the absence of supplementary feeding.

That body weights are generally maintained at similar levels from November to January also extends to data on other age-classes (Mehlitz and Siefke 1973; Ueckermann and Hansen 1983; Petrak,1987). Mehlitz and Siefke (1973) showed carcase-weights of fawns to differ very little from November to end of January. Although for later months their results were based on only very small samples, they showed fawns in East Germany to lose weight from end of January until end of April (that is most weight losses in fact occurring after completion of our catching period), and to not attain any growth again until June over their previous highest weights. Pemberton and Dansie (1983) using data on two live-catches made in successive months for one site did find significant weight losses by mature does during February, but were unable to test losses in other months.

Whilst few females were culled during the present study for reasons discussed above, more thorough analysis of seasonal weight fluctuations in the case of more the extensively culled males was hampered due to the fact that most parks carried out their cull before the catching season started, or predominantly restricted it to within one of our time-periods. The greatest weight losses in the case of adult males, however, clearly occurred during the rut in October before commencement of our catching season (as has been previously shown by a number of authors: Baker 1973, Sterba and Klusak 1984, Ueckermann and Hansen 1968,1983). Although most body weight data during this study were collected in winter, live-weights were available for three bucks weighed on the 4th October 1988 (110kg, 104kg, and 98kg) in park 'G', and 'entire-carcase' weights of adult bucks (>2 years) averaged 88.5 kg (n=31, SD=15.4) in early September in park 't'. In contrast, mean live-weights of adult bucks did not exceed 75 kg in any of our study parks during the main catching season (Nov-Mar), with few individuals over 80 kg ever being recorded in winter.

Results of carcase weight variation between November and beginning of March (i.e. the period comparable to our live catches) are thus rather inconsistent, suggesting that weight losses in some years are often very slight, and the seasonal pattern of change is variable between years.

c.) Variation of live weights within sites between years is described fully in 3.2.2. below. However, it is clear within the present context, that differences in weights experienced in parks from year to year were small (even when catches took place in differing months) in comparison to those between parks, unless accompanied by major changes in stocking density from one year to the next.

The provision of supplementary food in the parks, and possibly more importantly the very mild winters experienced during the study from 1986/7 onwards may also have contributed to the lack of significant differences directly associated with differences in catching date. For all the reasons outlined in a. to c. above, a consistent correction factor for progressive weight loss overwinter would not have been possible to produce, even if it had been thought appropriate to do so. Actual weights recorded (Table 3.1) are therefore retained unmodified for further analyses, although comparisons within each of our three sub-divisions of the winter-catching period will be explored where sufficient data are available. We may nevertheless conclude at this stage that very wide, significant variation exists in body weights of fallow deer between the study parks, even when those comparisons which may have shown differences due to weight losses overwinter are disregarded.

Comparisons of Milk versus Yeld does

Studies on Scottish red deer, have shown non-lactating (yeld) hinds to be significantly heavier than lactating (milk) hinds (Mitchell et al.1976, 1986), and many studies of this species have sub-divided their data into yeld and milk hinds accordingly. While the reproductive status in relation to age and condition is discussed further in Chapter 4 , the possibility of a confounding effect of reproductive status in the above results for mature does needs to be considered here. In contrast to the above studies of Scottish red deer on open-range, but in common with Ratcliffe's (1987) work of that species in populations in Scottish forests, yeld females occurred in much lower numbers than milk does in most of our fallow deer populations.

The condition of udders was assessed during live capture and scored as '*milk*' if milk could be extracted from the teat, '*n-milk*' if no milk was obtained but the udder showed signs of recent use, or '*yeld*' if no signs of use during that year were apparent. Treating each year and park separately ANOVA analyses showed no significant differences between live weights of lactating, n-milk, and yeld does in the great majority of cases; the one exception to this occurred in park 'E' during just one of the four years it was sampled (1986/7) when yeld does there were heavier than either milk or n-milk does. Comparisons of *yeld* with '*milk plus n-milk*' females also remained non-significant ($p > 0.05$, ns). On pooling samples for all available winters for each park statistical significance could also be attained in the case of park 'K', but the relationship was in the opposing direction with milk does in fact being heavier here than yeld or n-milk does. As catches only took place from the end of November, milk production will have been greatly reduced in the majority of does even at the start of the catching season. The does still in milk in park 'K' during February, may have been those in especially good condition, reflected in such prolonged strong lactation, as well as by their high body weights.

3.2.2 Variation of body weights within sites across years

In order to summarise any general trend in body weights between the study years an overall parks-average was calculated for each age/sex class (Table 3.4), giving equal weighting to results from each of the six most regularly caught herds (A, B, E, F, I, J). For cases where data are not available for all six parks an average is shown in brackets based on half this sub-set of parks still retaining one of each from the 'low'(A & B), 'medium'(E & F), and 'heavy'(I & J) weight sites). While changes in this value between years were quite small (<10%) for all age/sex classes, in the case of fawns of both sexes the same pattern was apparent, i.e. weights were lowest in 1985[1] < '88 < '86 < '87. England has experienced exceptionally mild winters since 1986, and the rather low weights recorded in the first year may reflect the relatively cold and early onset of low temperatures during the first winter of study.

For individual parks, examination of Table 3.1 shows variation in live weights between years to have rarely exceeded 15% for any age-class (mostly < 10%), in contrast to the variation shown between parks above (i.e. 30 - 65 %; see 3.2.1). Nevertheless an overall analysis of variance entering parks and year of study as main effects, showed significant effects of year of study in addition to the between park effects described above, as well as interactions of the two effects for all age/sex classes (with the exception of male fawns). This indicates that weights generally varied significantly between years in some parks, but the inter-year effect differed between sites.

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[1] Figures of years given in the text refer to the catching season commencing in November of the year stated and ending in the February of the following year, e.g. '85 denotes the winter of 1985/86.

Table 3.4: Overall variation in mean live weights between years of study.

Equal weighting has been given to results of catches in each of the six parks caught most regularly (A,B; E,F; I,J), to allow a general comparison between years. (Figures shown in brackets are calculated from a reduced set of three parks, using one of each of the above pairs, when samples from all six were not available).

Year	Female			Male		
	Fawns	Yearlings	Adults	Fawns	Yearlings	Adults
1985/6	(22.7)		(39.7)	(25.7)	(43.1)	
1986/7	23.7	(36.9)	41.0	(26.6)	(42.7)	(61.8)
1987/8	24.4	36.0	41.5	27.8	(44.4)	61.9
1988/9	23.5	36.0	41.1	26.4	(45.6)	64.6

Table 3.5 : Results of one-way analyses of variance comparing live weights recorded within individual parks in different years of study (1985/6 - 88/9).
Significance values for ANOVA are indicated by astrix(p<0.05 *, <0.01 **, < 0.001 ***) In the case of significant results, any contributing pairs of years which showed significant differences by themselves (Tukey-Kramer test) are also indicated,
(where 5 = 1985/6 , 6 = 1986/7 , 7 = 1987/8, 8= 1988/9; **bold** figures highlight those significant comparisons where both samples were caught during the same months).

Females

Park	Adults		Yearlings		Fawns	
B	ns		ns		*	6:8
E	***	5:**7**,8 ; 6:7,**8**	***	5:6 ; 5:**7**	***	6:7
F	***	6:7 ; 6:8				
G	ns		ns		ns	
I	***	5:6,7 ; 7:**8**	ns		ns	
J	ns		*	–	***	7:6,8
K	***	7:8	***	7:8	*	7:8

Males

Park	Adults		Yearlings		Fawns	
B	**	6:7	ns		ns	
E	***	8:5,**6**,7	***	8:5,**6**,7	***	6:5,7
G					ns	
I	*	–	ns		ns	
J	***	6:7,8	**	6:7	*	6:7
K					ns	

(only samples providing weights of at least five individuals in a given age/sex category per year were included. For full details of sample sizes and mean weights see Table 3.1)

Subsequent one-way analyses of variance within the adult doe age-class showed no significant effect of 'year' on mean weights in parks 'A, B, G, and J' ($p > 0.05$), despite a wide variation in catching dates (Table 3.1). The overall heterogeneity in the case of adult does was noted to be due to variation between years in the remaining four parks (E, F, I, and K). Results of these analyses of variance are presented in Table 3.5; pair-wise comparisons of catching years (t-test) are also given, showing which years contributed most to the overall heterogeneity.

The most conclusive comparisons within parks across years are of course again those based on weights recorded during the same month in the different years of capture, such as in parks 'E' (1986 > '88; '85 > '87; $p<0.05$.) and 'I' ('87 > '88 , $p<0.05$). Interpretation of these changes of adult weights between years, however, must take into account that values obtained in successive years are not truly independent, due to recaptures for that age category.

Few significant differences could be shown for other age/sex classes within parks if caught in the same or consecutive months in different years, except in the case of park 'E'. Catches in this park provided the largest sample size for all categories, and allow us to distinguish between all four catch years on live-weight alone for at least two age/sex classes, despite actual differences between years usually being well within one sample standard deviation. It is interesting to note here that where significant differences could be established these always occurred in the same direction for fawns of both sexes, female yearlings, and adult-does, while for adult and yearling males a consistent opposing deviation (88 > 85,86,87) arose (Table 3.5). All four catches in this park took place between 10th December-10th January, and no effect of capture date was apparent.

Some of the most striking examples of changes in weights in successive years evident from Table 3.1 occurred in Park 'K' for all six age/sex categories. Here, in addition to the first catch taking place at the end and the other at the beginning of winter, the density of deer in park 'K' was reduced quite drastically from nearly 6/ha in 1987 to only 3/ha in 1988.

3.3 SKELETAL SIZE

The aim in this section is to investigate variation between populations in the **adult skeletal sizes** achieved, while results on individual growth rates are discussed in the subsequent section (3.4). As discussed in 3.1 above, skeletal measures of fully grown, adult animals have an advantage over body weight parameters in that they are not affected by seasonal variation.

Previous studies based on a variety of measurements of carcase material have shown skeletal growth of fallow to reach an asymptote very early on in life . Thus Chapman and Chapman (1975) found no increases in jaw length of male or female fallow beyond three years old. Jackson (1974) confirms such results for female fallow, but Mehlitz and Siefke (1973) state that in the case of males full jaw length is not reached until 5-6 years old. Our own results based on carcase material from park 't' (Fig. 3.2) show fallow jaw lengths to consistently increase until 3 years in females and 5 years in males. Data collected concurrently in the same park from red deer, are given by way of comparison, and shows that growth continues considerably longer into life in that species. Petrak (1987) presents data on hind foot lengths (canon bone + phalanges) for fallow deer, showing this parameter (which is readily comparable with our measure of canon bone length) already to have reached an asymptote at two years of age for both sexes.

Results of measurements of head length and canon bone length are summarised in Tables 3.6 and 3.7 respectively for male and female fawns, yearlings, and adults two-years and older in each study site. Bearing in mind the early completion of skeletal growth of female fallow outlined above, any differences in the age structures of our 'adult' samples will have had little effect on the mean skeletal lengths obtained for this sex. Mean canon bone length attained by yearlings is seen to only be slightly below the value for adults, while more significant increases are still apparent in the length of the head beyond 20 months of age. Coefficients of variation (SD/mean) for data on head length and canon bone length are not surprisingly, at around 3 %, somewhat lower than those for body weights (ca. 9 %) for all age and sex categories. The same trend of increasing in skeletal size across parks is nevertheless again apparent down both Tables 3.6 and 3.7, the parks in these Tables still being presented in order of increasing mean body weights.

Adult females from 1988/89 catching season again provided the most extensive set of parks with adequate samples of similar size permitting the necessary assumptions for parametric ANOVAs to be met. Significant heterogeneity occurred between parks for both measures (head length: $F_{9,324}$ =17.6, $p< 0.0001$; canon bone: $F_{8,304}$ =19.5, $p< 0.0001$). Comparisons between pairs of parks for adult does on head lengths are shown in Table 3.8 for 1988/9.

Correlation coefficients, comparing live-weight, head-, and canon bone- length for all adult does measured in each year of study, are presented in Table 3.9, showing strong significant correlations in all cases. The close similarity in ranking of parks in Tables 3.8 and 3.2 (that is, if arranged in order of mean weight and mean skeletal size respectively), also emphasise the close association between these different parameters. Using the 1988/9 winter as an example, mean adult female body weight across parks was positively correlated with mean canon bone length ($r= 0.79$, $p< 0.01$) and with head length ($r= 0.63$, $p=0.05$), and the two skeletal measures were also strongly correlated with each other ($r= 0.87$, $p< 0.005$; see Table 3.9 for other age/sex classes).

Only a single population (Park 'D') showed a major change in its relative ranking on weight and the skeletal measures, showing very high values for adult skeletal measures. This indicates an atypically low 'flesh-coverage' at a given skeletal size perhaps due to adult animals in this park now experiencing worse conditions (food availability /density) than those experienced in early life during their period of active skeletal growth. While records available for park 'D' are confined to those from one catch-up, growing female fawns and yearlings indeed ranked lower amongst our sample of parks than did adults based on their skeletal measures. If this 'outlier' site is omitted from the above correlations these all become more highly significant even for weight : head length ($p< 0.02$).

While this one example does illustrate the potential usefulness of ratios of body weight/skeletal measures as an index of condition, the very high degree of correlation of the measures across most of our sites indicate that little extra information can be obtained by this index here. Ratcliffe (1987) uses a regression of red deer carcase weights on jaw length to illustrate which of his study herds were of 'good' or 'poor' condition, by judging whether their scatter of points fell above or below the overall regression line. Similar plots of our results of adult-doe live weights on head length (Fig. 3.3a-c) in each year of study indeed separate out our park herds of good and poor condition, but in fact very much in the same way as was indicated by using live body weight alone (Table 3.2). These figures do, however, emphasise that even though only few individuals ever reach large skeletal sizes in the 'low-weight' parks, the few who do usually show lower weights than would be predicted by their skeletal parameters; hence, low weights may be taken here as being indicative of poor condition.

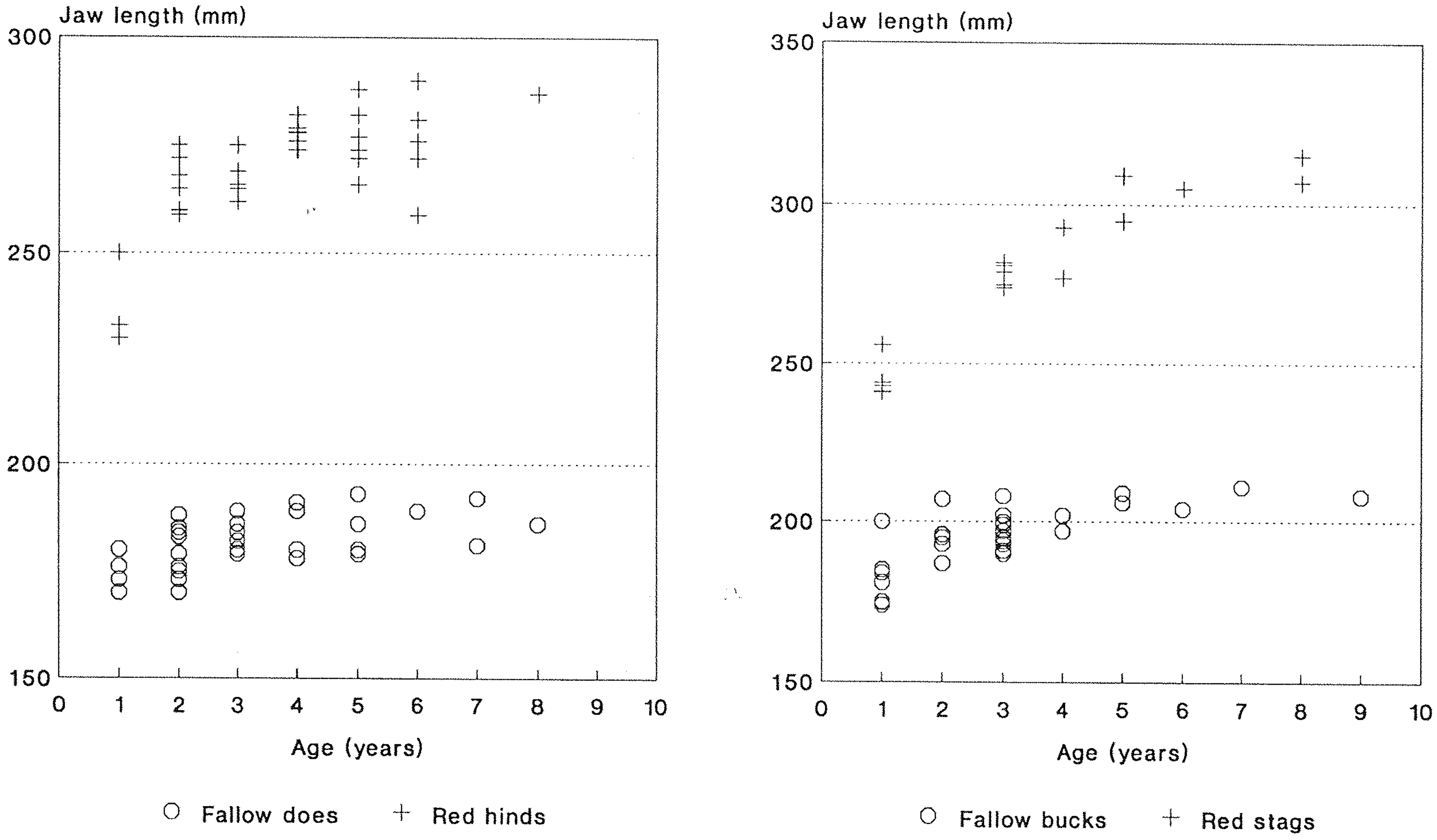

Figure 3.2 : Plots of jaw length on age for female and male fallow deer at park 't'. data for red deer from the same park are shown for comparison. (All males were culled in September, and all females during November 1987).

Table 3.6a :

Average head-lengths (mm) of Female fallow deer in 11 British parks during winter. (Catch-up period: Early=17Nov-18Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar ; n= number weighed, sd=standard deviation).

Park	Year	Females > 2 years length	n	sd	Female Yearlings length	n	sd	Female Fawns length	n	sd	Catch-up Period
A	86/7	250	3	2.7	-	-	-	-	-	-	E
A	87/8	246	8	11.0	226	4	3.4	190	8	10.2	E
A	88/9	245	8	6.0	230	5	10.2	-	-	-	E
B	86/7	253	46	9.0	240	29	11.0	199	5	16.0	M
B	87/8	250	31	8.3	236	8	4.7	207	11	10.4	L
B	88/9	250	43	6.6	238	16	3.7	205	27	9.0	L
C	87/8	258	25	5.2	245	16	7.7	208	14	4.2	L
D	88/9	263	59	6.4	246	27	4.8	205	29	8.5	M
E	86/7	252	66	6.3	233	34	7.0	-	-	-	E
E	87/8	253	41	7.3	240	20	5.2	206	11	10.0	M
E	88/9	253	65	6.8	243	35	7.0	202	95	5.8	E
F	86/7	254	18	4.5	-	-	-	-	-	-	L
F	87/8	256	20	4.1	-	-	-	197	3	13.7	M
F	88/9	257	19	5.4	237	3	4.0	216	6	4.9	L
G	86/7	252	20	6.7	236	17	6.9	206	9	11.4	L
G	88/9	257	18	6.4	240	11	4.0	210	3	2.3	L
H	85/6	260	4	5.3	-	-	-	-	-	-	L
H	88/9	261	13	6.2	250	4	6.2	-	-	-	L
I	85/6	252	17	10.8	245	3	6.7	209	11	4.8	L
I	86/7	257	29	8.4	237	10	2.4	199	15	5.7	E
I	87/8	261	13	9.3	234	4	14.6	209	3	3.8	E
I	88/9	256	30	6.2	241	16	4.5	201	14	7.8	E
J	86/7	261	31	6.0	251	17	8.8	214	12	6.7	L
J	87/8	256	41	9.9	242	12	11.0	211	23	6.0	E
J	88/9	259	58	6.4	246	19	5.7	211	19	4.8	M
K	87/8	258	39	5.4	244	11	3.8	219	20	7.8	L
K	88/9	260	24	7.3	243	17	4.2	203	11	6.4	E

Table 3.6b :
Average head-lengths (mm) of Male fallow deer in 11 British parks during winter. (Catch-up period: Early=17Nov-18Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar ; n= number weighed, sd=standard deviation)

Park	Year	Males > 2 years length	n	sd	Male Yearlings length	n	sd	Male Fawns length	n	sd	Catch-up Period
A	86/7	-	-	-	-	-	-	-	-	-	E
A	87/8	265	5	11.7	-	-	-	200	6	11.0	E
A	88/9	265	3	8.6	-	-	-	192	6	6.0	E
B	86/7	282	14	8.3	243	5	5.7	210	11	7.7	M
B	87/8	275	13	8.9	246	5	9.9	211	14	5.4	L
B	88/9	276	6	9.7	256	12	4.7	215	17	7.3	L
C	87/8	289	7	11.3	258	3	1.5	220	10	15.5	L
D	88/9	281	4	8.4	263	10	3.2	211	31	9.2	M
E	86/7	275	16	10.4	242	5	3.5	216	4	4.7	E
E	87/8	280	38	10.3	251	11	6.4	213	10	8.9	M
E	88/9	285	41	7.4	257	12	6.6	205	13	7.5	E
F	86/7	-	-	-	-	-	-	-	-	-	L
F	87/8	-	-	-	-	-	-	220	4	7.5	M
F	88/9	-	-	-	260	3	3	219	5	9.6	L
G	86/7	-	-	-	-	-	-	-	-	-	L
G	88/9	-	-	-	-	-	-	-	-	-	L
H	85/6	-	-	-	-	-	-	-	-	-	L
H	88/9	-	-	-	-	-	-	219	5	4.1	L
I	85/6	287	9	11.6	257	3	4.0	220	5	7.7	L
I	86/7	282	13	12.9	253	10	9.7	206	14	6.8	E
I	87/8	294	8	13.0	258	4	7.9	209	5	3.5	E
I	88/9	299	14	13.1	267	11	9.6	208	16	7.9	E
J	86/7	290	17	7.7	270	12	10.1	225	14	3.9	L
J	87/8	290	18	14.2	263	14	3.7	215	16	7.2	E
J	88/9	294	9	11.3	271	9	9.7	223	24	5.7	M
K	87/8	-	-	-	-	-	-	228	15	6.3	L
K	88/9	-	-	-	264	4	5.9	215	11	4.1	E

Table 3.7a :
Average canon-bone (mm) of Female fallow deer in 10 British parks during winter.
(Catch-up period: Early=17Nov-18Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar ;
n= number weighed, sd=standard deviation)

Park	Year	Females > 2 years length	n	sd	Female Yearlings length	n	sd	Female Fawns length	n	sd	Catch-up Period
A	86/7	275	3	5.9	-	-	-	-	-	-	E
A	87/8	273	8	9.3	262	4	9.4	234	8	10.0	E
A	88/9	277	8	5.5	268	5	7.6	-	-	-	E
B	86/7	275	46	7.9	269	26	6.9	247	5	14.5	M
B	87/8	275	31	8.0	274	8	4.9	251	11	9.2	L
B	88/9	277	40	5.5	277	14	5.9	252	23	10.2	L
C	87/8	283	25	4.1	282	16	4.6	256	14	5.7	L
D	88/9	287	59	5.6	286	27	4.8	254	29	8.0	M
E	86/7	280	65	5.7	276	34	5.1	-	-	-	E
E	87/8	281	20	5.9	279	20	5.9	254	11	5.9	M
E	88/9	280	63	5.8	282	35	6.4	254	92	6.1	E
F	87/8	281	20	5.9	-	-	-	243	3	11.9	M
F	88/9	282	19	5.0	281	3	3.2	267	6	4.6	L
H	88/9	285	13	6.6	280	4	4.6	-	-	-	L
I	85/6	291	17	11.1	285	3	11.6	260	11	9.2	L
I	86/7	287	29	7.1	280	10	5.1	254	15	5.3	E
I	87/8	281	13	7.9	277	4	5.3	262	3	1.7	E
I	88/9	281	30	5.9	277	16	13.8	251	14	8.5	E
J	86/7	285	31	5.4	287	17	9.0	260	12	6.7	L
J	87/8	281	41	10.7	282	12	5.2	257	23	9.3	E
J	88/9	285	56	6.1	284	20	5.1	261	18	5.9	M
K	87/8	290	39	5.8	286	11	5.6	266	20	5.4	L
K	88/9	290	24	4.6	288	17	5.4	258	11	6.5	E

(no canon bone measures available for park 'G')

Table 3.7b :
Average canon-bone (mm) of Male fallow deer in 10 British parks during winter. (Catch-up period: Early=17Nov-18Dec, Middle=1Jan-26Jan, Late=5Feb-6Mar ; n= number weighed, sd=standard deviation)

		Males > 2 years			Male Yearlings			Male Fawns			Catch-up
Park	Year	length	n	sd	length	n	sd	length	n	sd	Period
A	86/7	-	-	-	-	-	-	-	-	-	E
A	87/8	301	5	7.4	-	-	-	251	6	9.5	E
A	88/9	302	3	65.0	-	-	-	247	6	8.2	E
B	86/7	307	4	2.2	283	5	9.0	251	10	25.9	M
B	87/8	302	13	12.7	297	5	8.0	261	14	6.2	L
B	88/9	309	6	9.9	301	12	6.8	266	17	12.6	L
C	87/8	314	7	3.5	302	3	6.8	268	10	7.4	L
D	88/9	313	4	9.9	307	10	2.4	265	32	9.1	M
E	86/7	307	14	5.2	294	5	8.3	-	-	-	E
E	87/8	310	32	4.9	300	11	5.8	267	9	8.2	M
E	88/9	309	31	4.9	311	10	5.2	259	11	11.3	E
F	87/8	-	-	-	-	-	-	278	4	4.8	M
F	88/9	-	-	-	313	3	7	277	5	10.8	L
H	88/9	-	-	-	-	-	-	268	5	10.8	L
I	85/6	319	9	8.4	315	3	15	272	5	6	L
I	86/7	318	12	6.4	307	9	4.5	260	14	9.4	E
I	87/8	314	8	5.2	303	4	8.5	258	5	5.3	E
I	88/9	313	14	6.4	305	11	5.9	263	16	7.5	E
J	86/7	313	17	7.6	311	12	8.8	273	14	5.3	L
J	87/8	315	18	11.1	307	14	4.2	268	16	9.7	E
J	88/9	316	5	6.8	309	11	9.4	273	22	6.4	M
K	87/8	-	-	-	-	-	-	280	15	4.4	L
K	88/9	-	-	-	313	4	4.1	274	11	4.7	E

(no canon bone measures available for park 'G')

Table 3.8 :
Comparisons of mean skeletal measures of Adult Females in different deer parks as assessed at winter live-catches. Multiple comparison tests (Tukey-Kramer's) indicate pairs of parks differing significantly in mean values; # = p<0.001, * =p<0.05 .
Results are for data from catches in 1988/9, (for sample sizes see Tab. 3.6 & 7).

a) Mean Head length

Length (mm)	PARK	A	B	E	I	F	G	J	K	H	D
244.9	A	\									
250.4	B		\								
253.4	E	*		\							
256.1	I	#	*		\						
256.9	F	#	*			\					
257.1	G	#	*				\				
259.2	J	#	#	#				\			
259.8	K	#	#	*					\		
260.7	H	#	#	*						\	
262.8	D	#	#	#	#	*	*				\

b) Mean Canon-bone length

Length (mm)	PARK	B	A	E	I	F	H	J	D	K
276.7	B	\								
277.1	A		\							
280.3	E	*		\						
280.7	I				\					
281.7	F	*				\				
285.0	H	#					\			
285.2	J	#	*	#	*			\		
286.5	D	#	#	#	#	*			\	
289.6	K	#	#	#	#	#		*		\

Table 3.9 : Correlation analyses between body weight, head length and canon-bone length, assessed at live capture.

Values shown are Pearson's correlation coefficients and (sample size).

a) Using data for all individual deer caught in all parks and years combined

(all correlations sig. at $p<0.001$)

Age class	Weight vs Head length	Weight vs Canon bone	Head length vs Canon bone
Female fawns	0.69 (344)	0.74 (325)	0.76 (334)
Yearling does	0.56 (324)	0.61 (299)	0.50 (307)
Adult does (>2 years)	0.58 (790)	0.49 (726)	0.49 (743)
Male fawns	0.70 (262)	0.78 (252)	0.78 (260)
Yearling males	0.64 (144)	0.63 (138)	0.62 (137)
Adult males (>2 years)	0.67 (239)	0.39 (206)	0.39 (209)

b) Using park-mean values determined at different sites (parks A to K).

Results shown are for 1988/9 data, when the widest range of sites was sampled; for individual park-means see Tables 3.1, 3.6, and 3.7.
($p<0.05$ *; $p<0.01$ **; $p<0.001$ ***)

Age class	Weight vs Head length	Weight vs Canon bone	Head length vs Canon bone
Female fawns	0.48 ns (8)	0.77 * (7)	0.89 ** (7)
Yearling does	0.63 * (10)	0.80 ** (9)	0.73 * (9)
Adult does (>2 years)	0.62 * (10)	0.79 ** (9)	0.89 ** (9)
Male fawns	0.81 ** (9)	0.91 *** (9)	0.93 *** (9)
Yearling males	0.54 ns (7)	0.58 ns (7)	0.12 ns (7)
Adult males (>2 years)	0.97 *** (6)	0.74 * (6)	0.85 * (6)

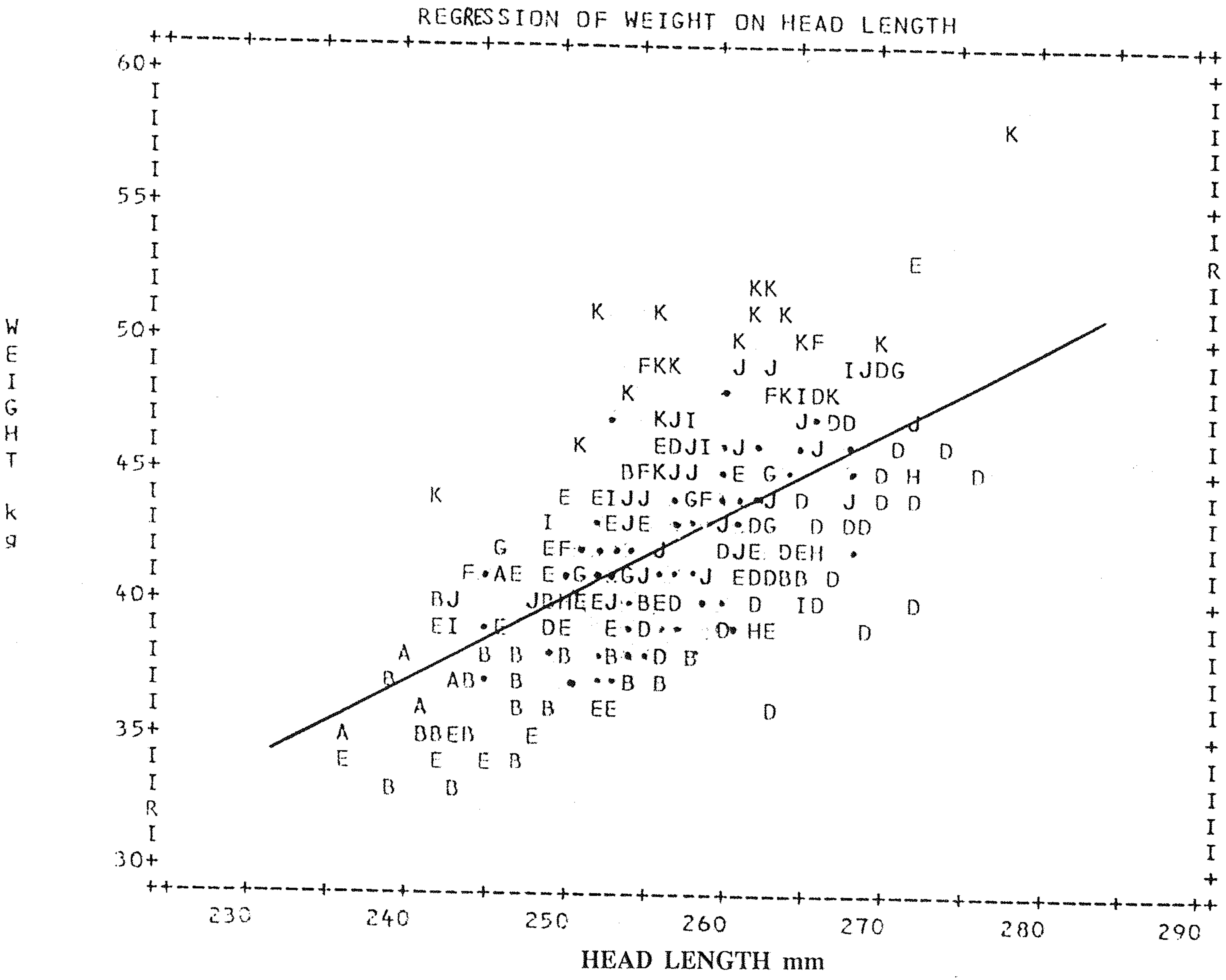

Figure 3.3a : Plot of live weight on head length for Adult females caught during winter 1988/9. (10 parks were sampled; 322 cases for which both measures are available have been plotted; Letters A to K indicate parks of origin; • = multiple park occurences). Equation of line: $Y = -42.293 + 0.328 X$, $R^2 = 40.3\%$, $p < 0.0001$).

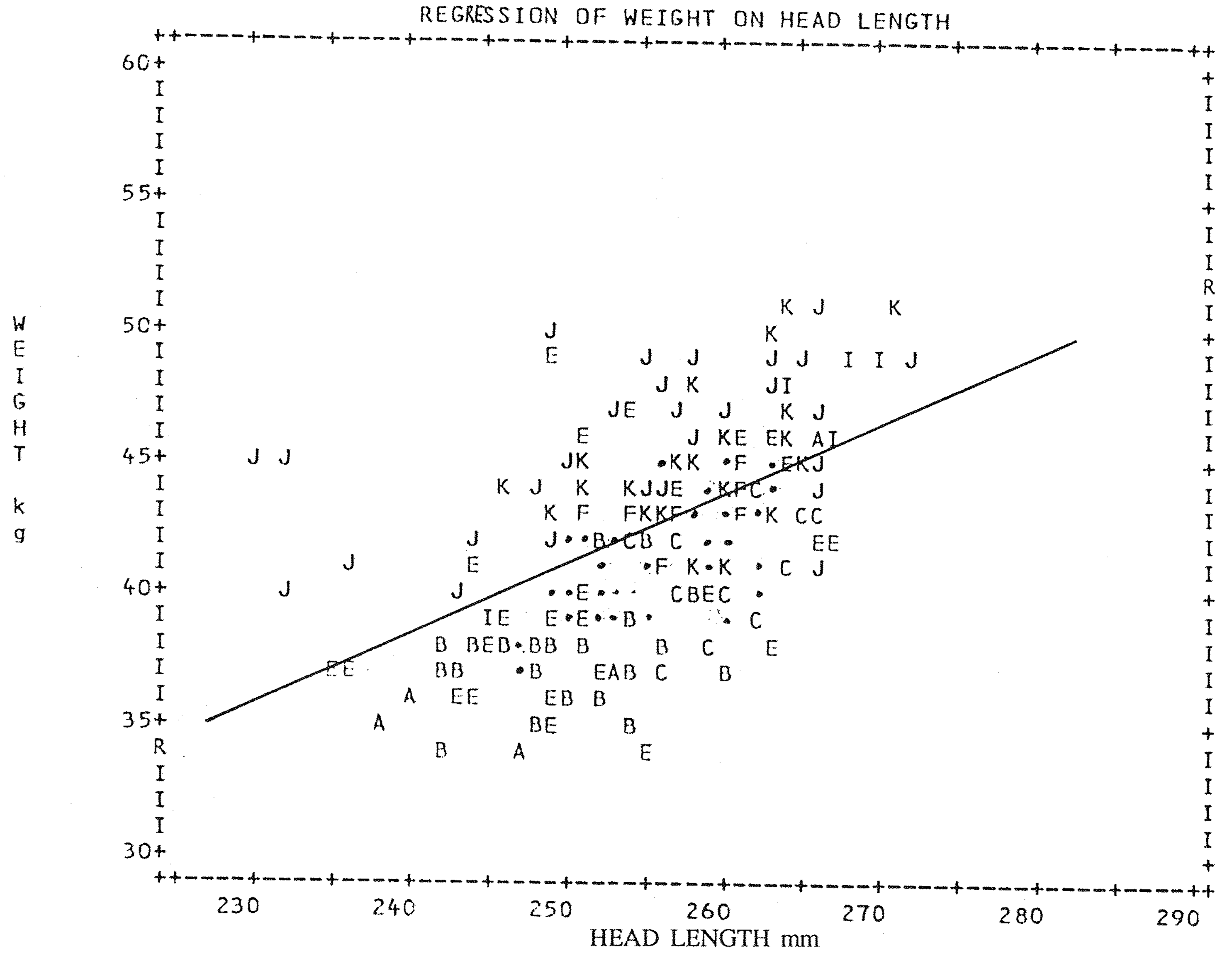

Figure 3.3b : Plot of live weight on head length for Adult females caught during winter 1987/8.
(8 parks were sampled; 215 cases for which both measures are available, have been plotted; Letters A to K indicate parks of origin; • = multiple park occurences). Equation of line: $Y = -29.187 + 0.279 X$, $R^2 = 30.6\%$, $p < 0.0001$).

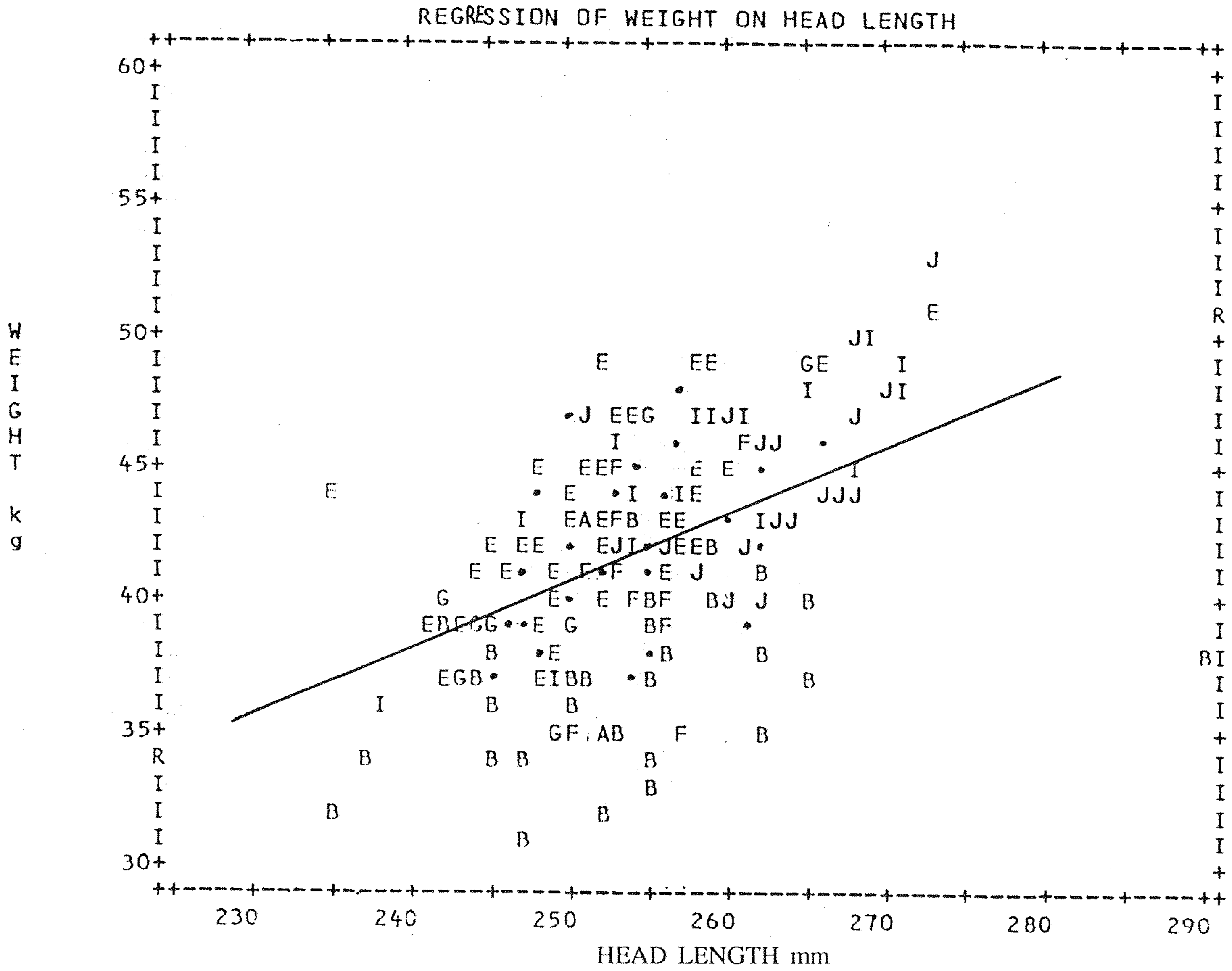

Figure 3.3c : Plot of live weight on head length for Adult females caught during winter 1986/7.
(7 parks were sampled; 206 cases for which both measures are available, have been plotted; Letters A to K indicate parks of origin; • = multiple park occurences). Equation of line: $Y = -27.032 + 0.269 X$, $R^2 = 26\%$, $p < 0.0001$).

3.4 GROWTH

There are two main options available for investigating growth rates of deer in our study populations :

i.) Utilization of the average measures recorded in successive years for each known cohort (i.e. animals born in the same year), weighed as fawns in one year, yearlings the next year and so on (using data from Tables 3.1,3.6, and 3.7), and

ii.) Utilization of data on **individuals** recaptured in successive years, thus providing a more direct measure of actual growth increments which can be achieved over a set period of time in those parks where sufficient recapture data are available to date. For those animals which were first caught and tagged as fawns or yearlings the actual age in years when handled as 'adults' is also known, making an accurate division of the latter age-category possible[1].

Weight gain

In addition to the regular catching-operations in the winter, a total of 115 fallow fawns were tagged soon after birth in the summer in 8 different British park populations, and were if possible sexed and weighed at that time. Searching for newly born fawns, which are usually well hidden in any available cover such as nettles or bracken, is very time consuming and in order to catch a high proportion of those born such searches need to take place daily in all sites throughout the fawning season (June+July). The wide geographical distribution and size of the study sites precluded such daily searches, and only a relatively small sample of fawns (numbering from 2 to 20 in each park per year) were caught during this study, mostly when visiting the parks for other data collection in the summer (see sections 2.3; 2.5).

Weights for 84 fawns (40 f, 44 m) judged to be less than three days old at handling were obtained in the eight parks combined (1987-89); no significant differences in mean birth weights could be demonstrated between parks within this sample. Using the above pooled data, female 'birth' weights were recorded to average 4.3kg ($n=40$, $\sigma=0.62$) and males 4.7kg ($n=44$, $\sigma=0.71$). That is males tended to be larger than females even at birth (males > females, $t=2.25$, $p< 0.03$). On the basis of average weights determined during winter live catches for fawns, yearlings

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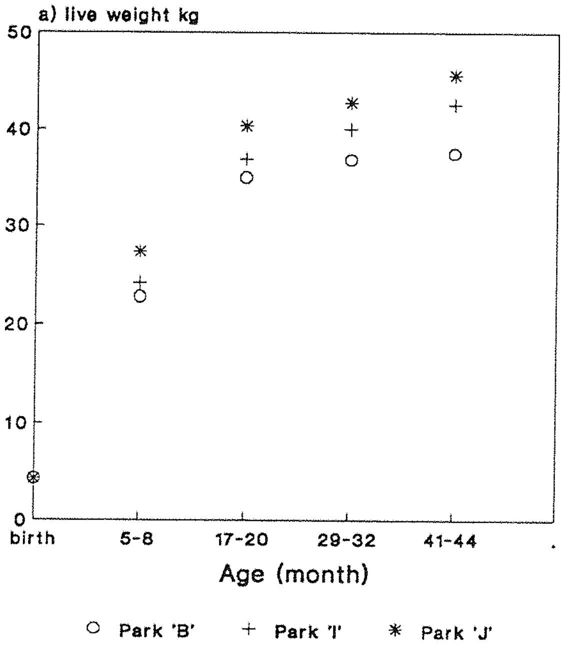
[1] see footnote page 41.

and adults (Table 3.1), it can be noted that growth is extremely fast during the first five months of life. Thus female and male fawns already reached on average 58% and 42% respectively of mean adult winter weights recorded during 'early' winter catches in November / December (see Table 3.1), while at 17 months on average they only fall short 11% and 30% of those maxima. Sexual divergence on weight is already highly significant in the first winter, males being heavier than females by an average of 13% at 5 months, 21% as yearlings and 54% as adults (pooled data from all 'Early' live-catches, Tab. 3.1). Males thus not only continue their growth for longer than females, but also grow faster early on.

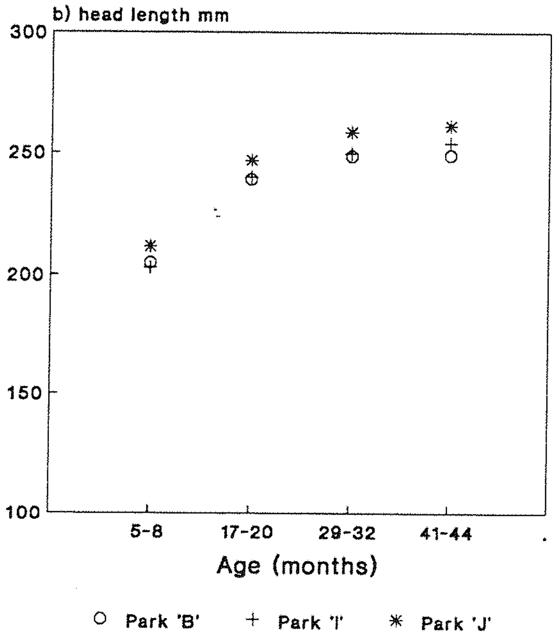
Known aged animals, tagged and recaptured in a number of parks, allow us to follow growth in some further detail. The time scale of this study, however, means that not very many known aged animals (having been aged as juveniles) are as yet over four years old; low mortality rates have also made intended back-extrapolation after death of animals of unknown year of birth (aged by tooth sectioning) unproductive. Furthermore the practice of live sales has resulted in tagged animals often leaving the parks after only one or two years of study. As the proportion of animals tagged in the parks increases, individual data are of course progressively becoming more and more extensive and valuable, and will continue to be monitored in the future. The data presented here hence only provide an early preview of this part of the work.

Samples of reasonable sizes of known 2, 3 and in some cases 4 year old females, in addition to fawns and yearlings were available in three populations. Plotting firstly the mean of all known aged animals born between 1985-87 against age at weighing, provides a generalised growth profile for does in each of these parks (Fig. 3.4a). The main difference apparent between sites is that the animals in the park with the highest weights as fawns (5-8 months) continued to gain weight faster in their second year, though gained little in the third, while the others gained weight more steadily during the second year and showed a less definite levelling off in the third; that is to say animals from populations of lower mean adult weight, also took longer to reach that adult size.



(Mean weight kg)

Age in months		Park B	Park I	Park J
5-8	$\bar{x}$	**22.8**	**24.1**	**27.3**
	S.E	0.35	0.38	0.28
	n	77	42	52
17-20	$\bar{x}$	**35.0**	**36.9**	**40.3**
	S.E	0.30	0.38	0.43
	n	62	33	48
29-32	$\bar{x}$	**36.8**	**40.0**	**42.7**
	S.E	0.63	0.71	0.77
	n	15	8	23
41-44	$\bar{x}$	**37.5**	**42.5**	**45.6**
	S.E	0.60	0.81	0.72
	n	2	3	12
all does >2 years		37.9	43.1	44.3
	n	161	89	128
	S.E.	0.22	0.39	0.26



(Mean head length mm)

Age in months		Park B	Park I	Park J
5-8	$\bar{x}$	**205.0**	**203.0**	**211.7**
	S.E	1.56	0.95	0.79
	n	43	43	54
17-20	$\bar{x}$	**238.8**	**239.7**	**246.8**
	S.E	1.19	1.06	1.21
	n	53	30	48
29-32	$\bar{x}$	**248.6**	**249.7**	**258.4**
	S.E	1.12	1.22	1.38
	n	15	12	21
41-44	$\bar{x}$	**249.0**	**254.0**	**261.0**
	S.E	3.50	2.70	1.40
	n	2	3	7
all does >2 years		251.2	256.3	258.5
	n	120	89	130
	S.E	0.73	0.89	0.67

Figure 3.4 : Mean live weights and head lengths attained by known aged females in three parks. Available data for all does of known age handled at live catches 1985-89 have been pooled. (Only few animals which were tagged as juveniles - and are hence of known age - have yet been weighed at over 3 years of age).

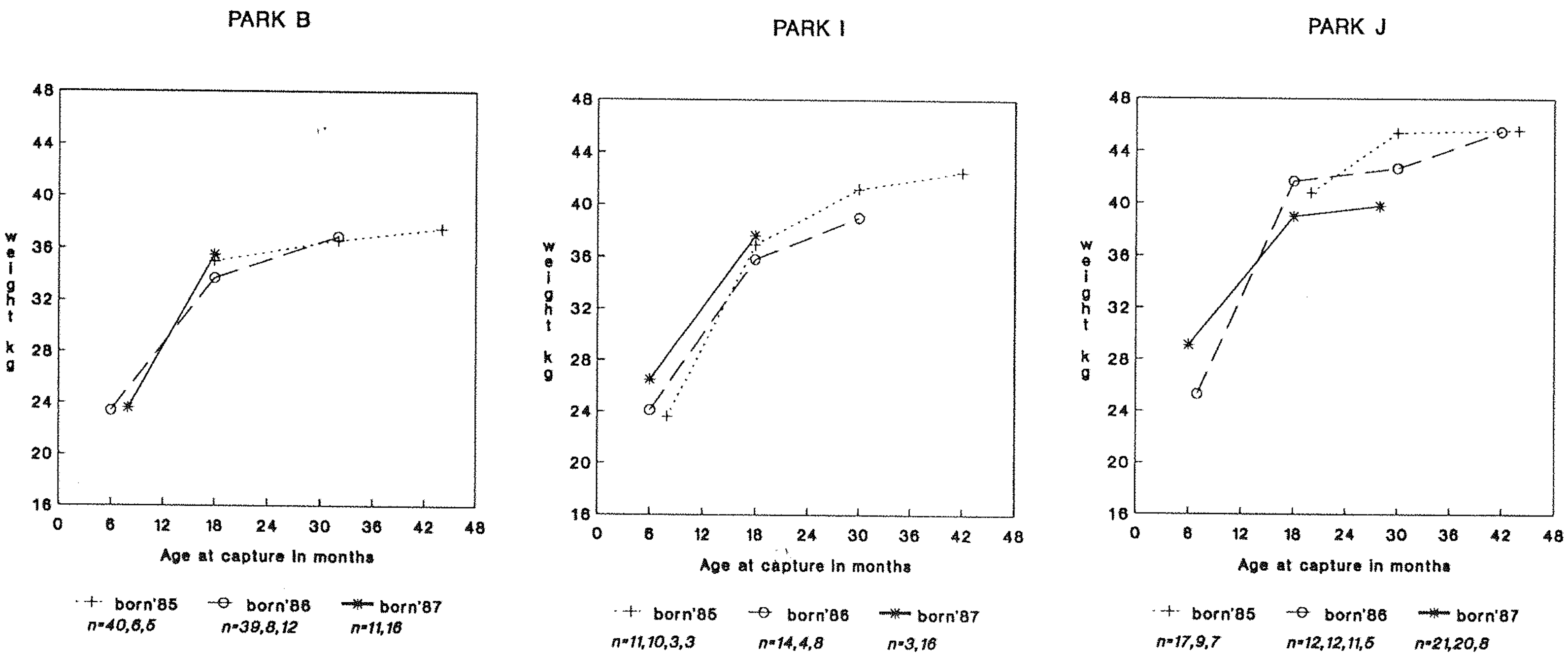
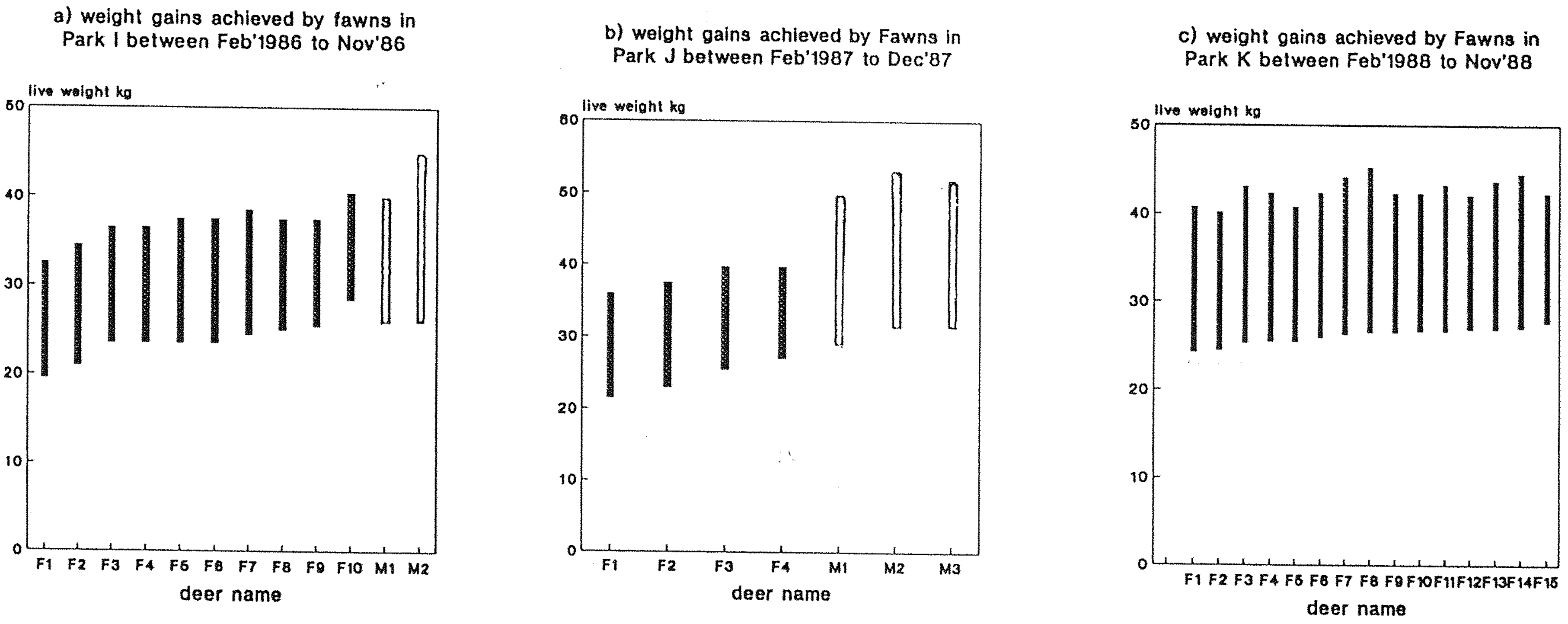


__Figure 3.5__ : **Mean live weights attained by different cohorts of Female Fallow weighed at various ages.** Based on recaptures of known aged animals tagged as fawns or yearlings. Lines have been fitted merely to highlight cohorts, and do not indicate linear growth between points. ($n_{x,y,z}$ = sample size in successive years).



a) weight gains achieved by fawns in Park I between Feb'1986 to Nov'86

b) weight gains achieved by Fawns in Park J between Feb'1987 to Dec'87

c) weight gains achieved by Fawns in Park K between Feb'1988 to Nov'88

Figure 3.6 : Increments in live weights achieved by individual animals weighed as fawns at the end February, and again as yearlings in the following November or December. Note similarity in increments amongst cohort members within each population, irrespective of initial weights at 8 months of age. (females = filled bars; males = clear bars).

Figure 3.5 re-plots the above data when split into the three separate cohorts born in 1985, 1986, and 1987 respectively, each sampled in a number of successive years. Within each park differences apparent among fawns of these female cohorts tended to converge with age , rather than early differences between cohorts being wholly maintained or exaggerated later; however, this result is to date based only on rather small samples from the higher age groups, especially for the cohorts born in the later study years.

Individual variation in pattern of weight gain determined from recaptures of **individual** animals weighed as fawns (at 8 months) and again as yearlings (17-18 months) was generally quite small (e.g. park I: mean weight gain Feb. to Nov. =13.1, n=9, σ=0.73). That is to say, both initially light and initially heavy fawns usually gained near equal amounts of weight over their second summer and therefore the original deviations were maintained, despite the fact that in percentage terms the smaller animals actually grew faster during that period. These results are illustrated graphically in Figure 3.6. In each of the three parks shown, one live-catch was carried out at the end of February and another the following November or December. This allows us to establish the actual increments in weights and skeletal sizes that may be achieved over those 9 months (from ca. 8 to 17 months of age), while minimising the confounding influence of winter weight loss. Highest growth rates beyond 8 months of age were attained by males in Park 'J' (1987, n=4), who gained on average 21.4 kg in the 9 months to November, equivalent to an increase of 75 grams per day. Females of the same age recorded average growth rates up to 62 g d^{-1} (Park K -1988, n=15). From 20 to 29 months of age some males still attained growth rates in excess of 60 g d^{-1} , while does never gained more than 25 g d^{-1} over the same period.

Further results on birth weights and growth in terms of weight gain are presented in Chapter 4 (Reproductive success) in relation to birth date, and maternal age and condition.

Skeletal growth

The general pattern of skeletal growth has already been introduced above (section 3.3). Increases in 'head-lengths' measured on known aged females 0 to 4 years of age are compared across a number of parks for does born between 1985-87 in Figure 3.4b to portray a generalised pattern of growth for head length, comparable to those for weight gain in Figure 3.4a. Bearing in mind the strong correlations demonstrated above (Table 3.9) between body weight and skeletal size, it is not surprising to find that results here for skeletal growth again mirror those for weight gain extremely closely; differences in skeletal growth rates between the populations are seen to be in the same direction as those for weight gain, although separation between them is less clear based on this character.

Although only a single catch-up was held per park during any one winter, measurements based on different cohorts in successive years indicate that mean head and canon bone length of fawns at catch-ups during the 'Late'-winter catching-period were generally longer than those from the 'Early' period (Tables 3.6 & 3.7). Our data thus suggest here, that unlike body weight and in contrast to Mehlitz and Siefke's (1973) study based on cull data from free-ranging fallow, significant skeletal growth of fawns in parks may continue during the winter months.

3.5 EFFECTS OF ECOLOGICAL CONDITIONS ON BODY WEIGHT & GROWTH

The above sections of this chapter have illustrated the wide variation which exists between our different fallow populations, and to a lesser degree between years, in the mean body size and growth rates achieved by the animals. We are now able to proceed to explore the possible causes of this variation. The wide range of density-dependent and density-independent factors which may be involved and how these might be expected to influence body size and growth were introduced in 3.1. These factors will be considered here in relation to body weight under three main headings: 1. climate, 2. population density and 3. forage availability and supplementary feeding, before 4) exploring their combined influences in multivariate regression models.

Data presented in the above section have shown variation in body weights between parks to be closely related to variation recorded in other parameters of physical size and growth (see 3.3 and 3.4). Thus in populations where mean body weights were low, in general so were the skeletal sizes attained by the animals;

employment of indices of condition obtained from live animals (e.g. weight÷head length or weight÷canon bone), which take into account differences in 'fleshiness' in relation to a given skeletal size, yielded no discriminatory power in separating populations other than that obtained by use of body weight alone. While analyses presented below will be limited to factors affecting body weight, parallel investigations of the other physical measures would hence be likely to yield very similar results.

During the winters of 1986/7, 87/8, 88/9 live-weight data were collected in 7, 8, and 10 parks respectively. Analyses drawing comparisons across this sample of parks in relation to ecological conditions were (unless otherwise indicated) repeated for each catching year at a time, in order to avoid exaggeration of statistical significance through replicated use of those variables which were unchanged or non-independent between years.

3.5.1 Effects of climatic variation

Climate may be expected to exert influences on the condition of deer directly, through increases in thermoregulatory cost due to cold temperatures, precipitation and wind chill, but also indirectly by effects on primary (vegetative) production. Thus for grasses to be able to achieve growth, critical minimum temperatures must be exceeded, and the grass 'growing season' has been defined as "the period when the annual curve of mean monthly screen temperature exceeds 5.6 °C " (Gloyne 1968). The yield of grass is strongly affected by rainfall and soil type; for dairy pastures Young (1982) uses a combination of these two factors to allocate scores of growing conditions. Thus, high summer rainfall (Apr-Sep) over clay loams and heavy soils provides 'very good' growing conditions, while low summer rainfall on shallow soils over chalk or rock affords only 'poor' conditions. Other detrimental factors on yields include poor drainage and waterlogging (Young 1982).

As well as limiting primary productivity, the length and severity of the winters will also effect reductions in the digestibility and nutritional value of the vegetation that is available (Milne 1974). In at least some sites or years the climatic effects on food resources may be outweighed by increased costs of thermoregulation due to cold temperatures and wind chill (Blaxter et al. 1963; Moen 1973; Simpson, 1976). Simpson, studying energy metabolism in red deer, demonstrated that they were less well adapted to cold weather than hill-sheep, having a metabolic rate exceeding that of sheep by 30 %. Clutton-Brock and Albon (1983) showed weights of male red deer on Rhum in different years to be inversely related to the previous winters temperature, although this effect might well in part be explained with a parallel effect on the onset of the growing season. Effects of cold weather on deer may also be negated to a varying extent dependent on differences in the availability of shelter offered by topography or dense vegetation (Staines, 1977; Grace and Easterbee, 1979; Ratcliffe, 1987; Putman and Langbein 1990).

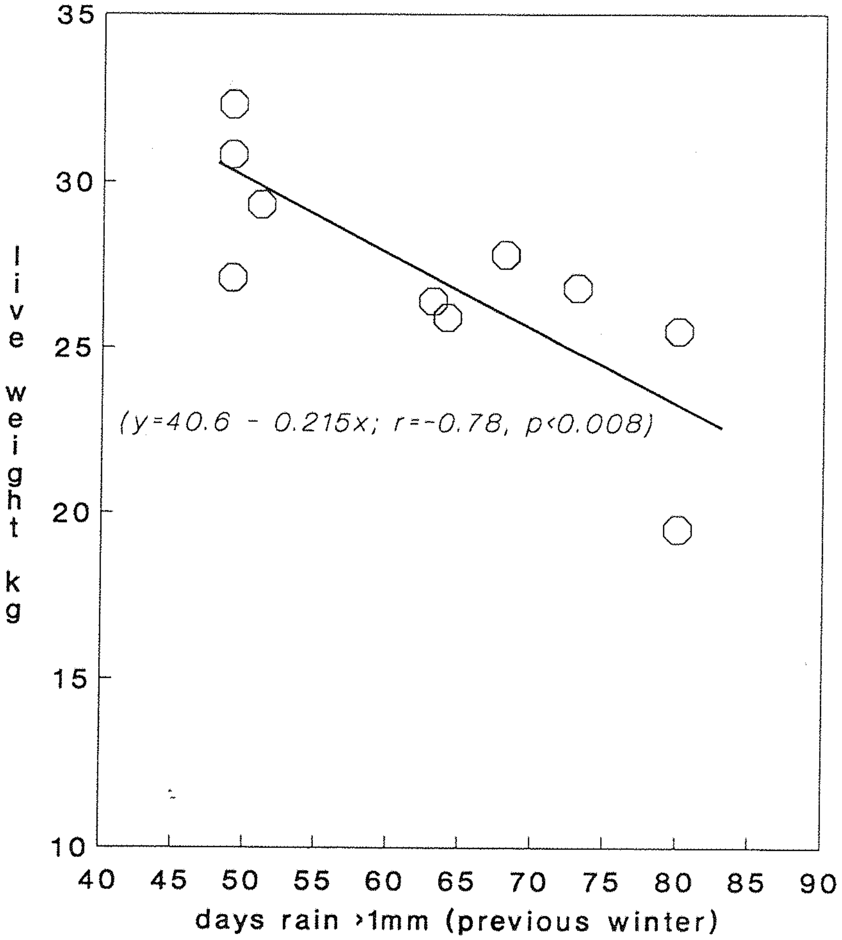
Meteorological variables (including monthly mean temperature, total precipitation, no. of days when rainfall exceeded 1mm, no. of days of snow-lie, no. of days of ground frost) were extracted from Monthly Weather Reports (HMSO) for the nearest weather station of similar altitude for each of our parks from Dec'84-Mar'89. Length of the growing season was then also calculated for each site according to Gloyne's (1968) criteria (see above).

Figures 2.1 summarises major climatic differences recorded between the study sites; (complete annual weather data are shown in Appendix II). Wide variation between parks is noticeable in particular in the average duration of growing seasons (i.e. park 'A' 220 days, park 'G' 320 days), which overall were at their shortest in 1985 (inter-park range: 207-294 days) and longest in the very mild winter of 1988 (inter-park range: 229-366 days) for all sites. Mean duration of growing seasons over the four years of study, assessed according to the criteria described above, showed a strong linear relationship with the computationally much simpler average of the monthly mean temperatures from November to March :

$$\text{Growing season} = 138.6 + 30.2 \times \text{mean winter temp. } ^\circ C \; ; \quad (R^2 = 99.2\%,\ n=7,\ p<0.0001).$$

The two parks (A, B) consistently showing the lowest live-weights had conspicuously high winter precipitation levels [measured either as total rainfall Nov-March, or the number of days when rainfall exceeded 1mm; these two measures of rainfall were in fact highly correlated across sites ($r=0.96$; $p< 0.001$, $n=10$; see also Fig. 2.1a)]. Only parks 'A' and 'H' were located more than 100 m above sea level (298m & 185m respectively), reflected in the associated low mean winter temperatures recorded at these sites.

Figure 3.7: Plot of mean live weights on rainfall(Nov-Mar.) for Male Fawns in 10 different parks during winter 1988/9.



Strongest univariate relationships of weights and meteorological variables, were found between mean live weights recorded in the winter of 1988/9 with the number of days of rain in the previous winter, and were consistent across all six different age and sex categories ($r > -0.7$, $n > 8$, $p < 0.01$); e.g. male fawns Fig. 3.7). In 1987/8 such inverse correlations of weights with precipitation were improved if using total-rainfall (mm) in place of no. of days of rain ($r > -0.66$, $n > 7$, $p < 0.05$). Both the study sites subject to very high winter precipitation levels (parks 'A' & 'B') are very poorly drained and prone to waterlogging; the reasons underlying the inverse relationships shown are hence likely to be related to increased leaching of soil nutrients, as well as increased thermoregulatory costs of wet winter conditions. Live weights also showed negative correlation with rainfall in the summer (May+June) before capture, but these associations were generally not statistically significant, or as in the case of adult does in 1986/7 significant just at the 10 % level. While a positive correlation with summer rain might have been expected as this should result in heightened primary production, a similar inverse effect of summer precipitation has previously been found for carcase weights of male red deer on the Isle of Rhum (Clutton-Brock and Albon, 1983).

Correlation coefficients between mean live weights and i.mean winter temperatures, ii.the number of winter days of ground frost, and iii.days of snow cover, consistently indicated inverse relationships as would be expected. Associations were strongest for fawns of either sex, and adult males (e.g. days of groundfrost 1988/9 : $r < -0.69$, $n > 7$, $p < 0.05$), but weak for adult females ($r = -0.5$, $n = 10$, $p > 0.1$) and yearling males ($r = -0.22$, $n = 8$, $p > 0.1$). Fawns may be expected to be affected more by cold temperatures due to their lower body sizes and fat reserves in comparison to adults, while adult males are particularly prone to loss of fat reserves during the autumn rut; a similar sex difference in effects of winter climate was shown for red deer by Clutton-Brock et al. (see above).

Length of the growing season was shortest in Park 'A' where the lowest body weights were also recorded. Univariate relationships of live weights on this variable were, however, mostly non-significant at the 5 % level. Inspection of the data shows that park 'B', where generally very low weights were recorded, to have one of the longest grass growing seasons; omission of this park from correlation analyses in fact produced significant correlations for several age/sex classes. The fact that park 'B' also experiences very high winter rainfall (see above), suggests interactive effects of these climatic variables in the analyses.

Rainfall in the previous winter was the strongest climatic correlate with body weights in univariate analysis above, and was not significantly correlated with the length of the growing season (e.g. 1988/9: $r=0.08$, $n=10$, $p > 0.1$). Entering rainfall as the first of a number of climatic variables offered in a stepwise multiple regression, the length of the growing season showed a significant partial correlation coefficient with the residual variance in male fawn weights in 1988/9 ($r= 0.61$, $n=10$, $p< 0.05$), explaining an additional 12 % of the total variance. Multivariate regressions on climatic factors in the case of the other age/sex categories, however, did not improve the fit of regressions of body weights over those using rainfall alone, based on comparisons of R^2 values.

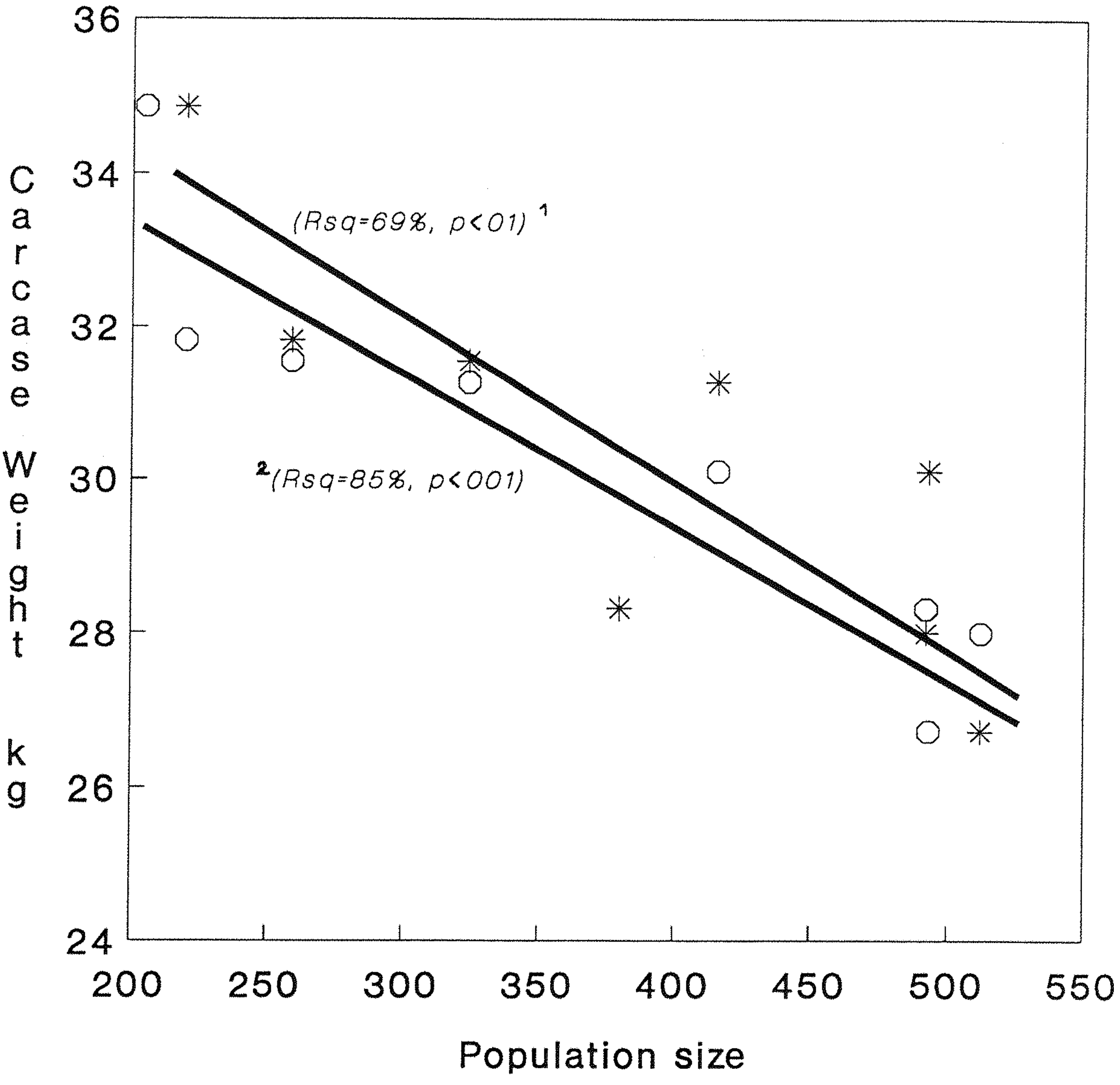
3.5.2 Effects of density and forage availability

One of the questions central to this study concerns the effects of density on performance of the deer, and thus exploration of the hypothesis that "body weights will decrease as density increases", is pertinent here. One major reason behind such a supposition is that as density increases the quantity of high quality forage available per deer will necessarily decrease. For comparisons between parks a straight forward stocking density, assessed merely as numbers per unit of the total area available, will therefore not usually be a good index of the plane of nutrition of the animals. (As not only the proportions made up of pasture may vary between parks, but also its productivity and quality, and availability of other forages [such as for example acorns, chestnuts etc.] offered by the habitat.) In comparisons within a park across a number of years the situation can be rather less complex, and here the Simple Stocking Density (SSD) of animals per unit of the total park area is likely to be a useful measure to relate to body weight, provided that no major management changes have occurred alongside changes in herd numbers.

Within park comparisons

Park 'G' provides us with such a simple system where the pasture management and feeding practises have remained relatively constant over the last nine years, but population size has fluctuated considerably between 160 to over 500 head. Since 1980 numbers increased gradually for the first four years, remained relatively

Figure 3.8 : Mean carcase weights of yearling males in relation to changes in population density (park G 1980-7)



✳ density current year [1] ○ previous year [2] constant for the next two, before being reduced again during the last two years. The herd was provided with supplementary feed from November to March only.

While live capture has only taken place in 2 years at this park, **cull-data** were available from 1980, providing an 8 year time span. Each year a large sample of males were culled ($17 \leq n \leq 58$) at 15-18 months old[1]. A regression of the annual mean 'skinned-clean-carcase' weight (whole weight minus viscera, head, feet, and skin) on stocking density (SSD), assessed in the autumn just before the beginning of the cull, showed a significant inverse linear relationship (R^2=69.3%, $p<0.006$, Fig. 3.8). Such a clear, linear density relationship has often been difficult to demonstrate in studies on wild deer, and here strongly supports our hypothesis that weights will decline with increasing density. If the same mean weight values are now re-plotted against density in the previous year, (that is the density just after each cohort was born), the regression is improved still further, now explaining 84.6% of the variance ($p<0.0005$, Fig. 3.8). This points to the particular importance of conditions (for the juveniles directly, and also for the dams on which they are dependent at that stage) experienced during their first year of life.

Similar analyses to the above could be repeated for three other parks (parks 'q', 'r', 's') for which reliable mean carcase weights, as well as density records, were again available for six or more years, although less extreme fluctuations in herd sizes occurred in these sites. Each of these three parks already presents a more complex systems than park 'G' above, due to the presence of other deer species and/or domestic livestock such as sheep or cattle, in addition to the fallow population.

No significant correlations of body weight and density (SSD) could be demonstrated in Park 's', where spring densities remained between 2.7 - 3.3 stock units (SU)[2] per hectare throughout the 11 year period for which data are available.

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[1] *Yearling males predominate in the cull in most parks and thus provide the highest numbers of carcase data available for any age class. They are also particularly useful for comparisons across years, as they usually have the lowest variance around the mean of any of the readily distinguishable age classes.*

[2] *While in most of the main study sites fallow deer where the only ungulates present, in order to be able to account for any other livestock, densities have been expressed in stock units (SU) ha^{-1}. Stock units were calculated assuming the relationship 1SU= 1 fallow = 1 sheep = 0.5 red =0.25 cattle. (see section 2.5.2)*

Wider fluctuations of density did occur in park 'q' (spring density range 2.8 - 5.1 ha^{-1}), but here recent increases in density have been accompanied by significantly greater amounts of supplementary feed per animal being provided during winter. Trends for increasing yearling male and adult female body weights with increased spring density (parallel to increased provision of winter feed) were noted here, but were non-significant ($p<0.05$).

In park 'r' fluctuations in **spring** densities over 7 years, from 1982-88, were confined between 1.7 - 2.4 S.U. ha-1, and no correlation of annual densities as measured at that time of year with carcase weights was found. However, highly variable numbers of other livestock (sheep + cattle) were grazed in the park each year from April to November (often exceeding the deer numbers); a significant inverse relationship between male yearling fallow carcase weight and **late summer** stocking density could be shown (R^2=66.5%, p=0.025). In contrast to the earlier case described above (for park 'G'), in park 'r' this regression was not improved by re-plotting carcase weights on the stocking density in the previous year.

A further example which well illustrates the importance of conditions during the juvenile 'growth' years on body weights, is furnished by cull data collected in Park 'B'. Although no accurate density figures for the early 1980's are available for this park, it is known that deer numbers at that time were at close to twice those kept there since the beginning of our study, and supplementary feeding in those earlier years was restricted to hay provided merely during spells of severe weather. During the winter of 1981/82 large numbers (over 100 head ≈ 12%) of this herd were found dead ; since then the herd has been significantly reduced and is provided with greater quantities of more varied supplementary feedstuffs. Although direct statistical analysis of body weights against density are not possible here, changes in annual mean body weights since 1980 for different age-classes of females in this park indicate that fawns and yearlings born into the relatively improved conditions in recent years, now attain body weights close to the average of weights calculated across a range of other British parks. However, the adult does, many of which were born in less favourable earlier years, have not been able to compensate as yet; their mean weight still falls near 10 % short of the average weight achieved by adult does in winter calculated across all our study sites (Table 3.1; 3.4).

Live capture data collected since the commencement of this study so far ranges only over 2 to 4 years in any one park, hence in general precluding meaningful regression analysis of **live weights** on density within any one park across years. ANOVA analyses nevertheless did show significant mean live-weight changes between years within a number of parks (see section 3.2, & Table 3.5), which in some cases were associated with inverse changes in density. Aside from changes in averages of adult weights, (which are not in fact completely independent of each other from year to year due to recaptures), the most statistically conclusive differences were shown for male fawns within Park 'E' (see 3.2.2). Only very minor changes in annual densities took place there (spring SSD 3.7-3.9, 1985-88), and hence no density-dependent relationships could be demonstrated in this case. Differences found in this case are thus more likely to have been associated with changes in winter severity and other climatic factors between years, as discussed above in 3.5.2.

Between park comparisons

During the winters of 1986/7, 87/8, 88/9 **live-weight** data were collected in 7, 8, and 10 parks respectively. Fallow deer were either the only or clearly predominant livestock in all these sites throughout the year, with the exception of park 'H' where red deer always outnumbered fallow. For the reasons discussed in introduction to this section, all comparisons across this sample of parks were confined to any one catching year at a time. Nevertheless, comparisons across parks still immediately present more complex systems than 'within-park' comparisons, due to highly variable habitat composition between sites. It is thus not entirely unexpected that correlation analyses of body weights with stocking densities (based merely on numbers of stock units per hectare of the total park area) in i.spring, ii. autumn, or iii. winter, did not give significant results ($p > 0.05$, n.s.) for any age or sex class.

Using the alternative Grazing-Area-Density ('GAD' - see 2.11), thus taking into account the area of good grazing available per animal (in contrast to bracken, woodland, coarse grazing, waste ground etc.), correlations between live weights and density also remained non-significant for all the six age/sex classes.

Our estimates of variation in density in relation to food resources could be further refined by including information on differences between sites in the vegetative production of pastures. Values for pasture production (kg per m^2), which was measured in two to four 1m x 1m exclosures set up in eight of the main study parks at the end of March'87, and cut at the end of July'87 (Plate 7), varied widely between parks (Fig. 3.9). In contrast to this earlier growth, regrowth values from August to the middle of October showed very little variation between sites. The actual effective 'density' of deer in relation to grass forage availability could thus be calculated (Fig. 3.9) as the amount of grass production/m^2 per deer in each of the study parks:

Grass Forage availability (1Apr- 31July incl.) =
(available grazing area x production [kg/m^2]) ÷ (nos. of stock units present in spring)

(As the vegetation exclosures could not be moved at regular intervals throughout the year, the figures for grass production do not take into account the current effects of grazing pressure itself on grass growth, but nevertheless should serve here as a good relative measure for comparisons between sites)

While in some parks grass productivity was assessed for longer periods in a number of separate years, the 1987 (Apr-July) grass production figures were the most complete set available for a wide range of parks, and were thus used for testing correlation with body weights in all years. Significantly, live weights and grass production *per se* [and not merely when considered as grass production per stock unit] were found to be closely correlated (Spearman's Rank correlation)[1] for every age and sex class in 1987, and without exception occurred in the predictable positive direction (Table 3.10). Re-using the same 1987 production values for correlation analyses with body weights from the two other catching-seasons again showed congruent, though on the whole statistically less significant results (Table 3.10).

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[1] Non-parametric rank correlations, which do not assume linearity, were used at this stage of the analysis, as samples of parks available, especially in the earlier study years, were very small for some age/sex classes.

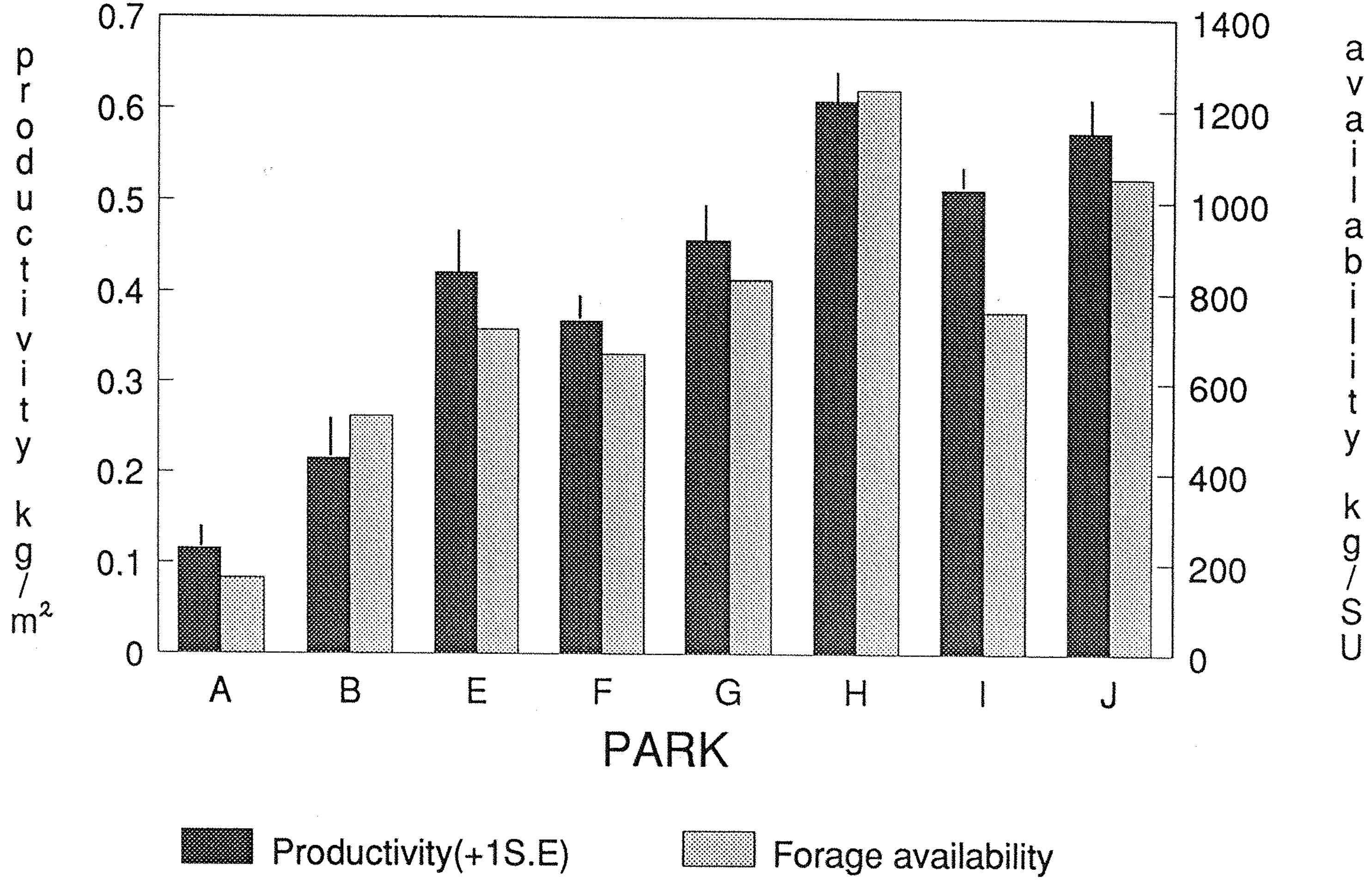

Figure 3.9 : a) Pasture productivity (Apr.-July'87) assessed in growth exclosures, in each of 8 different parks (kilograms dry matter increase / m^2). b) Forage availability calculated as : [productivity of total park area ÷ nos. stock units present in spring 1987].

Table 3.10 : Correlations of population-mean body weights with i.pasture productivity, ii. forage availability per deer.

Pasture productivity per m^2 was assessed in exclosures between Apr-July; forage availability is calculated as total spring/summer grass forage production per stock unit present in either a. spring or b. the following winter. Non-parametric (Spearman's) Rank-correlation coefficients and significant values are shown (* $p<0.05$; ** $p<0.01$; ns $p>0.05$; - but note high +ve coefficients also in cases where correlations missed significance at reduced sample sizes).

Age/Sex	No. of Parks	(i) Pasture productivity per m^2	(ii) Spr/Sum Forage availability	
			a) per deer in spring	b) per deer overwintering
1988/9				
Adult fem.	8	0.59 ns	0.54 ns	0.59 ns
Yearling fem.	8	0.90 **	0.90 **	0.90 **
Fawns fem.	7	0.75 *	0.68 ns	0.75 *
Fawns male	8	0.57 ns	0.57 ns	0.57 ns
Yearling mal.	6	0.77 ns	0.71 ns	0.77 ns
Adult males	6	0.94 *	0.89 *	0.94 *
1987/8				
Adult fem.	6	0.89 *	0.89 *	0.71 ns
Yearling fem.	5	1.00 **	1.00 **	0.90 *
Fawns fem.	5	1.00 **	1.00 **	0.90 *
Fawns male	6	0.83 *	0.83 *	0.77 ns
Yearling mal.	5	1.00 **	1.00 **	0.90 *
Adult males	5	0.90 *	0.90 *	0.90 *
1986/7				
Adult fem.	7	0.93 **	0.89 **	0.93 **
Yearling fem.	6	0.94 **	0.83 *	0.94 **
Fawns fem.	5	0.80 ns	0.80 ns	0.80 ns
Fawns male	5	1.00 **	0.90 *	1.00 ns
Yearling mal.	i.d.			
Adult males	i.d.			

(pasture productivity was assessed only in 8 main study sites - see text)

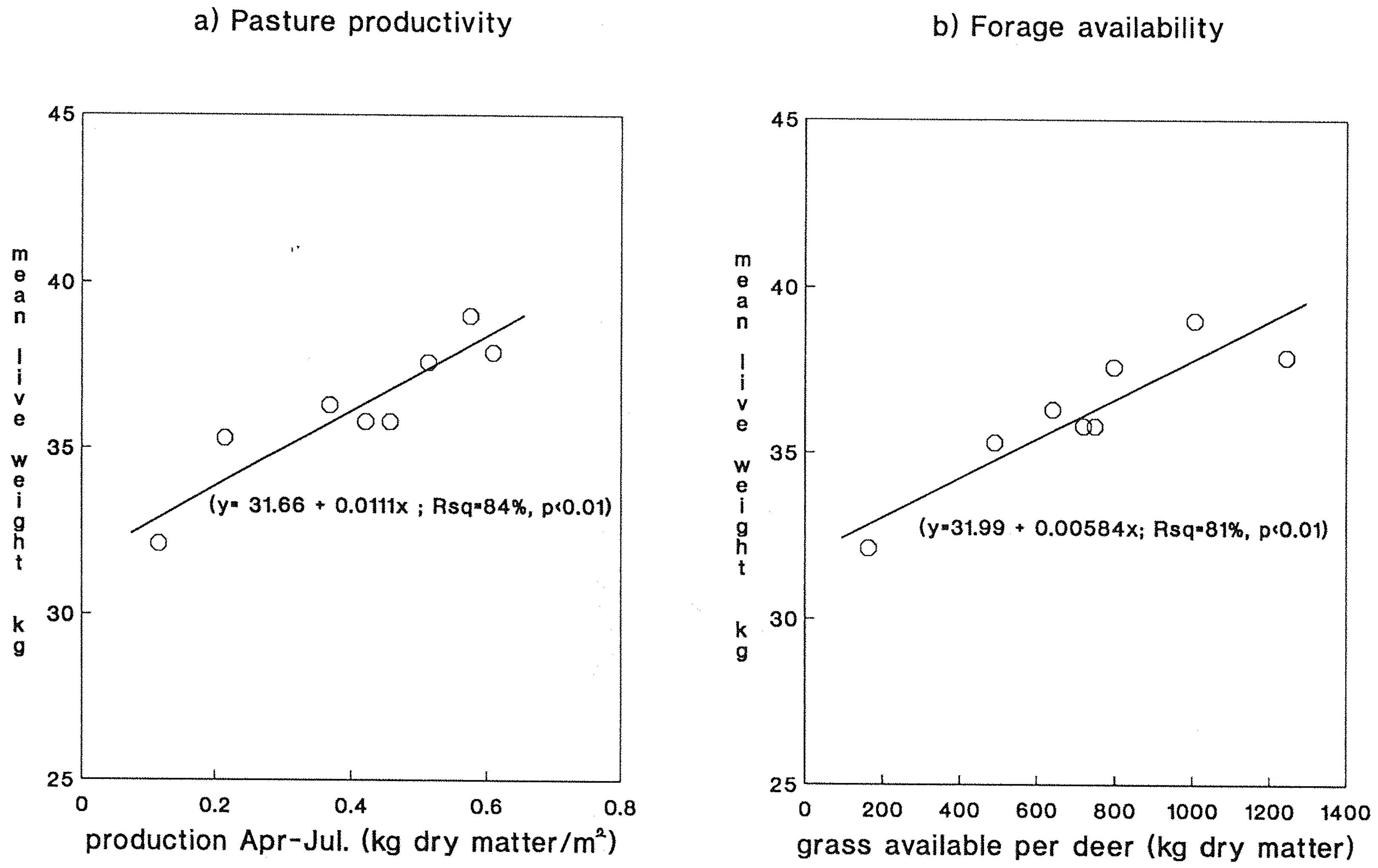

Figure 3.10 : Regression of mean yearling-female live weights (1988/9) on a) pasture productivity and b) forage availability based on data from 8 different park populations.

Weights of yearling females in 1988/9 provided us with the largest sample of parks for which significant associations were detected. Plots of these data show the relationship to be approximately linear; least-square regression lines were fitted on grass production m^2 (R^2=84%, $F_{1,6}$=30.9, p<.001; Fig. 3.10a) and on forage availability per animal (R^2=81%, $F_{1,6}$=25.9, p<.001; Fig. 3.10b). Park 'A' showed particularly low pasture productivity; relationships amongst the remaining sites nevertheless remained significant even when this outlying case is disregarded. The actual relationship obtained for female yearling bodyweight (1988) and total summer forage production per animal was :

Yearling fem. Liveweight [kg] = 31.99 + 0.00584 forage availability [kg] $[R^2= 81\%]$

A very similar relationship was obtained for adult does using average body weight over the duration of the whole study (1986-8) as:

Adult fem. Liveweight [kg] = 36.80 + 0.00609(forage availability [kg]) $[R^2=72.2\%]$

For adults too, the relationship with grass production alone was equally significant. While it was unexpected that such production values per m^2 alone, irrespective of the density of animals exploiting this resource, would give such a clear relationship with the observed body weights, importantly these relationships remained significant when productivity was multiplied by the area of available pasture per animal. It would appear that the range of densities in our sample of parks is insufficient to show up the direct density relationship here; in other words all those parks which were similar in their primary pasture production, had very similar grazing densities (GAD) associated with them. Neither unfortunately did deer densities change dramatically over the four years of study in any of those sites where grass production was measured.

The regression lines obtained above are of course likely to become non-linear as grass production levels approach zero. Mean yearling female weights below our intercept of 32 kg have indeed been recorded in the past (e.g. in park 'B' by Pemberton and Dansie 1983); it is pertinent to note in this context that occurrence of those extremely low weights in 1980/1, were followed by a large-scale die-off (12% of the herd) during the following winter at that site ! (see Chapter 6).

In addition to measurements of the vegetative production, the actual available 'standing crop' of grass was assessed at various times of the year in each site (see section 2.9). Values for standing crop cuts at the end of March are shown in Table 3.11 by way of example. Quantities obtained from sample cuts taken later in spring and summer were not directly comparable between parks because of differing regimes and timing of chain-harrowing and/or cutting of the pastures. However, the quantity of available grazing per deer in most sites is only likely to have been a limiting factor during winter and early spring before the re-start of the growing season. While wide variation did occur in the standing crop (Dry matter/m^2 and [DM x area] x SU^{-1}) of grass between parks during winter and early spring, no significant correlations of standing crop sampled in November, January, or March with live-weights could be shown. This is perhaps not surprising considering the relatively high stocking densities of some of the sites which produce deer of above average weight. Thus differences in other variables, such as possibly supplementary feeding and winter severity, may be off-setting the effects of these high density conditions in the univariate analyses presented so far.

Table 3.11 :
'Standing-crop' of grass on good pasture areas at the end of March.
Average dry weight grams per m^2, sampled in 2-8 quadrats per site, + (standard error).

				Park			
Year	A	B	E	G	H	I	J
1987	257	250	350	381	100	213	227
	(18.4)	(48.4)	(48.7)	(31.6)	(7.4)	(30.3)	(20.9)
1988	226	193	293	285	-	153	217
	(43.4)	(27.9)	(52.0)	(44.2)		(21.3)	(15.4)
1989	211	160	-	237	-	85	283
	(67.2)	(39.6)		(39.1)		(24.5)	(11.7)

The quality of standing crop samples was also assessed in terms of energy-content, digestibility, and crude protein content at different times of the year. Qualitative analyses could not be completed during the present study ; preliminary results available so far for the eight main study parks suggest that within park variation between different areas of pasture sampled were nearly as great as differences between sites.

3.5.3 Effects of supplementary winter feeding

Some supplementary feedstuffs were provided for the deer in all our study parks, such feeding, however, being mostly restricted to the winter months (late November to March). The type of food provided varied widely between parks and years from hay only, to hay plus silage, or root crops, corn, and concentrated compound feeds. For all those estates who could provide reliable information of the total amounts of supplementary feedstuffs distributed each year during the winter, the percentage dry matter, metabolisable energy, and digestible crude-protein given were assessed using food composition tables (MAFF, 1977). At first sight, based on total quantities of wet weight of feed offered per deer, most parks appear to offer quite similar amounts of supplements (Table 3.12). However, once actual dry matter and nutritional content are taken into account very wide differences become apparent[1]. Having divided the total amount of feed provided in each park by the number of stock units in winter using this supply, this was further divided by a standard of 135 feed days in order to obtain a comparable figure of the average daily contribution of supplementary feed to the metabolism of the deer at each site during winter. Mean values of supplementary feed provided per deer per day in this study at each site are shown in Table 3.12. The average daily winter energy requirement of an adult fallow doe (1SU) after Ueckermann (1971) lie in the region of 11 MJ. Using this value it can be seen that supplementary feeding alone nearly fulfils such requirements in some parks, while in others over 80 % still needs to be obtainable as residual natural winter forage offered by the habitat.

Amounts of supplementary feed (metabolisable energy, and crude protein per animal) given in each park during the winter before capture were strongly positively associated with mean live weights recorded for all age sex/classes. At levels of supplementation exceeding the daily requirements of the deer, such relationships are likely to become non-linear. Scatterplots against body weight indeed indicated this

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[1] A general trend is discernible across parks/years for more supplementary feed to be provided per deer the smaller the total herd size. This may possible be due to larger estates tending to opt for cheaper, and hence usually lower quality feedstuffs in order to keep the overall feed costs down. A minority of park managers at present seem to work out the levels of feeding to reflect current herd numbers, instead tending to still rely on what has 'traditionally' been provided.

Table 3.12 :

Amounts of supplementary feedstuffs provided overwinter.

Values shown are averages caculated over the 4 years (85/86 - 88/89), and represent amounts given per stock unit per day during winter (mid-November to March). Types of feeds ranged from 'dry' feeds (e.g. maize or pelleted concentrates) to 'wet' feeds (e.g carrots or sileage), reflected in the highly variable dry matter- , protein- , and energy-content levels shown.

Park Code	Amounts per Stock unit per day Dry matter (kg)	Wet weight (kg)	Crude protein (kg)	Metabolisable energy content (MJ)
D	0.05	0.37	0.033	0.67
E	0.17	1.09	0.061	1.84
B	0.22	0.90	0.013	2.22
G	0.38	0.83	0.044	3.39
A	0.56	1.64	0.040	4.77
F	0.63	0.99	0.062	6.17
H	0.78	0.91	0.058	9.94
J	1.08	1.49	0.064	9.16
K	1.32	2.07	0.241	16.36
I	1.44	1.65	0.182	10.14

Table 3.13 :

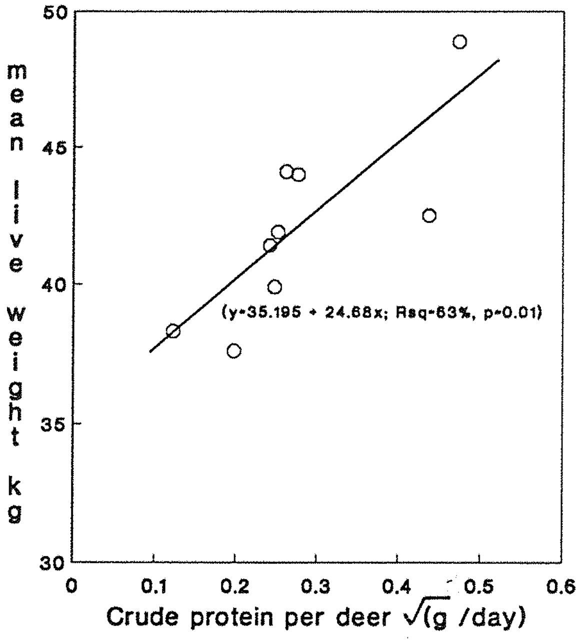
Correlations of mean live body weights and amounts of supplementary feed provided per stock unit per day during the winter before capture.

Pearson's correlation coefficients and significance values are shown. Values of crude protein were transformed for correlation analyses by taking square roots, to achieve linearity - see text).

Mean Weight	No. of Parks	Metabolisable Energy	$\sqrt{\text{(Crude Protein)}}$
1988/9			
Adult fem.	9	0.83 **	0.80 **
Yearling fem.	9	0.81 **	0.73 *
Fawns fem.	8	0.55 ns	0.54 ns
Fawns male	9	0.59 ns	0.57 ns
Yearling mal.	7	0.95 ***	0.93 ***
Adult males	6	0.60 ns	0.78 *

($p<0.05$ *; $p<0.01$ **; $p<0.001$ ***, one-tailed test)

a) Crude Protein



b) Metabolisable Energy

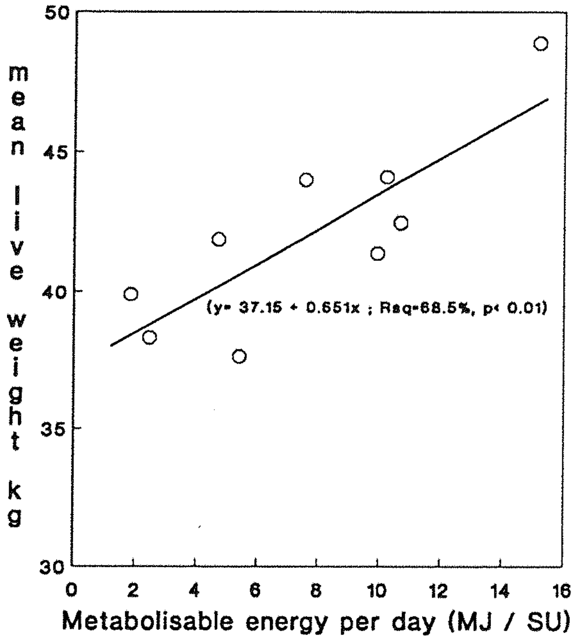


Figure 3.11 : Regression of mean adult-female live weights (1988/9) on a) square root of crude protein, and b) metabolisable energy, contained in supplementary winter feed provided daily per stock unit (1 stock unit = 1 fallow deer).

to be so in our sample of parks in the case of amounts of crude protein provided per animal; a square-root transformation applied to this independent variable improved the linear fit of plots with body weights (Fig 3.11a). Plots of weight on metabolisable energy in contrast showed a better linear fit throughout the range of available data without transformation (e.g. Fig 3.11b). Correlation coefficients and significance values between body weights and feed variables are presented in Table 3.13, showing results for 1988/9, when the largest set of data from different parks was available for comparison. Associations were strongest for yearlings and adults of both sexes, and only quite small differences in correlation coefficients arose when using crude protein rather than energy values; the one exception to this were adult males, whose weights did correlate significantly better with protein than with energy content. (For fawns comparisons shown here of course relate to food supplements provided before their birth [i.e. to their dams during gestation] and are hence not surprisingly less conclusive). Positive correlation coefficients were also obtained for all age/sex categories when repeating the above analyses with live weight data and feed recorded in 1986/7 and 1987/8, but generally missed statistical significance ($p > 0.05$, two-tailed) for the smaller samples of parks available in those catching seasons.

3.5.4 Multivariate analyses of live weights on park variables

Having seen above the important independent influences which climate (on its own or indirectly through its effect on primary production and forage availability) and supplementary winter feed may have on deer body weights, it is perhaps not surprising that relationships with simple stocking densities could not be demonstrated clearly by univariate comparisons across our sample of parks. Stepwise multiple regression analyses (Snedecor and Cochran, 1967) were carried out using live-weight data for the 1988/9 winter, in order to investigate further the effects of stocking density when the relationships with supplementary feeding or primary production are accounted for. The 1988/9 season again provides us with live-weight data for the largest sample (n=10) of study parks, for which most of the relevant independent variables could be also ascertained. [Note - all R^2-values given in the text below have been adjusted down for the available degrees of freedom in each analysis].

High, significant, coefficients were consistently obtained from univariate correlations of live-weights and metabolisable energy offered per deer during the winter before handling. Relationships of the residual variance in live weights and density and/or climatic variables were examined for each age/sex class:

For yearling females the highest partial correlation coefficient was shown by the density of animals in spring (GAD) per unit area of available pasture ($r= -0.73$, $df=7$, $p< 0.05$), accounting for a further 18 % of the variance in live weights. For adult does (retaining the same sample size of 9 parks across all variables) the partial coefficient with density was not significant ($p > 0.1$), a better explanation of the residual variance being achieved by inclusion of mean temperature during the previous winter ($r= 0.73$, $df=7$, $p< 0.05$). In the case of male fawns univariate linear regression of weights on supplementary feed the previous winter (i.e. during their gestation) were not significant. However the number of days when rain exceeded 1mm during that winter was strongly correlated with fawn weights ($r= 0.78$, $df=8$, $p< 0.01$). After accounting for this effect spring grazing density (GAD) again increased R^2 by a further 18 % ($r=-0.65$, $df= 7$, $p< 0.05$).

The amount of grass produced per m^2 of pasture (Apr-July) had also been indicated in earlier univariate analyses (3.4.1) as showing strong linear relationships with live weights in winter. For adult females none of our other independent factors, which were not highly inter-correlated with production per $m^{2,}$ could improve regression on productivity alone. For yearling females pasture production accounted for 81 % of the observed variance in weights, and only an additional 3 % was explained by inclusion of spring density (GAD) which here showed the highest partial coefficient with the residual variance ($r= -.55$, $df=7$, $p > 0.1$ ns). In the case of male fawns not surprisingly primary production was itself less closely related to body weights than for older animals ($R^2=50\%$, $df=8$, $p< 0.05$); but here the mean temperature in February (during their gestation) was correlated with the residual variance ($r= -0.76$, $df=7$, $p=0.01$), accounting for a further 27 % of the variance in live-weights. For the remaining three age/sex categories step-wise multiple regression models incorporating more than one independent variable did not improve on the explanatory power provided by the earlier univariate comparisons alone.

The above analyses serve well to illustrate that, while over the range of our available sample of parks differences in climate and management regimes mask the effects of stocking density on body weights to a certain extent, density nevertheless still exerts important discernible effects. The variety of climates in addition to differences in supplementary feeding and other density related factors thus results in nearly all our sites being quite unique in the conditions they offer to the deer.

In the above step-wise models the independent effects of either grass availability, supplementary feed per animal, or climatic variables dominate the regressions to the exclusion of one another; however, all three factors are clearly implicated as influencing body weights. From a predictive point of view a more valuable model is likely to be obtained by use of a combination of variables (which are not significantly inter-correlated) from each of these three groups of factors. Total primary production is clearly influenced by climate, in particular due to the high correlation of winter temperatures with the onset of the annual growing season. However, values of i. summer forage production in relation to density (total [Apr-Jul] production ÷ deer nos. present in spring), ii. mean winter temperature (Nov.-March), and iii. supplementary metabolisable energy (per animal Nov.-March) show no strong inter-correlation. Inclusion of all of these three variables provides the following predictive equations based body weight data for 1988/9 :

Yearling fem. live weight = $27.874 + 0.00472(C) + 0.195(D) + 0.646(E)$
$(R^2_{adj} = 89.2\%\ ,\ F_{3,4} = 20.2\ ,\ p = 0.007\ ^{**})$

Male Fawn live weight = $9.526 + 0.00605(C) + 0.241(D) + 1.976(E)$
$(R^2_{adj} = 76.4\%\ ,\ F_{3,4} = 8.53\ ,\ p = 0.033\ ^{*})$

Adult fem. live weight = $30.059 + 0.00194(C) + 0.474(D) + 1.174(E)$
$(R^2_{adj} = 62.7\%\ ,\ F_{3,4} = 4.91\ ,\ p = 0.079$ ns)

where : C = pasture grass production (1 Apr - 31 July) [kg per animal]
D = metabolisable energy in supplementary feed provided daily overwinter per animal [MJ]
E = mean winter temperature (Nov-Mar) [°C].

3.6 DISCUSSION

Fallow deer living within managed parks in England and Wales might in general be expected to experience relatively favourable conditions with regard to climate, food availability and shelter. Body weights and growth rates recorded in some of the park populations studied indeed rank amongst the highest ever recorded for this species, although others by comparison seem to perform quite poorly.

The range of average body weights determined for different age classes of fallow amongst our parks is summarised below in Table 3.14. Differences shown between populations span entire age classes, such that average yearlings in some parks already exceed weights achieved by adults in others. Live weight data for farmed fallow available from the literature are presented alongside for comparison and show these too to be highly variable, but in general to rank near the lower end our weight range recorded in parks. Directly comparable live data on free-ranging fallow according to age are less readily available. However, Jackson's (1974) data on whole carcase weights in the New Forest, England, again fall well within the above range, as do weights from the extensive amounts of data on german-gralloched weights reviewed by Ueckermann and Hansen (1983) once reconverted to whole-carcase weights (Table 3.14).

It is generally accepted that the size, weight and physical condition of deer of the same species living in different areas tend to reflect the quality and quantity of food offered by the habitat (e.g. whitetailed deer: Adams 1960, McEwan 1957, Teer 1984; blacktailed deer: Einarsen 1946; roe: Klein and Strandgaard 1972; fallow: Jackson 1974, Ueckermann and Hansen 1983; red deer : Mitchell et al. 1976; Ratcliffe 1987; reindeer: Reimers 1982). Additional variation in body size and growth might be introduced if differing genetic strains develop in different areas (e.g. for whitetailed deer see Smith and Chesser 1990). However, electrophoresis of blood proteins revealed no differences across a wide range of British park populations tested by Pemberton (1983), who argues that British fallow are highly inbred having originated from only a small number of reintroductions; having thus passed through an evolutionary bottleneck they now show only little genetic variation (Pemberton and Smith 1987).

Table 3.14 : Comparison of winter live body weights (kg) of Fallow in Parks, Farms, and Wild populations. The lowest and highest mean-weights recorded in any year in the parks used during this study are shown, together with comparable age-specific data available in the literature for farms and wild deer.

	No. of populations		Female Fawns	Female Yearlings	Female Adults (>2 yrs)	Male Fawns	Male Yearlings	Male Adults (>2 yrs)
PARKS: 'A' to 'K' (this study)	11	lowest mean :	19.3	32.1	36.3	19.5	40.2	51.9
		highest mean :	28.9	42.6	48.9	32.3	55.9	74.4
FARMS:								
Denmark[1]	4	lowest mean :	17.1	31.9	-	18.9	42.5	-
		highest mean :	27.3	42.7	-	31.9	51.4	-
New Zealand[2]	2	lowest mean :	-	33.5	-	-	-	-
		highest mean :	-	35.0	-	-	45.5	-
USA - New York State[3]	1	mean :	20.0	32.1	42.5	23.6	-	-
WILD: Populations								
England-New Forest[4]	1	mean :	20.5	-	38.6	22.5	-	63.2
Germany-various counties[5]	5	lowest mean :	16.6	30.6	38.2	22.9	-	-
		highest mean :	26.8	42.1	50.1	25.6	-	-

(Data for farms taken from Vigh-Larsen (1987) Denmark[1] ; Asher (1986) New Zealand[2]; Kerckerinck (1989) USA[3]; and for wild populations from Jackson (1974), New Forest[4] ; Ueckermann and Hansen (1983), Germany[5]. All are live or entire-carcase weights weighed in late autumn/winter, except for Germany, where gralloched weights have been converted back to entire weights using Jackson's (1974) regression equation; german deer weights for males are omitted, due to incompatible age breakdown.

During the current study differences in body weights attained by fallow within single parks between years showed clear-cut inverse relationships with population density. Such correlations are strongest with density as measured at the time of birth rather than the current year, emphasising the importance of environmental conditions during early life.

Between park populations however, much of the variance in body weights and growth rates could be attributed to differences in climate. Winter rainfall and mean winter temperatures were significantly correlated with both pasture production in the subsequent summer and deer body weights the following autumn and winter. The delay in onset of the growing season due to prolonged cold winter temperatures was implicated as being of particular importance, while areas with exceptionally high winter rainfall showed additional reductions in pasture production possibly related to water logging and leaching of nutrients from the soil. Similar indirect effects of summer climate on body weights have been shown for Scottish red deer by Albon (1983), where these are thought to act through changes in forage production of heather, *Calluna vulgaris* and *Erica spp.*. Feldhamer et al. (1989) link climatic influences on whitetailed deer condition to the effects of climate on yields of acorns and chestnuts, which may also be of some importance in our study parks. Conclusive evidence for more direct effects of climate on deer condition comes mainly from studies of deer close to the northern limits of their range. For example, the high costs of thermoregulation and importance of shelter for red deer on the Scottish Highlands have been demonstrated by Staines (1977), Grace and Easterbee (1979) and Ratcliffe (1987), and further studies there show that males of this species in particular are prone to the detrimental effects of cold temperatures (Clutton-Brock and Albon 1983; Watts 1980).

A much greater source of variation between populations in body size and condition than was anticipated at the start of this study, is introduced by surprisingly wide differences in the quantity and quality of supplementary feed provided per animal overwinter in the different parks. A general trend is discernible across parks/years for more supplementary feed to be provided per deer, the smaller the total herd size. This may be due to larger estates tending to opt for cheaper, and hence usually lower quality feedstuffs, in order to keep the overall feed costs down. A minority of parks managers at present seem to work out the levels of feeding based on current herd numbers, instead tending to still rely on what has 'traditionally' been provided. Once the effects of differences in forage production and supplementary feed were accounted for, significant amounts of the residual variation in body weights between populations were again explained by differences in stocking densities.

The influences of climatic variation and density-dependent factors implicated above in explaining differences between park populations, are likely also to be responsible for the relatively low weights of fallow recorded on many deer farms. However, it should be remembered that in addition to often being stocked at even higher densities than parks, most farms also offer a less diverse habitat. While fallow deer may be well adapted anatomically to feeding as preferential grazers (Hoffmann 1985), forage other than grasses also contribute >35% of the diet (>75% in winter) of wild fallow in southern England (Jackson 1977); in autumn up to a quarter of the diet may be made up of highly nutritious tree fruit such as acorns and chestnuts. Fenner (pers. comm) assessed isolated mature oak trees in Southern England (during 1989) to have yielded on average 82.8 kg (dry wt.) of acorns each, which equates with the entire basic food requirements of one fallow doe for over 2 months. Such standard trees form a characteristic part of the traditional British deer park landscape, and the associated natural food supplementation during the period leading up to the rut and onset of winter is likely contribute significantly to the attainment of the high mean body weights shown in some of our park fallow populations. On farms given over entirely to pasture the lack of shelter will also increase thermoregulatory costs throughout the year over those incurred in parks, where often extensive areas of cover are present (e.g. in the form of bracken, *Pteridium aquilinum*, or woodland). It is interesting to note in this context that the only farmed yearling does reported in Table 3.14 as having reached weights equalling the highest attained in our parks, were overwintered indoors as fawns .

Studies of Scottish red deer indicate that for this species over-winter weight losses may introduce confounding variance if sampled at different times of the year (e.g. Mitchell et al. 1976). Some such studies have therefore attempted to adjust cull weights according to dates of shooting based on mean weight losses observed between the beginning and end of the cull (Albon et al. 1986, Ratcliffe 1987). Albon et al. (1986), however, showed that overwinter weight losses (Oct-Feb) varied widely between years for Red deer in Central Scotland; thus losses among pregnant yeld hinds averaged 5kg (<10% of body weight) in 1972-3, but were at only 0.2kg negligible in 1973-74; losses among milk hinds have generally been found to be of a smaller order than for yeld animals (Mitchell et al. 1986). This indicates that major weight losses are not inevitable for that species, even in the relatively cold Scottish climate. For fallow deer in the forests of Northern Germany, experiencing climates more closely resembling that of our parks in England and Wales, no significant weight losses are noted before February (Mehlitz and Siefke 1973, Ueckermann and Hansen 1983, Petrak 1987). No consistent trends of weight loss could be determined during this study between catch-ups held 'Early' (Nov/Dec) and 'Late' (Feb) in winter, possibly in part due to the very mild winters experienced in England in recent years. Applying a weight-loss correction factor according to the catching date of each park was therefore thought unsatisfactory. Ideally a number of catches would have taken place at different times of the winter in each park. Although such repeated catches in at least some parks are now being planned, within the context of this thesis this was not feasible due to the large number of parks involved, in most of which the deer had never been handled prior to this study. We may nevertheless conclude that extremely wide, significant variation in the body weights of fallow deer exists between the study parks, even when all those samples which may have shown differences due to weight losses over-winter are disregarded.

Variation in body weights between park populations was already well established amongst the juvenile age-classes, emphasising the great importance of conditions during early growth. Average growth rates achieved over the first five months of life for females fallow ranged from 3kg per month in one park up to 5kg per month in another. During the following twelve months juveniles at both these sites achieved nearly identical gains (1.06kg and 1.14kg per months), thus maintaining but not greatly exaggerating these early differences. A similar pattern was seen amongst males showing mean growth rates to 5 months of age ranging from 3kg to 5.5 kg per months between parks, and 1.7kg to 1.9 kg per month respectively over the next year. Morphometric indices of condition and skeletal growth assessed during this study closely reflected findings based on body weight alone throughout all analyses. Skeletal growth as measured here by length of the head or of the mandible already reached asymptotes between 2 to 4 years of age [at least among females]. Amongst a wider series of body measurements on culled fallow deer in East Germany Mehlitz and Siefke (1973) found 'total body length' (upper-lip to tail) to increase for the longest period (7-8 years) in both sexes. Petrak (1987) however, relying on measurements made of total body length and chest girth of fallow in Germany, concluded that skeletal size on the whole is completed by three years of age for female fallow, and six to seven years in the case of males. Data on weight gain, as well as skeletal growth, in the present study indicated that deer from the heavier herds reached such adult size noticeably earlier; this is in line with the findings of several other authors who note that growth is completed more rapidly among ungulate populations expanding in favourable habitats (Klein 1968; Geist 1971; Skackleton 1973).

Skeletal measurements of yearlings and fawns made during February were generally longer than when measured in November. While such comparisons were unfortunately only possible within some of our highest performing populations, this result, in contrast to data from Mehlitz and Siefke (1973), shows that growth will not necessarily stagnate over the winter months.

The main aim in this chapter has been to illustrate the extent of variation which exists between our study populations with regard to body size, growth, and condition, and to explore the reasons which may be causing the differences shown in these parameters. The actual consequences of such variation, with respect to the reproductive performance and survival of the deer, form the subject of subsequent chapters. More comprehensive discussion of the implications of variation in body size and condition must therefore await the presentation of results reported there.

Chapter Four

FEMALE REPRODUCTIVE SUCCESS

Plate 9 : Fallow doe and fawn in autumn

4. FEMALE REPRODUCTIVE SUCCESS

4.1 INTRODUCTION

Eventual success or failure to recruit viable offspring to the population is influenced by a large number of factors determining the level of nourishment and care received by the growing young in the womb as well as beyond birth. In fallow deer, the burden of parental care falls almost entirely on the females, whereas male contribution to the reproductive effort is limited to the transfer of gametes; it is therefore in particular the females who hold the key to offspring survival, and hence to population increase or decline.

The purpose of this chapter will be to address the complex interactions between environment, behaviour, body condition and fecundity, which affect the ability of female fallow deer to produce young and subsequently rear them through to adulthood. Figure 4.1 provides a pictorial representation of different factors, and interrelationships amongst these, which may influence female reproductive success. How successful an individual will be at propagating its genes does not depend merely on the young reared in one year or season, but on the reproductive success over its entire lifetime (LRS); that is the total number of surviving offspring it produces and also the reproductive capability of those offspring. In addition to the successful production of offspring in any one year, evaluation of reproduction must therefore also consider the costs of rearing the young, the knock-on effects these may have on the mother's own future breeding attempts, and the influence of maternal care during early life on the future reproductive status of individual offspring. Among the many components of the system displayed in Figure 4.1, we may thus distinguish those related directly to the adult female herself (her body condition, age, life-span, fecundity, maternal behaviour, genotype and mate choice), and those pertaining to her off-spring (birth date, sex, condition, survival, and future reproductive success), while both these sets occur within the constraints imposed by a dynamic set of environmental conditions (population density, age/sex structure, habitat, and climate).

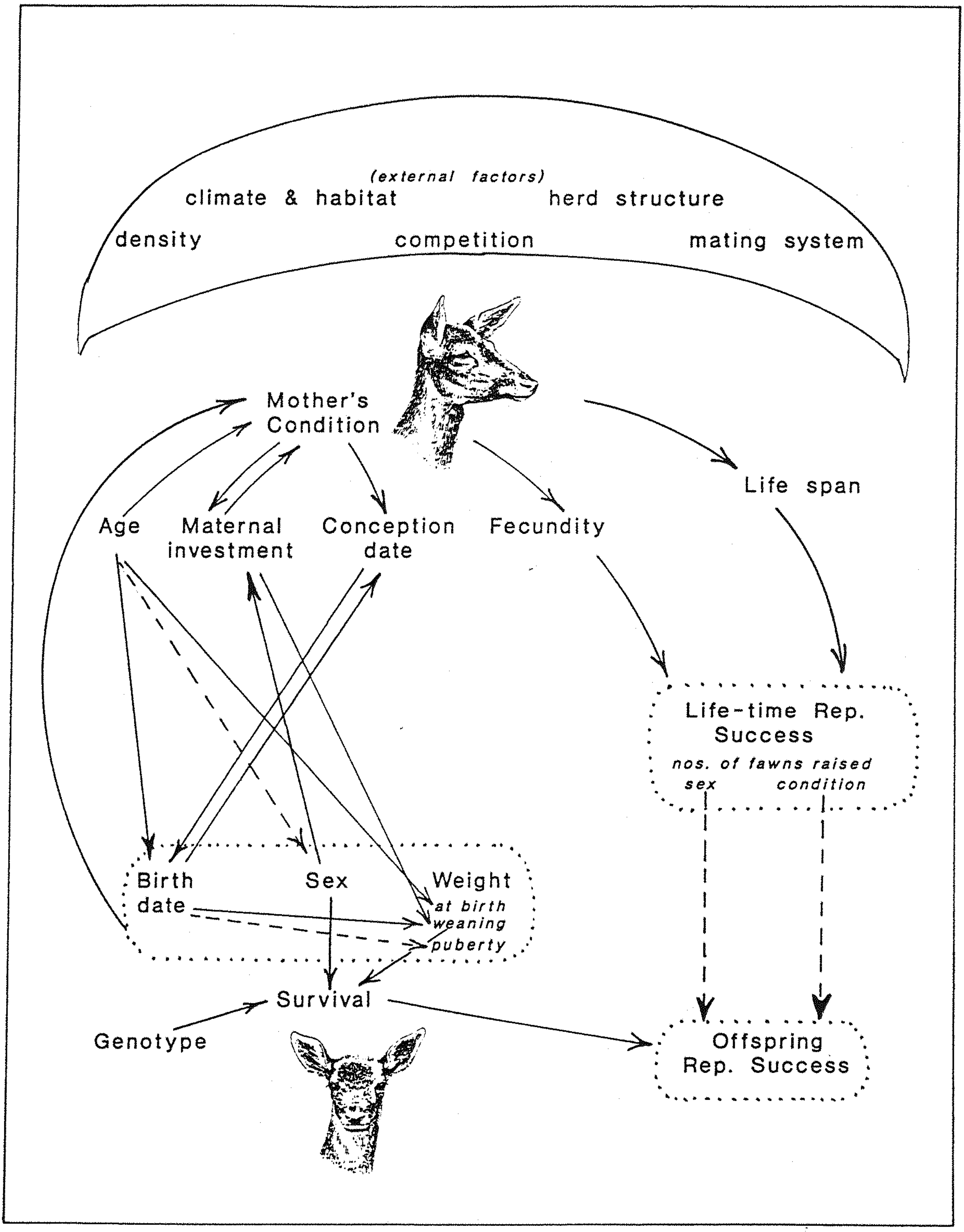


Figure 4.1: Schematic illustration of relationships between the condition of female deer, the success of their reproductive effort, and consequences on future breeding attempts. Interrelationships between the performance of mothers and their offspring are shown under an umbrella of additional external factors which influence all members of the population.

The general underlying concepts linking reproductive success of mammals to factors such as density, through for example changes in body condition, have already been introduced in Chapter 1. With regard more specifically to deer, relationships suggested by means of solid arrows in Figure 4.1 are supported by some previous field studies on at least one species from this family: Changes in reproductive performance may be effected through a) delays or advancement of the age of puberty, b) changes in the fecundity among adults and c) in multiparous species (e.g. moose, whitetailed and roe deer), by changes in litter size. Density dependent changes in deer fecundity were already being reported in the earlier half of this century (e.g. red deer : Darling, 1937 ; wapiti : Cowan, 1950; white-tailed: Morton and Chaetum, 1946; Chaetum and Severinghaus 1950). Morton and Chaetum's work on white-tailed deer in New York State showed populations living in the South, at lower density on ranges of better quality, to have significantly higher mean fecundity than those in the North. Density-dependent effects on reproductive success have also been the subject of several more recent investigations on a number of deer species (although not including fallow), which have greatly helped our understanding of the underlying reasons for such relationships.

Changes in reproductive rate are often shown to be exerted through body condition, which itself in the previous chapter was shown to be influenced by density-dependent, as well as independent factors. Rattray (1977) shows that in domestic animals nutrition can have pronounced effects on almost all stages of reproduction, from puberty, sexual development and reproductive efficiency to prenatal and postnatal foetal survival. Lowered reproductive rates in deer have frequently been found to be associated directly with low body weights (e.g. red deer: Mitchell, 1973; Clutton-Brock et al. 1983; Albon et al. 1986; reindeer: Reimers, 1983; whitetailed: Teer, 1984). Kelly and Moore (1977) and Hamilton and Blaxter (1980) demonstrated that red deer hinds must achieve a certain threshold weight before their probability of conceiving increases significantly; below certain thresholds ovulation thus seems to be suppressed. Body weight itself has been shown to be closely correlated (at least during late autumn) to other indices used to measure condition of deer (Robbins et al. 1974, Reimers et al. 1982, Mitchell et al. 1976, Kie et al. 1983, Albon et al. 1986). Thus, while Albon et al. demonstrate independent significant relationships of a number of measures of body composition with fertility in red deer, accuracy of models using a number of such indices was only marginally better than prediction of fertility on body weight alone.

Age at puberty in many mammals including several deer species is also related to body condition and in particular the level of nutrition available to the animals as juveniles (Sadleir 1969). Delayed puberty has been shown to be a major factor contributing to the low reproductive rates found, for example, in resource limited moorland red deer populations in Scotland (Mitchell 1973; Staines 1978; Clutton-Brock et al. 1982), where in populations with hinds of low body weights most females will not reproduce for the first time until they are two years old or more. In comparison, Ratcliffe (1984a, 1987) shows that Scottish hinds in a number of populations living in commercial woodlands, generally already conceive as yearlings. Pubertal deer thus seem to be especially sensitive to the body weight-fecundity relationship discussed above, and it has been suggested that critical ovulation weight thresholds may lie higher for such young females than for adults (Ratcliffe 1984a, 1987). That age may continue to be an important variable in relation to fecundity throughout the life-span, is illustrated by the positive correlation of age-related dominance ranks with reproductive success in red deer on Rhum, shown by Clutton-Brock et al. (1984).

The costs incurred by successful reproduction have themselves also been noted to lead to changes in body condition; thus females which recently produced young are, at least in harsh environments, found to be less likely to be fecund than those which were yeld that year (red deer : Mitchell and McCowan, 1986; Clutton-Brock et al., 1983; reindeer: Reimers 1983, Skogland 1985; white-tailed: Teer 1984). Maternal body condition may influence not only conception and production of young but also their survival, through changes in birth weights (e.g. for fallow, Asher 1986), and effects on birth dates. Reduced survival among red deer calves on the Isle of Rhum was shown to be correlated with a delay in birth dates, while the parturition dates of hinds were noted to be affected by timing and costs of reproduction in the previous year (Clutton-Brock et al., 1983, 1987b). Further, the costs of rearing male offspring were found to be greater than those associated with rearing females, probably because male deer tend to be heavier at birth and have faster growth rates (see Chapter 3) and hence heightened milk demands. The above studies also suggest that, as a consequence of these costs, subsequent reproduction is delayed to a greater extent after rearing a male than after a female off-spring.

These previous studies on deer, of which the above mentioned are only a small example, clearly provide us with a wealth of hypotheses to explain the relationships which may govern reproductive success in fallow deer.

Deer species, however, vary tremendously with regard to their body size, geographical ranges they inhabit, breeding seasons and other ecological adaptations of importance to reproduction (review: see Putman 1988). To what extent relationships shown previously in other deer species will also apply to fallow, as well as the relative importance of the differing factors involved, is therefore likely to vary greatly between species and populations.

Factors affecting the reproductive success of fallow deer have been studied comparatively little, with work to date restricted to general descriptions of reproductive performance of fallow in different populations based on data derived from culled animals (Sterba & Klusak, 1984; Chapman & Chapman, 1975; Baker, 1973), or dealing predominantly with physiological aspects of puberty and oestrus cycles (Fisher 1982, Sterba & Klusak 1984, Asher 1986).

My own studies of female reproductive success presented below are predominantly based on known individuals whose performance was monitored for up to a maximum of four reproductive seasons for each animal. Thus, while their complete LRS can not yet be addressed directly, comparisons are possible between the success of individuals, cohorts and populations over set time-spans, as are investigations of the variation in reproductive success between does of different age-classes or reproductive condition. Results are presented in particular on fawning and rearing success [4.2.1 & 4.2.5], parturition date [4.2.2], birth sex-ratios [4.2.3], and birth weights and growth [4.2.4], evaluating each of these whenever appropriate in relation to the age, condition and previous reproductive history of mature females.

Methodology used in making observations and assessment of reproductive variables was discussed in detail in Chapter 2. To recap briefly, data presented here for the most part pertain to eight of the study parks, where during the course of the present study large numbers of individuals were annually captured, weighed, aged, and tagged, and females checked for their reproductive status. Subsequent reproductive success of marked, known-aged animals was assessed in terms of their observed pregnancy, fawning success, parturition dates, birth weights of young, maternal behaviour and neonatal losses during the summer, and if recaptured, their condition the following winter. In some cases reproductive performance in the summer could also be related to observations made of the same animals during studies of the previous autumn's rut (see Chapter 5).

Throughout this presentation does of breeding age are described as **yearlings** if they were less than 2 years old at the previous rut (though in fact two years old by the end of gestation), while those referred to as **adult** were already over 2 years old at the rut. **Milk** does are those which had reared fawns in the previous summer; **yeld** does those which had not produced a fawn the previous year or had lost it soon after parturition.

4.2 RESULTS

4.2.1 **Fawning and rearing success**

Fawning rate

During three consecutive fawning seasons (1987-9) it was possible to determine the success or failure at carrying fawns through to the full term of pregnancy (fawning success[1]) in 674 cases, where the age of the doe (that is at least distinguishing as far as yearlings and adults) was also known. No multiple births were recorded, and hence all results presented refer to production of single offspring. Full details of percentage fawning success rates broken down by park, year, and age, are shown in Table 4.1; for clarity the actual numbers of does assessed each year, and the numbers known subsequently to have lost their fawns within two months of parturition, are also given. In some parks the number of tagged does available during particular years was rather low; as wide variation in percentage fawning rates between years within any one park only occurred where these were based on rather small samples, results for 1987-9 have been pooled for each park for further analysis of the effects of age on fawning rate.

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[1] 'Fawning success' rather than 'fecundity' (production of live fawns) is described, as dead neonates could not always be found; hence distinction between does producing still-born foetuses and those losing young within a short period of parturition was not always possible. Thus, while mean 'fawning success' rates include all does giving birth, 'rearing success' includes only those does with live fawns in August. Mean population fecundity, defined as the number of live fawns produced per female (Caughley 1977), would thus lie in between these values of fawning success and rearing success used in this presentation.

Table 4.1: Fawning success and early fawn losses in 8 British parks 1987-89

PARK	YEAR	YEARLINGS				ADULTS			
		Nos. fawned x/N	(%)	No.lost fawns early	% with fawns in August	Nos. fawned x/N	(%)	No.lost fawns early	% with fawns in August
A	1987:	1/2	50.0		50.0	5/5	100.0		100.0
	1988:	0/4	0.0		0.0	9/9	100.0		100.0
	1989:	0/2	0.0		0.0	3/4	75.0		75.0
	Total	1/8	12.5	0	12.5	17/18	94.4	0	94.4
B	1987:	5/5	100.0		100.0	9/13	69.2		69.2
	1988:	25/29	86.2		86.2	11/14	78.6	2	64.3
	1989:	8/10	80.0		80.0	26/29	89.7		89.7
	Total	38/44	86.4	0	86.4	46/56	82.1	2	78.6
E	1987:	2/3	66.7		66.7	11/14	78.6	2	64.3
	1988:	2/3	66.7		66.7	13/17	76.5		76.5
	1989:								
	Total	4/6	66.7	0	66.7	24/31	77.4	2	71.0
G	1987:	52/59	88.1	2	84.8	8/12	66.7	1	58.3
	1988:	42/47	91.5	4	83.0	58/62	93.5	1	91.9
	1989:					30/34	88.2	1	85.3
	Total	94/106	88.6	6	83.0	96/108	88.8	3	86.1
H	1987:	2/3	66.7		66.7	9/10	90.0	2	70.0
	1988:	2/3	66.7	1	33.3	13/14	92.9	3	71.4
	1989:								
	Total	4/6	66.7	1	50.0	22/24	91.7	5	70.8
I	1987:	7/8	87.5		87.5	25/26	96.2		96.2
	1988:	12/12	100.0	2	83.3	20/21	95.2		95.2
	1989:	14/15	93.3		93.3	27/28	96.4		96.4
	Total	33/35	94.3	2	88.6	72/75	96.0	0	96.0
J	1987:	9/12	75.0	1	66.7	13/15	86.7		86.7
	1988:	3/5	60.0		60.0	24/26	92.3	2	84.6
	1989:	18/21	85.7		85.7	31/39	79.5		79.5
	Total	30/38	78.9	1	76.3	68/80	85.0	2	82.5
K	1987:								
	1988:	3/3	100.0		100.0	16/16	100.0	1	93.8
	1989:	10/12	83.3	1	75.0	17/19	89.5		89.5
	Total	13/15	86.7	1	80.0	33/35	94.3	1	91.4
	Grand Total:	N=258	84.1	11	79.8	N=427	88.5	15	85.0

(All data on Does of unknown age class are omitted)

Average fawning rates of **adult** females varied little between these populations, and in fact exceeded 82 % in all but one park (Table 4.2). Reproductive rates of **yearlings** showed greater variation, ranging from 12.5 - 94.3 %. Fawning rates of yearlings were also, with only one exception, lower than those of adult does in the same park (Wilcoxon's matched pairs test, $p < 0.05$). While significant differences between yearlings and adults thus clearly exist, in many parks these differences were only quite small and yearlings also attained fawning success rates over 82 % in four sites.

Although all 'adult' does were known to have been at least two years old when conceiving, the actual true age in years was known in each park for at least some animals, albeit a smaller sample (i.e. those which were marked early on in the project, as fawns or yearlings and thus subsequently of known age). Fawning success at 1, 2, and 3 years of age, as far as data are available to date, is summarised in Table 4.3. Two-year old does overall also showed predictably higher average success rates than yearlings (weighted average two-year olds = 86.3 % > yearlings= 78.7%), but in contrast to the above results which included all 'adults', these differences were not statistically significant (Wilcoxon's pairs test $P > 0.1$).

The fawning success of two female cohorts (i.e. those born in 1985, and those born in 1986) was possible to compare as yearlings and again as two year olds in six of the populations. No consistent differences across parks in fawning success between these two cohorts could be shown at either age (Wilcoxon's pairs test $p > 0.1$, two-tailed).

As tagging began less than five years ago few of our animals of known age are yet even six years old. However, as reproductive rates have been shown to fall off in the later years of life in most vertebrates (Caughley 1970, review Clutton-Brock 1988), it was thought important at least to attempt to assess any further age-effects as far as possible. Among animals aged after death by study of tooth eruption and sectioning, no does with I1-incisors worn down to 5mm or less were found to be under six years old. Selecting therefore from our annual handling data (for all parks combined) all those does with incisors less or equal to 5 mm, and separately those with I1's over 7 mm, distinguishes amongst our adult sample a

Table 4.2 : Fallow deer 'Fawning' and 'Rearing' success (1987-89) in eight British deer parks.
(parks are arranged in order of increasing average adult female live-weight)

Park	Mean Winter Live Weight		Yearlings			Adults		
code	yearlings (kg)	adult does (kg)	n	% fawned	% with live fawns in August	n	% fawned	% with live fawns in August
A	32.5	37.7	8	12.5	12.5	18	94.4	94.4
B	34.9	38.0	44	86.4	86.4	56	82.1	78.6
E	35.2	40.7	6	66.7	66.7	31	77.4	71.0
H	37.9	41.9	6	66.7	50.0	24	91.7	70.8
G	35.5	42.1	106	88.6	83.0	108	88.8	86.1
I	37.1	43.8	35	94.3	88.6	75	96.0	96.0
J	40.3	44.3	38	78.9	76.3	80	85.0	82.5
K	40.5	45.8	15	86.7	80.0	35	94.3	91.4

(Wilcoxon's Test: $Z = 2.03$, $p = 0.02$ one-tailed, - fawning success yearlings < adults)

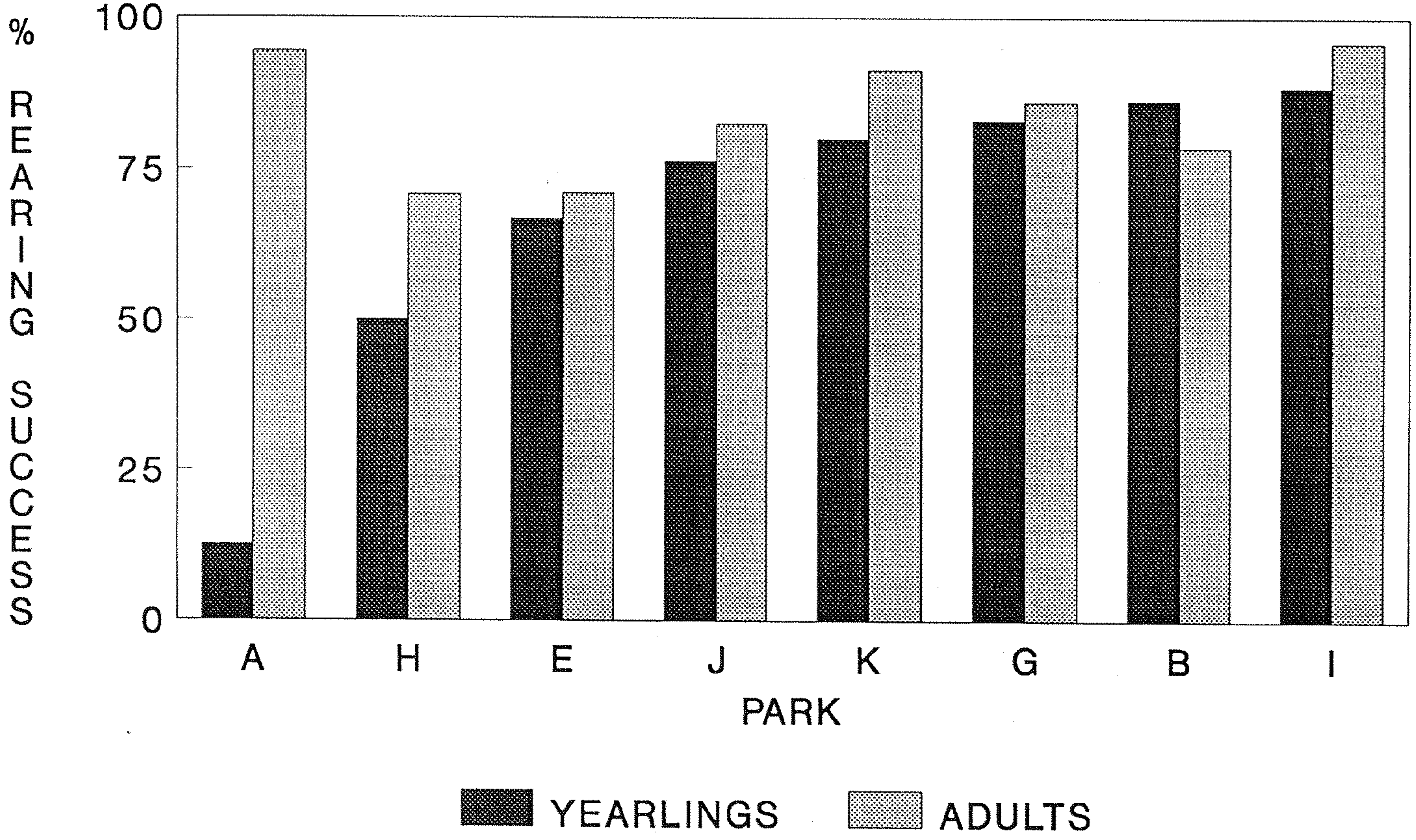

Figure 4.2 : 'Rearing' success in 8 fallow populations between 1987-89, achieved by females conceiving either as Yearlings, or as 'Adults' (>2 years old). ('rearing success' = % of does producing <u>and</u> rearing fawns through to at least August; sample sizes see Table 4.2)

Table 4.3 :

Percentage fawning success in relation to age at conception for a number of female cohorts.

Park	Cohort (year of birth)	Age at conception 1-year		2-years		3-years	
		n	% fawned	n	% fawned	n	% fawned
A	1985	2	50.0	2	100.0	-	
	1986	4	0.0	2	50.0	-	
	Total:	6	16.7	4	75.0	-	
B	1985	5	100.0	5	60.0	1	0.0
	1986	29	86.2	10	90.0	-	
	Total:	34	88.2	15	80.0	1	0.0
G	1985	55	94.5	48	95.8	17	82.4
	1986	47	91.5	6	100.0	-	
	Total:	102	93.1	54	96.3	17	82.4
I	1984	3	100.0	3	100.0	3	100.0
	1985	8	87.5	3	100.0	3	100.0
	1986	12	100.0	10	90.0	-	
	Total:	23	95.7	16	93.8	6	100.0
J	1985	12	75.0	8	100.0	7	85.7
	1986	5	60.0	6	50.0	-	
	Total:	17	70.6	14	78.6	7	85.7
Overall Total	1985	82	90.0	66	93.9	31	83.9
	1986	97	85.6	34	82.4	-	

group of 'old', as well as one of relatively 'young' does. Ninety-five percent of the 'old' does (n=41), and 90 % of the 'young' adult does (n=179) produced fawns. However, the 'old' group suffered a 15 % summer fawn-mortality compared to only 1.2 % recorded losses in the case of the younger group, giving respective rearing rates of 80% and 89 %. Thus, although does clearly continue to achieve high fecundity beyond our arbitrary (and perhaps rather low) dividing line of six years, these results do suggest that the rearing ability of old does may decline with age; this effect might be explained by a loss in grazing efficiency, which could cause a failure of adequate milk production.

Early losses (within 1 - 2 months of birth) of fawns averaged less than 5% of numbers born for both yearling or adult mothers across the eight parks. Losses of fawns during their first winter were also negligible amongst the populations included here. Patterns of rearing success (Fig. 4.2) thus closely reflect those of fawning success discussed above, with yearlings generally achieving lower rates than adults; on the evidence from some parks the yearling age group is nevertheless seen to have the potential to also achieve very high reproductive rates.

Effects of body weight on fawning success

The very wide variation which occurred in mean live-weights of does between parks, and the underlying reasons for these differences have already been extensively discussed in Chapter 3. In Table 4.2 parks are again listed in ascending order of mean live weight of adult females during winter, over that period for which their fawning rates have been calculated. While the lowest yearling fawning success rates were indeed recorded in the population (park 'A') which also showed the lowest mean live weights, adult fawning rates at that same site exceeded 90 %. Rank correlation analyses of percentage fawning success and mean live weights across the eight study sites were not significant ($p > 0.1$) for either yearlings or adults[1].

In order to explore further the extent to which differences in fawning rates may relate to differences in **individual** body condition, analyses were carried between reproductive success and each mother's live body weight the previous winter. For this, data for all sites were combined and animals then grouped into consecutive weight classes such that each contained 5 % of the entire sample.

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[1] Between park variation of fawning success in relation to body weight, density and other park characteristics is addressed in more detail in 4.2.6 using a wider range of populations.

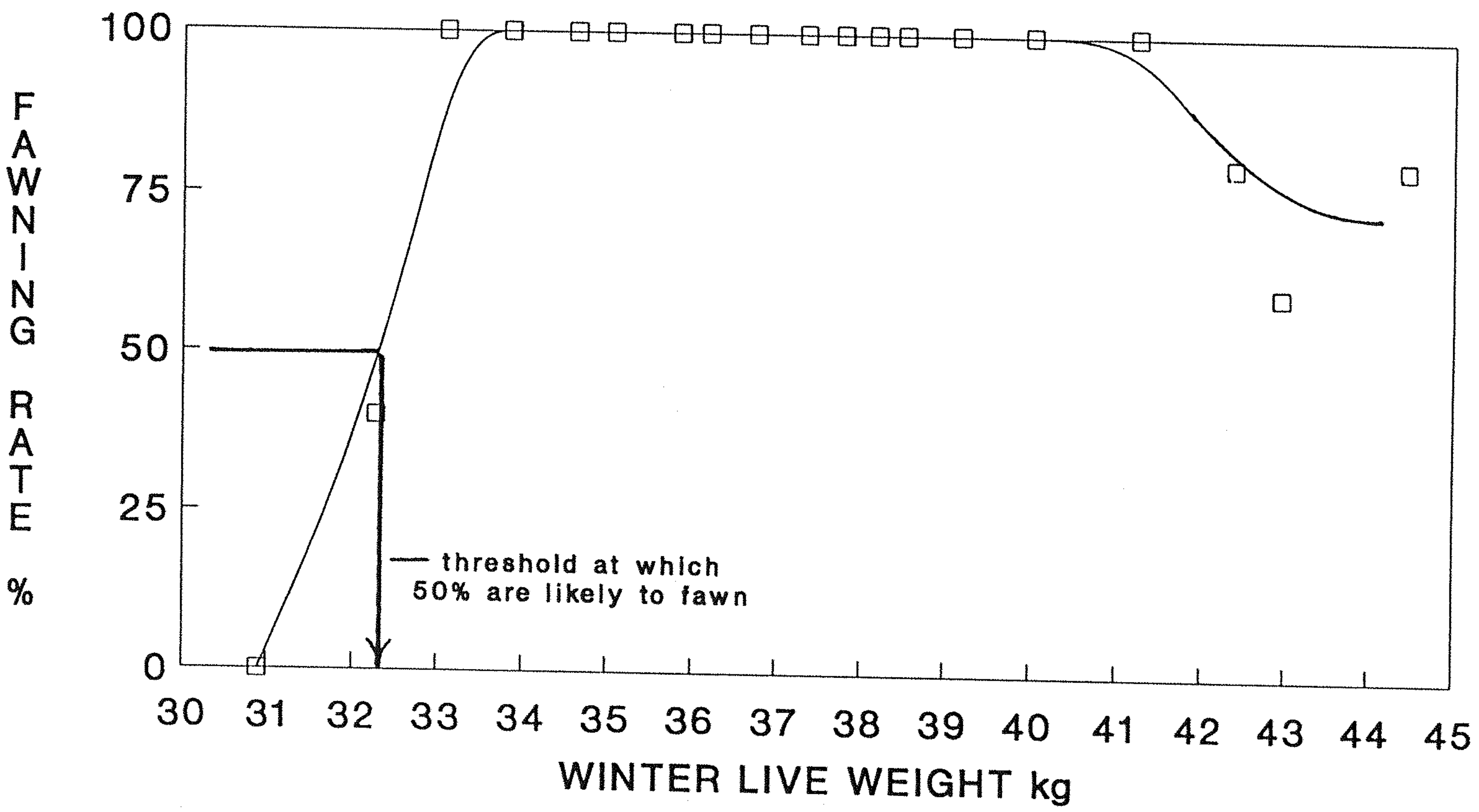

Figure 4.3 : Fawning success of yearling fallow does, in relation to body weight. (Combined data from 8 parks; each data point shown represents the percentage which fawned among 5 does in a given weight class)

The proportion of animals in each weight class which produced fawns was then calculated and plotted against weight, to explore whether or not there was evidence for a threshold weight for successful reproduction; analyses were carried out separately for yearlings and adults.

Fawning success of adult does exceeded 75% in each 5-percentile of the available sample (total n=240) and no direct link of fawning rate and body weight was apparent. (From Table 4.2 it is can be seen that even in park 'A', where the lowest average body weights were recorded, adult fawning rate is >90%).

Fawning rates of yearlings in contrast did show a relationship to body weight (Figure 4.3). Among the lightest group of animals (29 - 31.5 kg) none produced a fawn; thereafter fawning rate rose quickly to 100 % among animals of 33 kg and above. A threshold mean winter live-weight at which 50 % of yearlings are likely to produce a fawn, could be calculated (after Hamilton and Blaxter 1980, Albon et al. 1986) as 32 kg. The fawning rate remained at this very high (100 %) level for all 70 yearlings weighing between 33 and 42 kg, and in fact fell slightly for the few heavier animals.

Fawning rate in relation to reproductive history

Studies of ungulate reproduction have often assessed the reproductive success of milk and yeld females separately, since the costs of raising a calf one year may reduce fecundity at the following rut. Table 4.4 shows the percentage of fallow does known to have raised fawns in two consecutive summers for each park, the remainder having either failed to fawn or lost their young early in at least one year. The number of individually recognisable does, who reared fawns to weaning in two consecutive years only fell below 90 % in the three parks where mean adult body weights also fell below average over that period. Results for those sites where it proved possible to follow reproductive success of individual does for three consecutive years (Tab. 4.4) further support the finding that these very high rearing success rates continue to be attainable despite previous reproductive costs. For example Park 'I', which to date provides us with most individuals monitored for 3 or more consecutive years, showed 96 % (n=24) of does in this park to have produced in all of three years, as well as 83 % (n=6) of those for which data on four years are available.

Table 4.4 :

Percentage of individual Does producing & rearing fawns through to at least August in two or more consecutive years.
(parks listed in order of increasing mean female live-weight)

PARK code	raising fawns in 2 consec. years (n)	%	raising fawns in 3 consec. years (n)	%
A	14	71.4	3	33.3
B	13	69.4	4	0
H	11	63.6	no data	-
G	66	90.9	12	75.0
I	68	92.6	24	95.0
J	37	94.6	12	90.0
K	14	92.8	no data	-

Table 4.5 :

Comparison of Fawning success of previously Yeld or Milk adult Does.
(because of the low incidence of yeld does, data for all those parks containing at least some yelds have been pooled)

	Yeld	Milk	N-Milk
Fawned :	28	34	65
No Fawn:	8	1	5

Chi-square test (with Yates' correction) :
Yeld < (lower fawning rate) than Milk : $X^2 = 4.4$, df=1 , $p< 0.05$ *
Yeld < " than Milk+NMilk : $X^2 = 6.4$, df=1 , $p< 0.01$ **

(Yeld = no fawn raised in previous year
Milk = fawn raised in previous year & still lactating in December
N-Milk = fawn raised in previous year but udder dry in December)

As a consequence of the high consecutive reproductive success rates described above for milk does, samples of yeld does available for comparisons were very low in any one park. Using pooled data for all parks, yeld (adult) females showed lower fawning rates than those which were observed to have reared fawns in the previous year. If the analysis is repeated, including as 'milk' does not only those observed by myself in the summer accompanied by a live fawn, but also all those which were found to be still lactating during handling at November/December catch-ups, these still showed significantly higher fecundity than yeld females ($p<0.005$; Table 4.5). Studies of resource-limited red deer populations in Scotland have demonstrated that yeld females tend to show higher fecundity than lactating ones (e.g red deer : Mitchell et al. (1976, 1977); Clutton-Brock et al. (1982); but see also Hamilton and Blaxter (1980), who found no such difference for red deer on farms. Our unexpected, opposing result here may be due to truly sterile does forming a high proportion of the in any case low numbers of yeld adult females present in the parks. Large numbers of does were clearly able to reach the required body condition necessary for conception while still lactating during the rut, and indeed suckling bouts were frequently observed during the rutting period in some of the parks. That milk does of lesser 'condition' may in fact wean their fawns earlier than those in good condition, thus enabling them too to regain the required body weight thresholds by the rutting season, was also suggested by results of observations of suckling behaviour (see 4.2.5 below).

4.2.2 Birth sex ratio

The ratio of female to male off-spring produced in different years by each population could be estimated based on the number of fawns of each sex caught during the winter; an adjustment was made to this value to include any fawns found dead before winter relative to the proportion of the total fawn population caught; as neonatal mortality was generally low (see Table 4.1) such corrections in practice only produced minor changes.

Based on 10 parks where high proportions of the population were caught annually (& including over 1500 fawns in total), birth sex-ratios averaged 1.1 (S.d.+- 0.38) in favour of females within a range of 0.33 to 2.2 in individual park years (Table 4.6). Cadman (1971) and Chapman and Chapman (1975) amongst others have shown foetal sex ratios for fallow deer close to parity, and Ueckermann and Hansen (1983) present similar results for live births. At first sight our results at various sites in certain years seem to indicate wide deviation from the expected 1:1 sex ratio ; however, largest deviations from parity occurred where sample sizes were small, and chi-square analysis (or Fisher's exact test where appropriate) shows that they could have arisen by chance in all cases ($p > 0.1$, df=1 ; Table 4.6). Nevertheless, records provided for me on an additional fallow population (park 'u'), which was not part of the main set of monitored parks, do suggest a significantly skewed ratio in favour of female fawns there in 1987 (48:18, $X^2= 6.3$, $p<0.02$); this population also exhibited lower body weights of adult does than were recorded in any of the other parks during the study period.

It was not possible to evaluate differences in offspring sex-ratios between yearling and adult mothers in most individual populations, as sample sizes of fawns which were of known sex as well as having been matched with known yearling dams usually fell well below those required for contingency-table analysis. In park 'I', where 22 suitable matched mother-young pairs were available, yearlings produced 5 female and 7 male fawns, compared to 4 females and 6 males produced by adult dams. While such differences between yearlings and adults remained non-significant when data on birth ratios for all sites were pooled (yearlings: 16f,18m, adults: 39f,64m ; $X^2=0.9$, $p > 0.1$), on these data adult does at least are suggested to have male biased birth sex-ratios ($X^2= 3.1$, $p= 0.07$).

Table 4.6 :

Sex ratios of fawns born in 10 British deer parks.

Park Code	Year of Birth	Number of Female fawns	Male fawns	Sex Ratio f : m
A	1987	8	6	1.33
	1988	4	6	0.67
	(TOT)	**(12)**	**(12)**	**(1.0)**
B	1986	43	31	1.39
	1987	12	14	0.86
	1988	27	18	1.50
	1989	34	34	1.00
	(TOT)	**(116)**	**(97)**	**(1.2)**
C	1987	15	11	1.36
	1989	16	8	2.00
	(TOT)	**(31)**	**(19)**	**(1.6)**
D	1988	69	71	0.97
	1989	30	18	1.67
	(TOT)	**(99)**	**(89)**	**(1.1)**
E	1985	30	21	1.43
	1986	63	57	1.11
	1987	56	61	0.92
	1988	113	107	1.06
	(TOT)	**(262)**	**(246)**	**(1.1)**
F	1987	3	4	0.75
	1988	6	5	1.20
	1989	4	11	0.36
	(TOT)	**(13)**	**(20)**	**(0.7)**
G	1986	68	46	1.48
	1988	36	30	1.20
	(TOT)	**(104)**	**(76)**	**(1.4)**
I	1985	11	5	2.20
	1986	14	14	1.00
	1987	16	14	1.14
	1988	14	16	0.88
	1989	19	17	1.12
	(TOT)	**(74)**	**(66)**	**(1.2)**
J	1986	12	14	0.86
	1987	23	18	1.28
	1988	21	25	0.84
	1989	18	26	0.69
	(TOT)	**(74)**	**(83)**	**(0.9)**
K	1987	20	16	1.25
	1988	11	12	0.92
	1989	12	14	0.86
	(TOT)	**(43)**	**(42)**	**(1.0)**
Overall :		**828**	**750**	**1.10**

(Deviations from 1:1 sex ratio are not significant in any individual or pooled comparisons; [$X^2 < 2.7$, $p > 0.1$])

4.2.3 Parturition date

Effects of age

The date by which pregnant does had produced their fawns was assessed in seven of the study parks in each of two years for as many known individuals as possible. The date by which 50 % of does were known to have produced varied between parks from 11th June to 6th July for adult does, and 16th June and 17th July for yearling conceivers. The median parturition date for yearling does was found to be later than that of adult does in the same park in 9 out of the 10 park-years where a difference was found (Table 4.7a), such consistent differences being highly unlikely to arise by chance (Wilcoxon matched-pairs test: $p< 0.01$). Statistical comparisons of median parturition dates within single park-years was only possible in some cases due to sample size limitations; these differences between the age classes were, however, confirmed in park 'G' in both years of study, showing adults to fawn significantly earlier and yearlings later than the overall median date ($p< 0.05$). This result was also affirmed when data were pooled for all sites (Table 4.7b).

In order to assess further the magnitude of this effect of maternal age on birth dates, the deviation between each individual's parturition date and the adult median parturition date for its park that year was calculated. Having thus standardised for differences in fawning times between sites, the cumulative percentage of births achieved was plotted against the deviation from the adult median for yearling and adult conceivers (Figure 4.4). Parturition dates of yearlings are shown to have been an average of 11 days later than those of adults. That this delay is a result of later conception rather than longer gestation periods was confirmed through observations made of tagged does during the rut (see Chapter 5), when yearlings tended to be mated later than adults.

Between park variation

While the data on parturition dates presented above lend themselves well to analysis of relative differences between age-classes, comparisons of the actual dates of parturition between study sites is less well justified. Median parturition dates shown in Table 4.7a must be interpreted with care as they are based on records when individual does were first known to have produced. The accuracy with which they reflect the 'real' median is thus affected by the ease of observing the deer, and may have varied between parks due to differences in the amount and type of cover

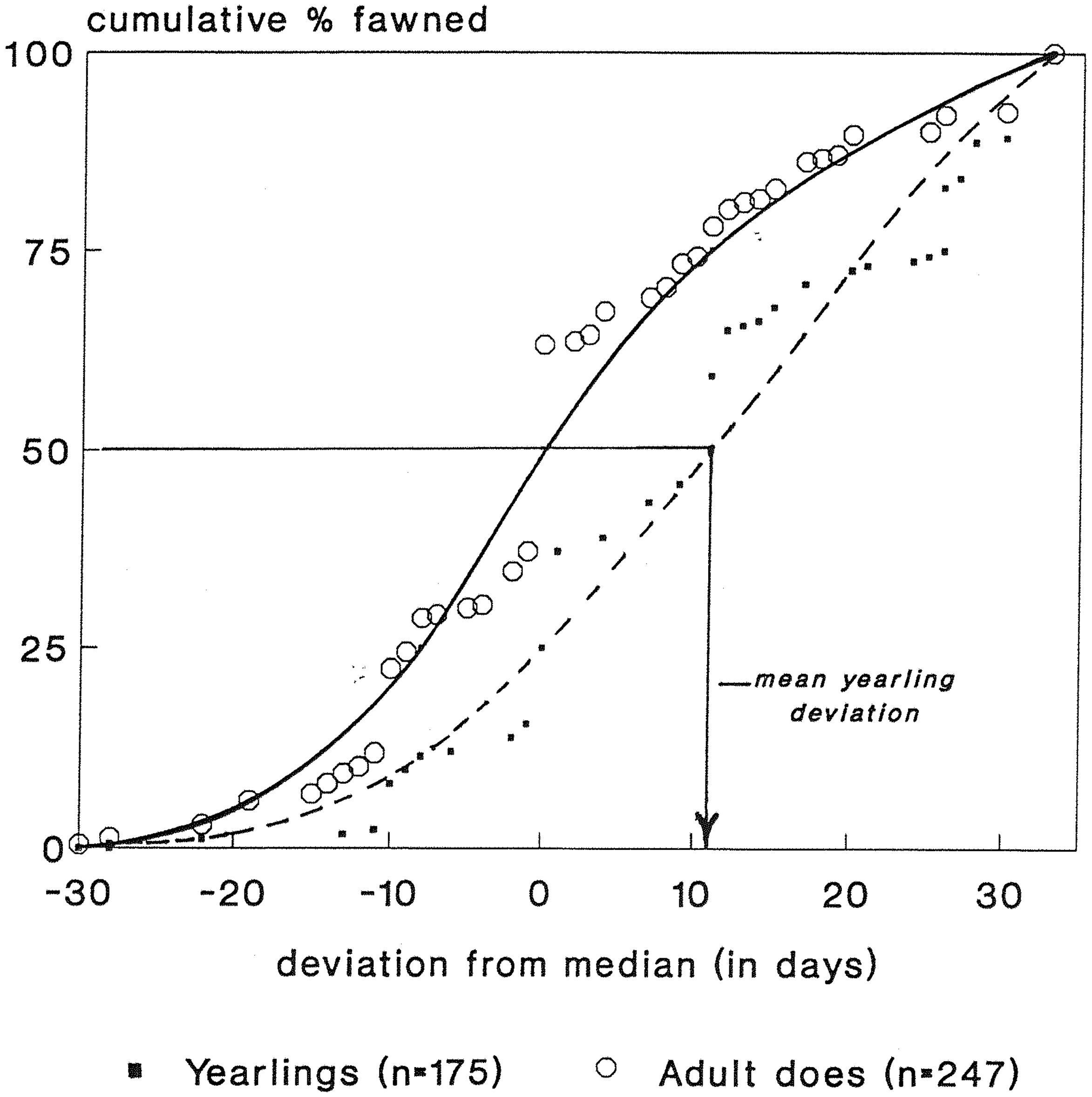

Figure 4.4 : Temporal pattern of parturition dates of adult and yearling does during June and July, based on data from seven British parks. (Individual parturition dates were all calculated as the number of days deviation from the median parturition date in that year for adults at their park of origin. Curves are fitted through consecutive quartiles)

Table 4.7a :

Differences in median fawning dates of females having conceived either as i. Yearlings or ii. Adults.
(Medians given are based on dates by which individually recognisable does were known to have produced - see text)

Park	Year	Median Fawning Date i. Yearlings	(n)	ii. Adults	(n)
A	1987	June 30th	1	June 30th	5
	1988	-	0	July 4th	9
B	1987	July 9th	5	June 24th	9
	1988	July 5th	25	June 27th	11
G	1987	June 23rd	53	June 11th	12
	1988	June 30th	42	June 20th	58
H	1986	June 25th	5	July 3rd	10
	1987	July 20th	2	June 29th	11
I	1987	July 1st	6	July 1st	24
	1988	June 26th	10	June 24th	19
J	1987	July 6th	9	July 6th	13
	1988	July 17th	3	July 2nd	24
K	1988	July 11th	3	June 24th	15
	1989	June 18th	9	June 15th	16

Table 4.7b :

Numbers of does producing before (Early) or after (Late) the overall Median fawning date, calculated among all does combined within any one park and year.

	Park 'G' 1987		Park 'G' 1988		Parks A-K 1987-9 pooled	
	Early	Late	Early	Late	Early	Late
Yearlings	23	30	15	27	69	91
Adults	10	2	35	23	87	65
Yearling vs. Adults :	$\chi^2 = 4.75$ $p < 0.03$ *		$\chi^2 = 4.96$ $p < 0.03$ *		$\chi^2 = 5.66$ $p < 0.02$ *	

present, and hence the visibility of the deer. However, observations made during the rut (Chapter 5), showed the peak of mating activity in each year in one park ('G') to occur between 8-10 days earlier than in all our other study sites; this difference is confirmed by the later parturition dates shown for that site in Table. 4.7a.

4.2.4 Birth weights and growth of offspring

Of a total of 84 fawns weighed at less than 3 days old (in all 8 parks combined) female fawns were shown to be significantly lighter (mean 4.3 kg) than male fawns (mean 4.7 kg, $t=2.25$ $p<0.03$). These results support the larger body measurements recorded for males amongst wild fallow fawns by Braza et al. (1988) in Donana, Spain.

No significant differences in off-spring birth weights could be shown between parks, despite the highly significant variation in maternal body weights. When using only birth weights of those fawns for which we were also able to determine the age of the mother our sample sizes were reduced considerably; nevertheless significant weight differences could be demonstrated between fawns born to yearlings and those born to adult dams (females fawns : yearling dams mean= 3.6 kg $n=6$, adult dams mean= 4.3 kg, $n=11$, $t=-3.37$ $p<0.005$; male fawns : yearling dams mean= 3.73 kg $n=7$, adult dams 4.8 kg $n=13$, $t=-3.98$, $p<.001$).

Differences shown above in birth weights, and also earlier in birth dates of offspring born to mothers of different ages, will only affect the reproductive success of the dams if they lead to long-term effects on the survival and reproductive chances of their young.

Effects of **birth date** on growth could be examined by comparing the body weights reached by known fawns at ca. five months (obtained during live-capture operations in Nov/Dec). Analyses were carried out on pooled data from a number of populations handled in Nov/Dec., as only a limited number of fawns in each site were tagged at birth as well as being recaptured later. **Male** fawns known to have been born between 1-7th June were found to be significantly heavier by the beginning of winter than those born 8-14th June ($t=2.3$, $p<0.05$), as well as being heavier than those born 15-21st June ($t=3.8$, $p< 0.01$). Data available for female fawns born in the first week of June were not sufficient for comparisons with those born later, while differences between weights of fawns born in the two later weeks were not significant for either sex.

Linear regressions of live-weight of fawns in Nov/Dec (at 5-6 months) on **birth weight** were not significant within any single site, although sample sizes available for such analyses were again rather small. Pooling of samples for several study sites here introduces confounding effects of differing environmental conditions (and consequently also differing maternal investment) experienced by fawns after birth. Nevertheless, on doing so significant positive relationships between fawn weights at birth and in early winter could be shown (males: R^2=31%, n=24, p<0.01; females: R^2=14%, n=21, p=0.1).

4.2.5 Suckling bout duration

For the females in many mammal species the energetic costs of lactation are higher than those of any other aspect of their reproduction (Moen 1973; Millar 1977, 1978; Randolph et al. 1977). For red deer, for example, Anderson (1976) estimates that the food requirements of milk hinds during the peak of lactation are twice as high as those of yeld hinds. The body condition of females during lactation is thus clearly likely to affect their offspring directly, through the quality and quantity of milk the dam is able to provide. In addition, a number of workers have attributed increased mortality (especially that due to predation) among whitetailed deer fawns, to differences in the maternal behaviour related to body condition (Langenau and Lerg 1976), and also to maternal age (Ozoga and Verme 1986a); that is does in poor condition, as well as inexperienced mothers, were observed to spend less time with their young.

Field work to assess individual fawning success and parturition dates took precedence over other work during this study, and hence only a limited amount of time could be spent specifically on observations of maternal behaviour. However, the duration of all suckling bouts observed were recorded opportunistically throughout other fieldwork in order to test two basic 'null-hypotheses' :

i) H_o = 'yearling' mothers suckle their fawns for bouts of the same length as do older does.

ii) H_o = suckling-bouts do not differ in duration between populations.

In many ungulate species the duration of individual suckling bouts, as well as the frequency of bouts, is known to decrease quickly with the age of the offspring (Lent 1974). A similar decrease was noted for fallow deer suckling behaviour during preliminary observations made over the first summer of this study. Two short-term projects, set-up in parallel to my own work in two of the study parks, confirmed this observation (Gordon 1987; West 1989), finding that suckling bouts averaged over 100 seconds for fawns up to 4 weeks old, but tailed off quickly (to around 60s) among fawns of 4-8 weeks of age. In view of the wide range of parturition dates among does within each park discussed in the previous section, and in particular the differences shown in such dates between yearling and adult does, analyses of summer suckling-bout duration must therefore carefully account for the age of each individual fawn observed suckling. Therefore only those suckling bouts, for which the age of the fawn involved was known at least to the nearest week, were included in comparisons of suckling-bout duration between maternal age-classes, and between populations. The number of bouts which could be accurately timed was further reduced as suckling bouts in many of the parks often took place inside dense cover, close to where the fawns had been lying-up; a clear view of the does with young fawns was thus often not obtained until after suckling bouts had occurred.

Data from park 'G' in 1987 offer the greatest sample sizes for comparisons of suckling bouts involving yearling does and adult does; those involving yearlings were on average shorter than those involving adult does for fawns less than 4 weeks old (yearlings :n=19, mean 96s; adults: n=21, mean 109s), as well as for fawns over 4 weeks old (yearlings: n=11, mean 48s; adults n=11, mean 51s), but these differences were not statistically significant for either group ($t<0.5$; $p>0.1$). Differences in the same direction between yearling and adult mothers were also shown for data from park 'K' collected by West (1989): ($p=0.07$ -one-tailed). These results for fallow, admittedly based on rather few data, are in contrast to findings for Scottish red deer by Cockerill (not dated, in Clutton-Brock et al. 1982), who found bouts involving first-breeders to be longer than those of other hinds. The small numbers of bouts involving known yearling mothers recorded in the remaining parks, preclude meaningful statistical analyses for these with respect to maternal-age.

The mean duration of suckling bouts recorded involving adult does (i.e. does already >2 years when conceiving) in various populations are shown in Table 4.8, distinguishing between bouts by fawns less than 4 weeks old, and those > 4 weeks.

Table 4.8: Mean length of timed suckling bouts (seconds) observed of fawns suckling from adult does (i.e. does having conceived at >2 years).

				PARK				All parks
	A	B	E	G	I	J	K	combined
Fawns < 4 weeks old:								
Mean (sec)	86	49	72	109	54	57	103	97.3
(sample size)	(5)	(4)	(9)	(21)	(5)	(9)	(7)	(60)
Standard Error	23.3	6.7	17.5	18.3	6.7	11.7	16.5	14.8
Fawns 4-8 weeks old:								
Mean	56	43	-	50	45	-	61	53.2
(sample size)	(12)	(11)		(11)	(11)		(24)	(69)
Standard Error	4.3	4.8		6.9	5.3		3.1	2.3

Among adult does analysis of variance indicated significant heterogeneity in suckling bout duration for fawns at 4-8 weeks old in comparisons across parks (Table 4.8; $F_{4,64}=2.74$, $p<0.05$); pairwise tests show these summer differences to arise mainly from the longer bouts observed in park 'K' than at parks 'B' and 'I'. Some further data on suckling bout duration were recorded later in the year during observations of the rut (late October) in two parks, at which stage the great majority of fawns will already have been over 3 months old. Pooling data for all bouts seen in October within both parks, irrespective of maternal- or fawn-age, average bout lengths had fallen to 34 seconds (range 15 to 43) and 49 seconds (range 24 to 85) in parks 'B' and 'G' respectively ($t_{11,23}=3.54$, $p<0.002$). Thus, while differences between populations during the first two months of lactation were only slight in most cases, the later result indicates that does in park 'B', where some of the lowest mean live weights and growth rates were recorded during this study (see Chapter 3), may start to wean their fawns earlier than in park 'G'. This conclusion, however, depends on two major assumptions. Firstly, that the shorter suckling bout duration is not compensated for by higher frequencies of suckling, and secondly, that duration of suckling bouts provides a good index of actual milk yield, at least for fawns of comparable age. Neither of these assumptions were possible to test during the current study, although Lent's (1974) review of various ungulate species does suggest that reductions in suckling-bout duration are generally accompanied by decreasing daily frequencies of suckling.

4.2.5 Between park variation in fawning success

Results presented in this chapter so far have all been based on the eight 'core' parks where I was able to undertake field studies of reproductive success by means of direct observation and handling of individually recognisable deer. Across this range of eight sites no significant linear correlations could be shown of fawning rate with mean live weight (yearlings or adults), or with simple stocking density [SSD] or grazing density [GAD] ($p > 0.1$). The failure to show significant relationships here is perhaps not surprising in view of the consistently high reproductive rates of females described above for most of these parks. However, lower reproductive rates were known to be attained among various other British park fallow herds. In order to extend the analyses to include such populations, data on fawning rates were extracted from herd records made by park rangers (see 2.7) in a number of additional parks. Parks were included here if census figures for the four years (1986-89) provided a breakdown into fawns, does, yearling males and adult males, as well as information on numbers of animals found dead or culled. Although such censuses seldom distinguished yearlings from adult females, they did allow calculation of the overall percentage of females of breeding age which had produced fawns. In combination with data on the 'core' study parks this provided information on annual reproductive rate for 4 years for each of 13 parks, which could be evaluated against a series of population, climatic and management parameters (see Table 4.9).

Analyses described below were carried out firstly using each year's record separately for all parks, thus providing 52 park-years. As such analysis may (through replication in successive years) overemphasise those features of a park or population that are unchanged between years or not independent of previous values, analyses were then repeated using the mean of each parameter over the 4-years in each park.

Correlation analyses between the population fawning rate and female body weight[1] remained non-significant even for this larger sample of parks. Similarly, no significant association was found neither with the total stocking density (SSD), or grazing area density (GAD). Amount and quality of **winter** feed supplements provided in relation to stock numbers, which in Chapter 3 were shown to be strongly

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[1] Where values of live weight were not available from catch-ups whole-carcase weight (total weight less bleedable blood) was substituted.

Table 4.9 : Correlation coefficients between population or management variables and Fawning-success in park deer. The mean and range of parameters over all park-years included (4 years * 13 parks) are also given. Results are shown from Rank-Correlation (Spearman's) analyses, and/or Mann-Whitney U-tests, using i) all park years individually and ii) park means over four years 1985-89.
(* $p<0.05$; ** $p<0.01$; *** $p<0.001$; NS not significant [one-tailed])

	Min.	Max.	Mean	(i) All park years	(ii) Average per park over 4 years
Fallow Fawning Success (%)	**41**	**96**	**72.5**		
Winter stocking density (mean stock units per ha)	0.5	8.2	3.3	R_s = 0.18 NS	R_s = 0.22 NS
Grazing density (mean stock units per ha. pasture)	0.7	11.5	5.4	= 0.08 NS	= 0.03 NS
Daily ration of supplementary food over winter					
as ME [MJ per animal]	0.1	26.7	6.1	= 0.45 ***	= 0.46 NS
and crude Protein [g per animal]	1.2	394	69.5	= 0.56 ***	= 0.63 **
Mean weight (within a park) of					
adult fallow doe (liveweight: kg)	34.7	48.9	42.1	= 0.12 NS	= 0.06 NS
yearling fallow buck (liveweight: kg)	35.3	55.9	44.2	= 0.39 *	= 0.42 NS
Mean monthly temperature (°C: Nov-March)	1.7	6.9	4.9	=-0.12 NS	=-0.36 NS
Total winter precipitation (mm: Nov-March)	167	747	345	= 0.18 NS	= 0.20 NS
Coldest mean monthly temperature (°C: Nov-March)	-0.5	7.1	2.8	=-0.01 NS	=-0.09 NS
Mean monthly temperature (°C: May & June)	9.7	17.5	12.8	=-0.12 NS	=-0.16 NS
Total precipitation (mm : May & June)	70	306	127	= 0.14 NS	= 0.45 NS
Total number stock units (overwinter)	39	1284	443	=-0.53 ***	=-0.56 *
Percentage of park area open to public	0	100	46.3	=-0.39 **	=-0.50 *
Level of public use [scale 0-9]	1	9	4.4	=-0.54 ***	=-0.61 *
or				Mann-Whitney U-test :	
Low / High disturbance : [below / above code 5]				Z= 1.98 *	=-1.17 NS
Deer species: [fallow only, red+fallow]				Z= 5.10 ***	= 2.64 **
Other stock (e.g. cattle, sheep): [present / absent]				Z= 0.93 NS	= 0.40 NS

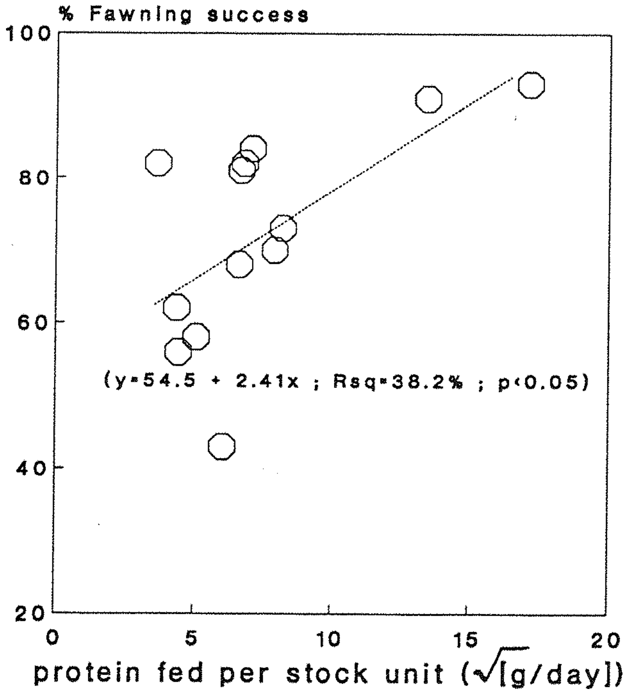

Figure 4.5 : Plot of fawning success in a range of fallow deer parks during 1988, against √(crude-protein) content of supplementary feed provided the previous winter. Fawning success rates shown here are based on mature does of all age classes combined in each site.

correlated with body weights, did also reveal significant direct correlation with reproductive rate ($p < 0.01$) here; the strongest associations were obtained with the amount of crude protein provided per deer in supplementary feed (Table 4.9), while correlations with metabolisable energy content of the feed were also significant. Hartfiel (in Reinken 1980) estimates the winter crude protein requirements of a mature fallow doe as 100g per day; signs of a fall off in reproductive rates during the present study were noted in parks providing less than 40g of crude protein per animal per day in the winter feed rations (Fig. 4.5).

A number of negative relationships concerned measures of public access, and also the presence of red deer in the parks in addition to fallow. Fawning rates show highly significant inverse correlations with the proportion of each parks' area which is open to the public (Spearman's r_s=-0.39, $p < 0.01$), and also when parks are ranked on a subjective estimate of the degree of public disturbance. Among the 13 parks, five had large numbers of red deer present in addition to the fallow; reproductive rates of fallow in these mixed populations were consistently lower than in pure fallow parks (Mann-Whitney U-test: z=2.6, $p < 0.01$). The parks carrying mixed deer herds were mainly those which also had extensive public access, and hence which of the two effects is the more important in relation to reproductive success remains difficult to resolve. An answer may lie in the fact that, although fallow fawning success showed no significant association with density, a negative effect was noted with increasing total stock units (that is irrespective of the park area available to them) in a park. This effect remained significant even when each **red deer** present was counted merely as one (rather than the usual 2) stock units; fawning success was, however, not correlated with the total herd size of fallow alone. This suggests that red deer introduce competitive effects, exceeding those expected through the simple increase in overall population size or stock unit density caused by their presence.

The relationships described in this section were generally significant both when using the average value of each parameter per park for the four years, as well as when using all park years as independent data points. While statistical assumptions necessary for application of more powerful parametric tests could be justified for a number of the parameters tested, no additional relationships were supported by such methods; coefficients and significance levels presented are therefore those applying to non-parametric tests throughout Table 4.9 .

4.3 Discussion

The high rearing success rates exceeding 0.9 offspring per mature doe, which were recorded in **some** park fallow populations during this study, show these to be reproducing at close to their maximum potential. Fallow deer usually give birth to a single fawn. The occurrence of twin-foetuses in culled pregnant does has been assessed by a number of workers at under one percent (Harrison and Hyett, 1954; Chapman and Chapman, 1975; Ueckermann and Hansen, 1983) each study being based on over 200 individuals; the incidence of surviving twins are likely to be lower still. Reports of populations with higher twinning rates are largely unconfirmed (Ueckermann and Hansen, 1983), and possibly influenced by inconclusive observations of two fawns seen following or attempting to suckle from the same doe. Pregnant fallow fawns also only occur extremely rarely (see below), and hence the potential to exceed 1.0 offspring per female (>1 year old) is very low.

Despite being kept at far greater stocking densities (2 to 6/ha) than those experienced by most wild or feral deer (< 0.5/ha), the average reproductive performance of deer in our study parks overall also compares very favourably with such data as is available from **wild** populations (Baker, 1973; Chapman and Chapman 1975; Sterba and Klusak 1984), and tends to be rather better than that at more intensively managed deer **farms** (Asher 1985, 1986; Vigh-Larsen, 1988), (see Table 4.10). While conception rates recorded for farmed fallow are often quite high, Asher's (1986) survey of New Zealand farms reports abortion rates ranging from 0.5 to 5.7 %, and early fawn mortalities exceeding 13 % in every year, leading to rather low rearing success in many cases.

Body condition

Studies on a variety of species lead us to predict that any effects of resource limitation on female reproduction will be seen first amongst those animals which are at the greatest competitive disadvantage, that is in particular pubertal individuals (e.g. horses : Welsh, 1973; 1975; sheep: Gunn, 1977; reindeer: Reimers, 1983; red deer: Mitchell, 1973; Ratcliffe, 1987; and see reviews by Sadleir, 1969; Hanks, 1981). Our results for fallow deer fully support such findings: a much wider range of fecundity was seen amongst yearlings than adults from different parks, and yearling reproductive rates were lowest in those parks showing lowest mean body weights.

Table 4.10: Comparison of Fawning and Rearing rates recorded among emparked, farmed and wild fallow deer. (figures given in brackets are pregnancy rates determined from post-mortem inspection of carcases, in cases where actual fawning data were not available)

	Number of sites monitored	Number of Does	Fawning rate %	Rearing rate %	Fawn Mortality %
Deer Parks					
Langbein (1990) : (this study 1986-89)	8	685	87.0	83.1	4.4
Chapman & Chapman (1975): (Richmond park - England)	1	113	(88.5)	-	-
Wild populations					
Chapman & Chapman (1975): (New Forest - England)	1	47	(89.0)	-	-
Baker (1973): (Blue Mountains -New Zealand)	1	70	(89.5)	-	-
Deer Farms					
Asher (1987) (New Zealand 1981-84)	3	668	91.6	75.6	16.2
Vigh-Larsen (1988): (Denmark 1986-87)	4	272	80.1	62.9	21.6

A threshold winter live-weight at which 50 % of yearling does are likely to produce fawns could be calculated to lie close to 32 kg. This is in general agreement with English (1984) and Asher (1986) who suggest that oestrus activity in yearling does on fallow farms in Australia and New Zealand commences at 28-30kg, and Vigh-Larsen (1988) who recorded a 50 % yearling fawning rate on a Danish farm where yearlings averaged 32.6 kg live weight at the end of winter. The level of these thresholds is surprisingly low, as equivalent weights have been recorded by us even for many female fawns at only 6 months of age in some parks (see Table 3.1a). However, fawn pregnancies were never observed during the present study, and although some such pregnancies have been reported in the past (Ueckermann and Hansen 1983, Asher 1985), these are clearly rare events everywhere.

Asher and Adam (1985) found birth weights of fallow fawns to be generally of the order of 10% of the mother's body weight in the case of adult dams, but a lower proportion (ca 8.5%, Asher pers. comm) for yearling dams. A yearling dam conceiving at our 32 kg threshold weight would accordingly be predicted to produce a fawn weighing around 2.7 kg. Only three live, but 6 dead fawns weighing less than 3 kg were found during this study, suggesting that such light fawns will have a very low probability of survival. Similarly, Asher and Adam for farmed fallow found mortality among fawns <3kg birth weight to be 67%, compared to 15% among those >3kg. Data for Soay sheep on the island of St. Kilda, Scotland, indicates that there amongst lambs of equally low birth-weights those with the heavier ewes as mothers will have higher chances of survival (Grubb, 1974), again accentuating the reproductive advantages of adults over yearlings.

Considering the low ovulation threshold weight for yearling does it is not surprising that a similar threshold could not be identified amongst our adult does, of which less than 1 % weighed under 32 kg during winter. Indeed for other species it has been suggested that such thresholds for adults lie in any case lower than for yearlings (Ratcliffe, 1987; but see also Albon et al., 1983). Such lowering of ovulation thresholds would fit in well with the greater ratio of maternal-weight : offspring birth-weight of adult does discussed above; i.e. Asher's figures (above) would suggest that an adult, in contrast to a yearling doe, weighing just under the threshold of 32 kg would still be likely to produce a viable fawn weighing over 3 kg at birth. (However, having seen plenty of undernourished deer, I would call into question whether an adult fallow doe of under 32 kg remains a viable entity herself, and surely due to its greater skeletal size such an adult would in fact be of poorer 'condition' than a yearling of equivalent weight). In practice average weights of adult females ranged from 36 kg to 49 kg between park populations (Table 3.1a), and adults were generally close to 10 % heavier than yearlings in each park. The average weight even of yearlings only fell below 33 kg in one of our parks, this being indeed the only site where fawning success was less than 50 % for that age-class in all years. Thus, although the consistently lower fawning success rates recorded for yearling than adult does confirm that resource limitation is acting in the same manner in fallow deer as has been shown in other ungulates, resources in most of our main study parks seem to have been at levels at which they are only just beginning to have a limiting effect on reproduction.

Costs of Reproduction

Milk does were also shown to have somewhat lowered reproductive rates, but only in those parks exhibiting below average body weights. Considering the very wide variation in female body weights between sites, these differences were again of a surprisingly small order when compared to, for example, the clear differences in fecundity shown between yeld and milk hinds for moorland red deer (Mitchell et al. 1976, 1977; Clutton-Brock et al. 1982). While fawning success amongst adult fallow does was not highly variable, the growth rates of offspring did vary considerably between the sites (see 3.4); this at least in part is likely to be due to differences noted between parks in the duration of strong lactation, (as indicated by differences in the decline of suckling bout lengths) and weaning times.

It seems probable that milk does in our poorer populations are able to ensure attainment of body weight thresholds for ovulation during the rut by weaning their fawns earlier if necessary. Fawns from a number of parks weighed in September were noted to have already achieved live weights of over 18 kg at that time; based on our poorest populations, fawns weighing just 18 kg at the beginning of winter have high chances of overwinter survival. Does may thus derive a greater increase in their reproductive success by ensuring a further conception through weaning their fawns, than they would gain from continued high investment in their current fawns once these already have a reasonable good chance of survival. Fallow does of superior condition on the other hand should be able to afford to continue to suckle young during pregnancy. Thus in park 'K' (x live weight 46 kg) many were found to be still strongly lactating when handled in early March, whereas in park 'B' ($\bar{x}$ weight 39 kg) more than 50% of does (excluding yeld animals) had already stopped lactating at the end of December, and none were lactating at a catch held in park 'B' at the end of February.

White (1990) suggests that in fawns close to weaning, rumen digestion supports maintenance requirements, while milk nutrients escaping modification by rumen fermentation are preferentially used for growth. If offspring are able to obtain most of their maintenance requirements from their own grazing activity well before they are weaned, the high protein supplement available to them from milk from mothers who are able to support continued lactation thus will allow them to gain a major growth advantage over young already weaned. The presence of a mechanism for early weaning is not difficult to visualise: thus lactation may stop if body weight falls close to the threshold for ovulation, while animals staying well above such levels can safely continue to invest in their current offspring without greatly increasing risk of failure to conceive. In northern red and reindeer populations, yeld females tend to be a much more common occurrence (Mitchell et al., 1976, 1977; Clutton-Brock et al., 1982; Reimers, 1983; Skogland, 1985) than shown in the present study for fallow deer. Females in these species may not have this option of early termination of parental care in favour of increasing their chances of renewed conception, partly because of the larger final body size and hence longer requirements of young for parental care, and also because of the earlier rut in these species.

Previous workers have indicated that threshold weights for reproduction themselves may alter under conditions of rising density or resource limitation (Albon et al. 1983; Ratcliffe 1987). Tyler (1990) shows that very heavy Svalbard reindeer often fail to conceive even when fat reserves exceed 17 % of body weight. We might therefore postulate that in circumstances where survival of young which are weaned early is reduced sharply (e.g. high density), sufficient reserves do need to be present to ensure continued lactation, in addition to those required for maintenance of pregnancy after conception.

The practice of 'flushing' of ewes to increase nutritional levels before mating (see e.g. Flowerdew, 1987) is known to result in an increase in ovulation rate as well as heightened proportion of twin births; similar results are also reported for whitetailed deer in contrasting habitats in North America (review by Sadleir, 1969). In most of our parks (and of course also in wild populations, but rarely on deer farms) a flush of high protein feed becomes available naturally during the often extensive seed fall associated with the mature oak, *Quercus spp.*, and chestnut, *Castanea spp.*, trees characteristic of traditional British deer parks. This may well be a factor contributing to the high reproductive rates recorded in our parks.

Age

Yearling fallow even in our 'heaviest' herds conceived and produced their fawns significantly later than older does. A similar delay in parturition of farmed red deer yearlings was observed by Hamilton and Blaxter (1980). Previous work on fallow, however, had suggested no difference in time of oestrus to occur if yearlings were kept together with older does. Asher (1986), on studying dates of first oestrus of 47 yearlings kept together with 17 adult does, found no significant difference between the two groups. A difference in fawning dates of yearlings and adults had been found on some northern New Zealand farms (Asher and Adam, 1985), but as yearlings were raised separately from older does in all these cases, Asher attributed the delay in conception dates to this variation in management. The clear differences in parturition and conception dates shown by our studies between yearlings and adult does, which are kept in entirely mixed age/sex herds, indicate that these differences are more fundamental, and suggests that pubertal does are likely to be less responsive to environmental stimuli (e.g. photo period, or priming odours) for the induction and synchronisation of oestrus than adult animals. Alternatively ovulation in yearling females might be delayed due to 'social stress' accompanied by increased adrenocorticotrophic hormone and secretory activity of the adrenal cortex (Christian 1965); thus Ozoga and Verme (1986) suggested that whitetailed deer fawns as well as yearlings may exhibit delayed oestrus activity due hormonal imbalance as a result of maternal domination. A delay in the attainment of the critical body weight thresholds for ovulation seems a less likely explanation of delayed conceptions, especially since Asher's work has shown no apparent relationship between the pre-rut liveweight and date of first oestrus for 16-month old does.

For red deer on the Isle of Rhum it has been demonstrated that a two week delay in birth dates had a significant detrimental effect on the survivorship of calves through the following winter (Clutton-Brock et al. 1987). The delay in birth dates of fawns born to yearling mothers demonstrated here (of on average 11 days) may on its own not decrease their chances of survival significantly, given the more temperate conditions of England. However, combined with the lighter birth weights also shown for fawns born to yearling mothers, it puts them at a clear disadvantage when compared to fawns born to adult does. In our park herds (where, in contrast to many farms, fawns are not separated from the remainder of the herd for weaning) fawns which enter winter relatively light have been found unable to compensate for such differences in relation to heavier cohort members during the following year (see Fig. 3.6). Such long-term effects of 'late' and 'light' birth thus suggest that not only survival but also the reproductive chances of fawns born to yearling mothers are likely to be impaired.

A further difference in the success of fawns may relate to the maternal behaviour and lactation rate of the dams. Suckling bouts observed of fawns with 'yearling' dams during this study were on average shorter than those with adult does (for fawns < 4 weeks old, as well as those > 4 weeks old), although these differences were not statistically significant. In contrast, Cockerill (n.d., in Clutton-Brock et al. 1982), found suckling bouts involving first-breeders to be longer than those of other hinds. Gauthier and Barette (1984) found that the reproductive experience of does of both fallow and white-tailed deer suckled their fawns more frequently than did older others, although no differences in mean suckling bout duration were shown. Although suckling rates are difficult to translate directly into milk yields in free living mammals, Sadleir (1980) showed milk yield of a captive black-tailed doe that produced twins in both years, was over 20% higher in her second lactating year. Studies showing higher frequencies of suckles from young does may thus reflect lower rates of milk let-down.

Langenau and Lerg (1976) attributed increased juvenile mortality observed amongst whitetailed deer at high density to the fact that undernourished females were less attentive to their young, thus making the latter more prone to predation; Ozoga and Verme (1986) suggest that maternal age may influence rearing success in the same manner.

In addition to any effects of late parturition dates on off-spring, Clutton-Brock et al. (1983) suggest that for red deer future reproductive performance of the mother is related to the previous year's conception date, with "a 1% decline in fecundity for every day's delay in the conception date of the previous calf". A similar effect could not be shown here for fallow. Fecundity of two-year old fallow does in our studies was generally as high as that of older does, despite their later parturition dates as yearlings. In fact an advancement, rather than a delay, in the mean parturition date in successive years could be demonstrated for particular cohorts; for example in Park 'G' the median parturition date for 1985 born does (n=48) was 23rd June in 1987, and 20th June in 1988.

Offspring Sex ratio

Ratcliffe (1987) for Scottish red deer found that high performance populations tended to have lower foetal sex ratios (female : male), although sex ratios did not in fact differ significantly from parity in any individual population. Birth sex-ratios in our study parks showed no significant linear relationships with either density, reproductive rate, or body weights across the range of sites. However, the most strongly female biased sex ratio (2.7:1 ; $p < 0.05$) was reported in that site were the lowest mean female liveweights were recorded at any time during the study. It seems likely that deviation from the 'normal' birth sex ratio is related to certain condition thresholds below which implantation failure, abortions, and neonatal mortality of males will increase. Thus for example in rats, *Rattus norvegicus*, reduction of food during pregnancy to starvation levels resulted in the resorption of embryos or still births (Russel, 1948). It had been hoped that during this study it would be possible to quantify differences between conception rates and actual birth rates. Unfortunately it has not yet proved possible to analyse the blood samples which were taken for pregnancy determination during live capture exercises; however, considering the very high birth rates recorded results could in any case only have turned up very few pre-partum losses.

Trivers and Willard (1973) speculate that mothers in poor condition should 'play safe' by producing 'less-costly' female offspring, which would suggest that yearlings and also very old animals might tend to avoid raising males. However, evidence for this concept is conflicting, as several studies provide evidence that malnourished deer tend to conceive a surplus of males (McCullough 1979; Skogland 1986; Verme and Ozoga 1981; Verme 1989), while others suggest the direct opposite (Clutton-Brock 1982; Clutton-Brock and Iason 1986). Clutton-Brock et al. (1984, 1985, 1986) develop the idea further based on studies of red deer, where they found that the balance between the likely success of a male and female offspring shifts dependent on the dominance rank of the hind. Thus, above a certain maternal rank sons outperformed daughters (in terms of LRS) while below this daughters did better than sons. Such an effect would explain the fact that male biased birth-ratios continued to be maintained in some of our low performance populations, where the majority of yearlings tended to fail to produce young at all although adult 'dominant' females continued to perform well.

Competition and disturbance

Does in parks which carry substantial numbers of red deer in addition to fallow were seen to have significantly lower fawning success than observed in 'pure' fallow parks. As this effect was not explained by the resultant increase in stocking density alone, it is possible that some competition is occurring between the species. Studies of competition in natural deer populations have generally shown wide ecological separation between coexisting deer species at least for most of the year (Hanley 1984; Jenkins and Wright 1988; and see recent review by Putman, 1988). Jenkins and Wright's work on whitetailed deer, wapiti and moose in Montana, however, also showed that during severe winters habitat selection by wapiti changed so as to cause far greater than usual overlap with whitetails; they concluded that while wide separation may occur at most other times, a high potential for interspecific competition does exist between all three species during harsh winters coupled with resource limitation. In a multi-species system in the New Forest, England, containing cattle and ponies in addition to fallow, roe and sika deer, Putman (1986) showed quite high degrees of niche overlap in habitat use and food usage between fallow and sika deer throughout the year, while food overlap with roe deer also reached significant levels in some winter months. Circumstantial evidence for competitive exclusion of red deer by fallow is given by Kean (1959) who notes that fallow have remained the dominant species in areas (such as for example Blue Mountains in New Zealand) where they have established high numbers before coming into contact with red deer.

In 'mixed' fallow and red deer parks used during the present study, the two species exhibited a high degree of spatial separation as well as clear differences in habitat use (Putman and Langbein, 1990). As a general rule, fallow herds tended to use a smaller proportion of a park's area than did the red deer; that is certain grazing and sheltering areas were used almost exclusively by red deer, but few were used only by the fallow. Contrary to these results, the smaller species (fallow) might be expected to outcompete the larger under the high density conditions typical of parks, because of their closer-feeding habit (e.g. see Challies 1985; Illius and

Gordon 1990). However, direct agonistic encounters with red deer may deter fallow from preferred areas in the parks; the frequent aggressive interactions between the species which are observed at feeding sites when supplementary food is provided during winter are perhaps the most obvious example of such effects. Observation of deliberate trampling of new-born fallow fawns by red deer hinds has been reported by some park keepers, and may be another contributory factor to explain the reduced reproductive rates of fallow recorded in some mixed parks.

The consequences of public access to some parks may manifest themselves in a similar manner to the competitive effects described above; that is exclusion from preferred areas for shelter or feeding (though in this case generally restricted to day-time). An as yet unknown factor in relation to the reduction in fawning success noted in 'public' parks is the number of fawns which may be lost as a direct result of disturbance (e.g. by dogs) during or close to parturition. Out of a sample of ten fawns tagged in park 't' all but one survived through to the next spring (Putman and Langbein, 1990). Tagging of fawns, however, necessarily took place at least some hours (usually 1-2 days) after birth, thus possibly missing that early period when dog-kills or mismothering would be most likely to occur. The question of early losses in these parks will be difficult to resolve until a good proportion of adults deer can be identified individually, as was possible in our core study parks.

Conclusion

Reproductive rates of fallow recorded during this study in British parks were generally higher, and the summer fawn losses lower, than those reported on many deer farms (Asher and Adam 1985, English 1984, Vigh-Larsen 1988). Vigh-Larsen emphasises that the unsatisfactory reproductive success of fallow recorded on Danish farms seems to be largely due to a lack of adequate supplementary feeding of deer kept at very high densities, as well as insufficient provision of shelter on farms in general. Differences in reproductive rates between our park populations were also seen to be closely related to levels of nutrition, effects of resource limitation being shown most clearly by lowered fawning success amongst yearling does. Winter body-weight thresholds at which 50 % of yearlings produced fawns were determined as 32 kg. Yearlings which did reproduce were seen to face further disadvantages, as they tended to produce lighter off-spring than adult mothers, as well as fawning on average 11 days later. The time-scale of this study so far precludes comparisons of the reproductive success of offspring born to yearlings and adults. Differences here should again be emphasised during harsh conditions limiting the growth of offspring. The very high reproductive success achieved by yearling fallow does in certain areas clearly demonstrates the potential for rapid expansion of populations under optimum conditions, while the great sensitivity of yearlings and their offspring to resource limitation should stem population increase as soon as sub-optimal conditions reoccur. From a management point of view in parks it may be preferable to concentrate any selective cull amongst the yearling does, ensuring that only yearlings of very good body weights, and hence high chances of producing good offspring, are allowed to go forward to become part of the main adult breeding herd.

The shelter requirements of newly born fawns in summer (see Ch.4), as well as those of the remainder of the herd during winter are more likely to be met in parks, which in contrast to farms generally give over extensive areas to rough grassland, bracken and woodland. In conclusion, studies in parks clearly demonstrate that fallow deer can continue to attain close to their maximum reproductive potential when kept at high stocking densities (> 5/ha overwinter), as long as such high densities are compensated for fully by supplementary feeding and provision of shelter in those months during which grazing conditions do become limiting.

Chapter Five

REPRODUCTIVE BEHAVIOUR AT THE RUT

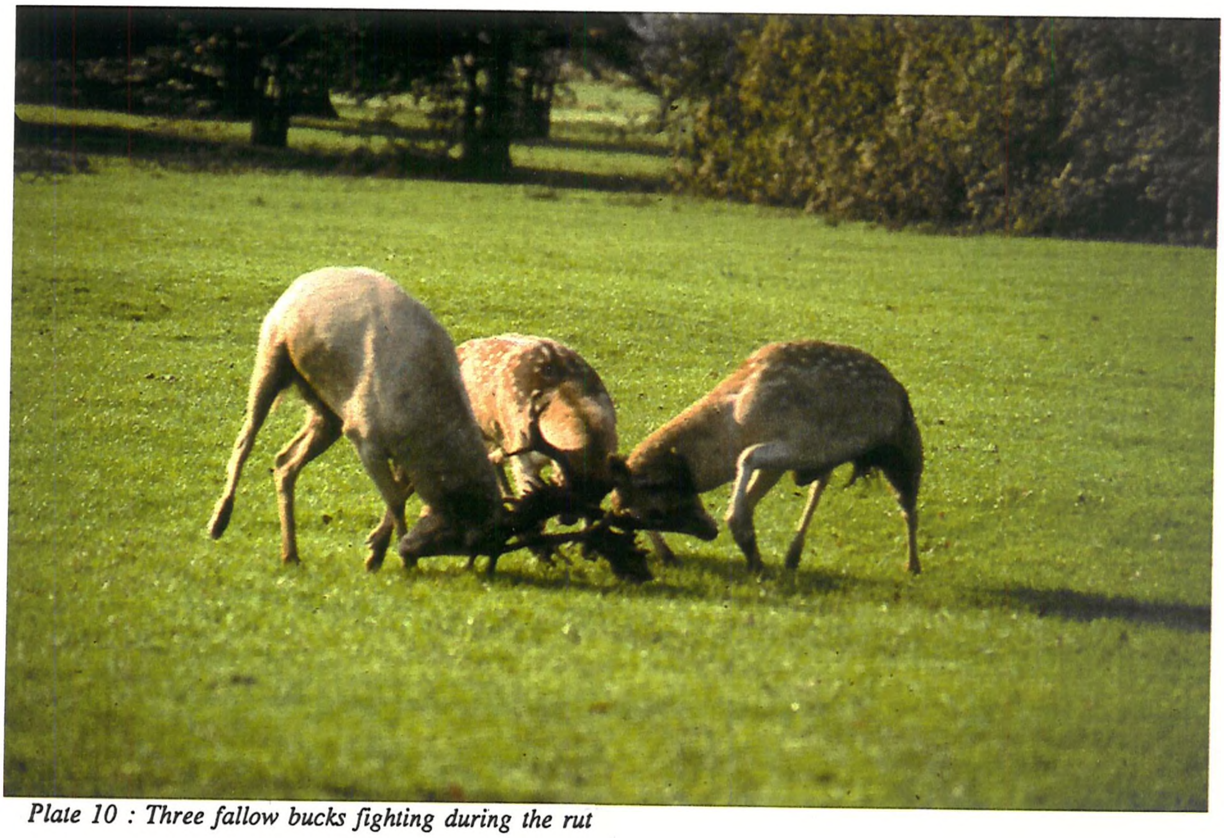

Plate 10 : Three fallow bucks fighting during the rut

5. REPRODUCTIVE BEHAVIOUR AT THE RUT

5.1 INTRODUCTION

The results presented in the previous chapter illustrate wide variation in reproductive success of fallow deer with respect to resource availability and age. Much of this variability can be explained in terms of differences in the body weights achieved by females, condition being closely linked to their ability to conceive and rear young successfully. Reproductive success may also, however, be influenced by the behaviour of the animals, ranging from their competition for mates and appropriate timing of mating activity, to parental care once the young are born. Such reproductive behaviour may not only be influenced by resource limitation, but also by vegetational habitat, climate, the presence of predators or human disturbance, and differences in the herd size and social structure. Whereas aspects of maternal behaviour have already been considered in the previous chapter, the aim of the present Chapter is to address the remaining question : Does male and/or female behaviour during the mating season vary between populations, and if so, does this relate to differences in density ?

The reproductive activity of mammals living in seasonal climates is generally timed in such a way that births occur at a relatively favourable time for nutrition of the lactating female and the weaned young, thereby increasing their chances of survival. Most births are confined to spring or early summer across a wide range of those mammals of the northern hemisphere, which produce young only once a year (see Hoffmann, 1973); amongst these fallow deer in fact produce their young later than most, that is during June or July. The length of gestation for farmed fallow deer in New Zealand has been assessed as 234 days (SD 2.7d) (Asher, 1986), and was estimated in Europe as 229 days by Prell (1938). The **rut**, defined as the peak time for mating activity and conceptions, thus falls within October and early

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[1] *Plate 10 (previous page) Fights between three fallow bucks are not uncommon during the rut, and sometimes ensue when a fighting pair drift into the territory of a third buck.*

November. Females usually exhibit their first oestrus at that time, but in the absence of conception cyclic activity will continue throughout winter and into early spring, with reoccurrence of oestrus at 22.4 day (±SD 1.3d) intervals (Asher, 1986). Conceptions therefore can, and indeed sometimes do occur outside the rut (e.g. Fisher 1983, Sterba and Klusak 1984). For farmed deer Asher (1986) however, found 82 % of does to conceive at first oestrus, and only 13 % during a later cycle.

During the present study regular observations of reproductive behaviours concentrated on the rutting period, although some supplementary data collected at other times will also be discussed below.

The traditional view of rutting behaviour in fallow, reported in most published accounts for this species, is a mating system in which individual mature males establish non-contiguous mating territories referred to as "rutting stands", and attract females by auditory and olfactory cues (eg. Chapman & Chapman 1975). However, early on in the project during my first series of observations of the rut in the autumn of 1985, I was struck by the quite vast differences in the level of activity and range of behaviours exhibited by the deer even between park-populations. While in some study parks males did indeed establish 'rutting stands' as described above, in other sites none of the mature males defended territories, while in others again territories were defended but were far from being 'noncontiguous'. The highly aggregated mating territories in the latter system are in fact analogous to lekking, which has only been recorded in a small number of ungulates: Uganda kob, *Kobus kob thomasi* (Buechner and Schloeth 1965), topi, *Damaliscus korrigum* (Montfort-Braham 1975); Kafue lechwe, *Kobus leche* (Schuster, 1976), and white-eared kob, *Kobus kob leucotis* (Fryxell, 1987). Lekking in fallow deer has recently become a subject of considerable scientific interest, with reports becoming available since my own studies began of leks in wild as well as enclosed populations (Schaal, 1986; 1987; Apollonio et al. 1989; Langbein and Thirgood, 1989; Thirgood 1990), which now also include published descriptions of one (Pemberton and Balmford, 1987; Clutton-Brock et al., 1988) of the three lekking populations observed during this study .

The flexibility of the mating systems of fallow deer from park to park offers an opportunity here not merely to describe a wide range of different systems, but also to explore the factors of the populations' ecology which may be causing this variation, and any consequential effects on actual population reproductive success. Previous explanations of variation in ungulate mating systems have concentrated on inter-specific variation (Estes 1974; Jarman 1974; Clutton-brock et al. 1982; Bubenik 1985). Comparisons within a species, however, whether between populations living in different environments, or within populations in different circumstances, avoid the problems of major differences between species masking subtle responses to environmental variation (Jarman 1982).

Density, sex ratio, and age structure of the population might be expected to affect territorial behaviour, while habitat structure may influence mating systems through its effect on sociality, degree of aggregation, and defendability of reproductive territories. Thus the aims of this section are 1) to define more clearly the different types of mating systems exhibited by fallow deer in parks, 2) to examine which factors of the population structure and vegetational environment are most important in influencing the mating system adopted by the population, and 3) to assess the benefits and costs to males and females adopting different mating strategies. A preliminary analysis of these questions, and an evaluation of my observations in deer parks against parallel work by Simon Thirgood on a number of free-ranging fallow populations has now been published (Langbein and Thirgood, 1989). Below I now provide a more detailed account of results relating to observations of emparked deer.

5.2 RESULTS

During the breeding season field observations focused on 9 of the study parks throughout Great Britain (Table 5.1). Within this sample continuous woodland made up less than 20 % of the park areas in seven sites, and nowhere exceeded 45 % ; most of the remaining area in each case consisted of permanent pasture with small numbers of widely dispersed mature trees. Population sizes ranged from 40 to 1200 fallow on areas extending from 16 to 820 hectares, resulting in a range of densities from less than 0.5 to over 6 deer per hectare during the period of study. Behavioural observations were collected in the same manner in all 9 parks (for detailed methodology see 2.5). The short time-span of the rut necessitated that field-work input concentrated on a different sub-set of sites in each year; however, a minimum of three observation days were made during the rut in any year for which a park was included in any comparative statistical analyses (Table 5.1).

Table 5.1: Days of observation in individual study sites during October and November from 1985-88.

Study Site	Year	Observation days in autumn rut
A	1985	4
	1986	6
B	1986	6
	1987	6
	1988	6
E	1985	5
	1986	4(*)
	1987	-(*)
G	1987	9
	1988	10
I	1986	7
	1987	5
J	1985	4
	1986	3
	1987	4
	1988	3
t	1987	7
	1988	9
v	1987	5
	1988	9
w	1987	5
	1988	5

(*) Observations continued by L.A.R.G., Cambridge.

5.2.1 The range of observed mating strategies

Confusion in the fallow deer literature concerning the use of terms such as "rutting stands" and "harems" have made comparisons between published studies difficult. It is therefore useful here to start with a description of the major types of mating strategies observed in parks, providing a framework for comparisons between populations and years. Male mating 'strategies' (that is, behaviour patterns leading at least in some cases to copulations with females) are considered here as a continuum, arranged with respect to the degree and type of territoriality associated with them (Fig. 5.1). It is possible broadly to distinguish between those strategies in which multiple or single territories are held by males, and those in which no territoriality is exhibited at all. Definitions presented below were used to allow identification of further reference points along this continuum.

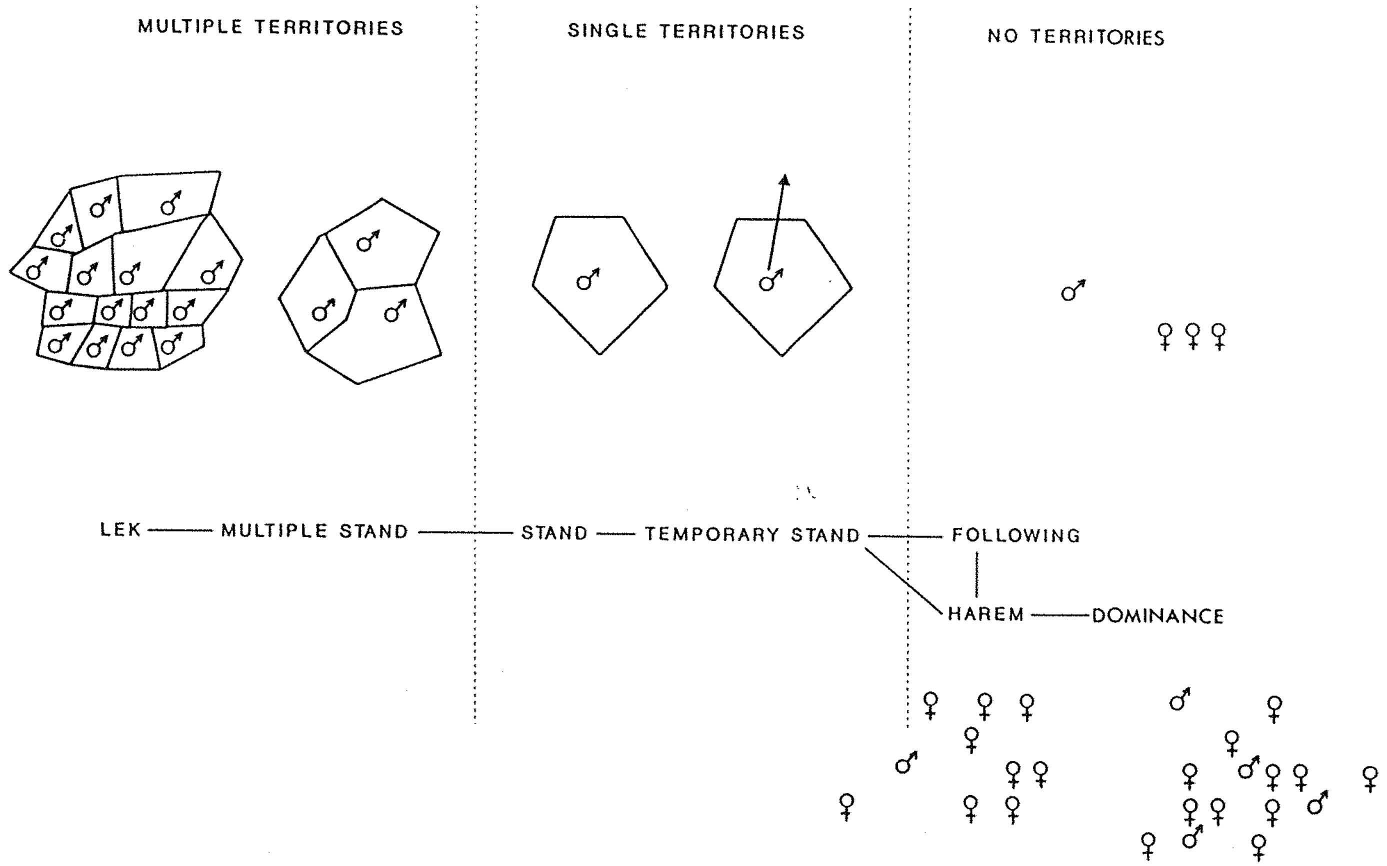
Territorial Strategies:

i. Stand:

The type of mating strategy traditionally described as "typical" for fallow deer (eg. Cadman 1966, Chapman and Chapman 1975) in which a single mature buck defends an exclusive reproductive territory against all other mature males for a large proportion of the day. Stands may vary greatly in habitat type, from open grassland to conifer thickets, and in size from 0.1 to 5.0 ha. In some cases they may contain feeding resources valuable to females, for example those stands which are situated under oak trees where females may forage for acorns; however many stands contain no obvious food resources. In a pure stand holding population reproductive territories do not abut onto adjacent territories, and may be clumped or widely dispersed in distribution throughout the populations range.

Some *Stands* were observed in most study parks, and formed the predominant strategy in parks 'I' and 'J'.

Figure 5.1 : Schematic view of the range of observed variation of fallow deer mating systems.



ii. Temporary Stand:

A similar strategy to the above but one in which the stand is only defended for a relatively small proportion, (that is only one or two consecutive hours), of the day. The stand holding buck will readily leave his territory, often in pursuit of females, or to take up an alternative stand in a different part of his range. Temporary stands often contain resources or are situated to intercept major female movement paths.

Temporary stands were the predominant strategy in parks 'A' and 'B', but were formed at some time in all 9 study sites. They occurred particularly around dawn and dusk, and seemed to be influenced by the daily feeding patterns of females. Temporary stands were frequently (but not always) situated in areas subject to extensive human disturbance in the daytime.

iii. Multiple Stand:

Reproductive territories of two or three mature bucks which are abutting but not overlapping. Such stands are not significantly reduced in size from that of a simple stand, but do not preserve the geographical separation from neighbours characteristic of that earlier strategy. Multiple stands may often be located on or near food resources, particularly so when they are only of a temporary nature, and females may visit multiple stands for feeding as well as reproduction.

Multiple stands were not found to be the predominant strategy in any park, and may possibly present a transitory stage in the development of one of the other systems described here. Thus, while in park 'B' a multiple stand was indubitably associated with a particular area of ground, in some ways the behaviour of the bucks here resembled the non-territorial Dominance-systems (see below) more closely than any of the territorial strategies; for example when a higher ranking male became alerted by courtship or mounting attempts taking place on an adjacent territory, he would usually come to displace (and sometimes literally exchange territories with) the current owner.

iv. Lek

Leks have been defined by Bradbury and Gibson (1983) as "assemblies of territorial males which females visit solely for the purpose of copulation". Males provide neither resources nor parental care and females have an opportunity for mate *choice. In fallow deer, lek breeding has recently been recorded in a number of populations (Schaal 1986,1987; Pemberton and Balmford 1987; Clutton-brock et. al. 1988; Apollonio et al. 1989; Thirgood 1990; and in this study in parks E, G, & J). In this study, fallow leks ranged in composition from 10-25 mature males, and were characterized by a reduction of individual territory size at the peak of the rut to as little as 5m*5m, and a high turnover of central territory ownership.*

Leks in parks were observed in open parkland (parks E and G) as well as in closed canopy woodland (park J). On all occasions when leks were observed in parks, lek-males accounted for significantly more matings than those adopting any other strategy.

Non-territorial Strategies

v. Following:

No territorial behaviour is exhibited by the buck, who follows individual does or groups containing reproductive females to achieve matings. Once female groups are located, there is little attempt to hold or herd them into a Harem (see below).

In parks this strategy was observed only after the main rut was completed. Males adopting this strategy were usually observed to closely pursue individual does exhibiting a late oestrus; continual harassment by the male often lead the doe to lie down and consequently become isolated from the group of animals she had been with. The 'following' male in such cases sometimes stayed close to the doe for several hours before copulation took place, or losing contact with her if the doe made a successful attempt at running off.

vi. Harem:

A group of females held by a single mature male for the purpose of obtaining exclusive mating rights. Other mature males are excluded from the group and the harem holder defends the females rather than a fixed territory. The harem holding buck will usually attempt to retain females within his group through extensive herding. (While some studies on fallow have also applied the term 'harem' the groups of oestrous females assembled within lek territories [e.g. Clutton-Brock et al. 1988] this term has been reserved here only for the non-territorial strategy described above).

vii. Dominance Group:

A multi-male mixed sex group in which one male is dominant over all others and achieves most matings. Subordinate males are tolerated in the group and there is a relatively low level of male aggression within the group, as compared to the other systems. No territorial behaviour is exhibited and the bucks move around the park with the relatively large feeding groups of females and fawns. The highest ranking male does attempt to keep all animals in a single group by occasional herding.

A clear distinction between Harems and Dominance groups on many occasions proved difficult in practice, as groups containing only a single mature male were not always challenged by any other males during the period of observation. Multi-male dominance groups on the whole were larger than harems, sometimes containing as many as 250 females and fawns. Within such large groups the sub-ordinate males which were tolerated in the herd usually mated only when the alpha-male was occupied simultaneously in a courtship or copulation with another female. More commonly when a sub-ordinate male attempted to mount with a doe in oestrus, the alpha-male would come to displace him from that area of the herd and take over the courtship of the doe concerned.

In most, if not all populations, a combination of these different **strategies** co-exist resulting in the population **mating system**. As indicated above, in park populations a single strategy could usually be identified clearly as being the most important strategy within the system, and bucks pursuing that strategy were responsible for the majority of matings. Other strategies were nevertheless exhibited alongside the predominant one during the rut itself, but their relative importance increased especially once the main reproductive phase had finished. Strategies thus varied not only between populations, but also through time; that is from the early stages of the main autumn reproductive period, through the peak of the rut, to post-rut reproductive activity during winter. Thirgood's work (in Langbein and Thirgood, 1989; and Thirgood, 1991) suggests that in wild populations several mating strategies may be of very similar importance even at the peak of rut.

5.2.2 Ecological factors influencing mating systems.

The common occurrence within park populations of mating systems with one clearly predominant strategy, combined with the relative ease in such populations of obtaining accurate measures of population parameters such as density and sex ratio, allow us to investigate in considerable detail the ecological factors which can influence mating systems.

For this analysis data were included from nine different study parks for which the mating systems were investigated for two to four years (1985-88 incl.). The ecological variables considered are listed in Table 5.2. Park-years were divided into three categories on the basis of the degree and type of territoriality of the mating system during the rut :

1. Multiple territories- lekking and multiple stands
2. Single territories- stands and temporary stands
3. No territories- harems and dominance

Statistical analysis

Differences between the three categories of mating system, in terms of single characteristics of habitat or populations were first tested using Kruskal-Wallis one-way ANOVAs (Table 5.2). Further univariate analyses were then carried out to make pairwise comparisons of the mating system categories for the same ecological variables (Mann-Whitney U-test, Table 5.2). Use of each park-year independently in analyses might over-emphasise those features of a park or population that are unchanged between years. In univariate statistical analyses a mean value for each parameter was therefore used, calculated from two years data for each park during which its overall 'mating-system-category' had not changed.

Linear discriminant function analysis (Norusis, 1985) was then used in order to assess which combination of ecological variables could best distinguish between our three mating system categories, given values for only a small number of variables. Discriminant analysis determines a number of linear combinations of variables, selecting coefficients such as to give the best possible separation between categories from the data provided. The goodness-of-fit of the model is estimated by comparing the total number for which category membership is predicted correctly, with the

Table 5.2 :
Univariate comparisons of population and habitat parameters between different mating system categories using mean values over 2 years per park from 9 parks.

		Territory System		
	Overall	Multiple vs Single	Single vs None	None vs Multiple
Total numbers	ns	-	-	-
Nos. of Bucks (> 4 years old)	*	ns	*	*
Nos. of Does (> 1 year old)	*	ns	-	-
Total density	*	*	*	*
Buck density (> 4 years old)	*	*	*	*
Doe density (> 1 year old)	*	*	ns	*
Sex ratio (Does : bucks >4 years old)	ns	-	-	-
Age structure of bucks (adult bucks/total bucks)	ns	-	-	-
Park area	*	*	-	*
Tree cover	ns	-	-	-

Overall comparison: Kruskall-Wallis one-way Anova; pair-wise comparison: Mann-Whitney U-test. (* : $p< 0.05$; ns : not significant).

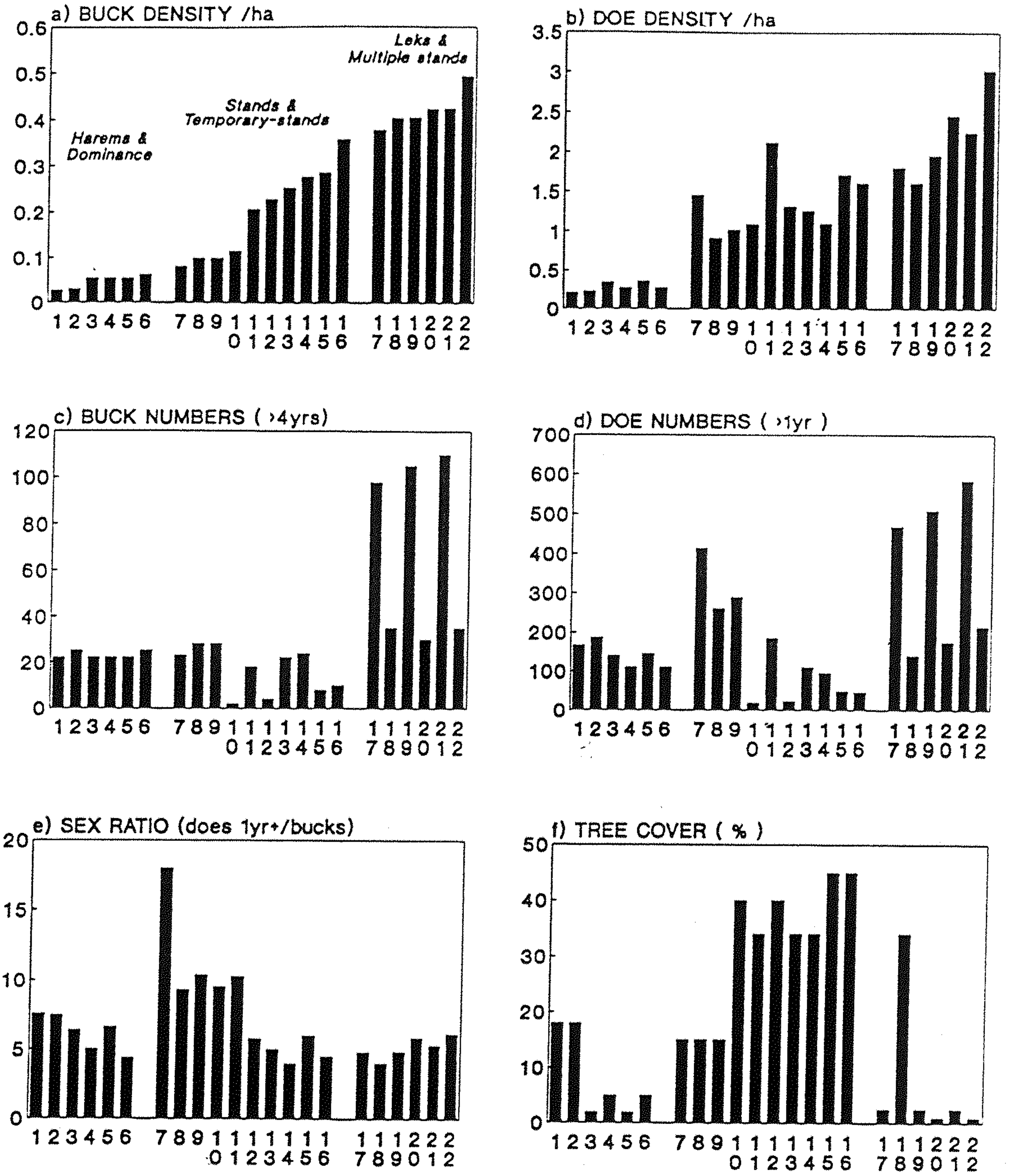
number which would be correctly classified by chance. This analysis was used here to suggest functions which might be used in future to predict the likely main mating system of other fallow populations.

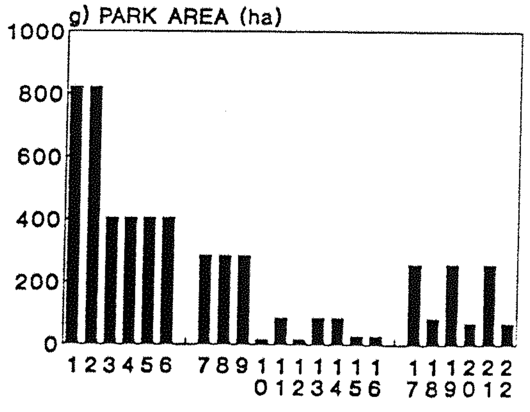
Univariate comparisons of mating systems and ecological variables

Single parameters showing significant differences ($p<.05$) in overall comparisons of mating system types were adult buck-density, adult doe-density, and total-density, as well as the actual number of mature bucks in the population, and total park area (Table 5.2). Most pairwise comparisons of different mating system categories also showed significant differences in these ecological variables (Table 5.2). While mean values were used in main analyses for the reasons outlined above, the considerable variability of some population parameters within sites between years (Figure 5.2) lends some validity to using park-years as separate data points. If this is done, total herd-size and numbers of adult females also showed significant differences in univariate comparisons, pointing to these as possible further important factors.

Surprisingly, differences in sex ratio were not significant in any of the above tests, sex ratio having been calculated as number of females per buck 1-year and older. Although fallow males reach sexual maturity as yearlings they are not usually able to compete for matings in the presence of 'adult' males until they are themselves fully grown at about 4 to 5 years. Sex ratios were thus recalculated as numbers of does per buck of 4-years and older, but no consistent relationships with mating systems were found with this measure either. Differences in the ratio of old to young bucks were also not significant between mating system categories.

In Fig 5.2a, all 22 park years have been arranged in order of increasing buck density. There is total separation along this gradient between the three main mating system types, with non-territorial systems occurring at low buck densities, single territory systems at medium buck densities, and multiple territory systems at high buck densities. A broadly similar relationship is shown with doe-density, with increased density associated with increased territoriality and the development of lekking (Fig 5.2b). There also appears to be a threshold level of approximately 30 bucks required for the formation of a lek (Fig 5.2c), although this may simply be an artifact of the three park populations in which lekking was observed. The results for doe numbers (Fig 5.2d) are ambiguous, great variation existing both between and





	Park	year	Mating sytem
1=	t	1988	Harem & Dominance
2=	t	1987	Harem & Dominance
3=	w	1987	Dominance
4=	v	1987	Harem & Dominance
5=	w	1988	Dominance
6=	v	1988	Dominance
7=	B	1986	Temporary Stands
8=	B	1988	Temporary Stands
9=	B	1987	Temporary Stands
10=	A	1985	Temporary Stands
11=	J	1988	Single Stands
12=	A	1986	Temporary Stands
13=	J	1986	Single Stands
14=	J	1985	Single Stands
15=	I	1987	Single Stands
16=	I	1986	Stands
17=	E	1987	Lek
18=	J	1987	Lek
19=	E	1986	Lek
20=	G	1987	Lek
21=	E	1985	Lek
22=	G	1988	Lek

Figure 5.2 Variation of population and habitat parameters in study parks, during years in which the fallow deer mating systems were studied. (All histograms arranged in order of increasing buck-density)

within categories. Little variation occurred in sex ratios with the exception of the single territory systems (Fig. 5.2e), and mating systems could not be separated on this variable. Single territory systems were associated with high cover availability (Fig. 5.2f), whilst non-territorial systems were observed only in parks of relatively large area (Fig 5.2g).

Variation of mating systems within sites

An example of the importance of buck density and number in influencing the population mating system was observed at Park 'J', where the mating system changed from year to year, reflecting the change in buck numbers in the population (Figs. 5.2c). In 1985 and 1986, buck numbers during the rut were low, 22 and 24 respectively, and a single stand system was observed. In 1987 however, the number of mature bucks was allowed to increase to 35, and a small lek of 10 bucks occurred in a woodland area of the park, as well as a temporary Multiple stand in the open. Convincingly, in the 1988 rut, with buck numbers once again reduced to 18, the population reverted to a single Stands system.

Although the gross mating system category was not observed to change in other parks, clear differences occurred in the degree of predominance of certain strategies from year to year. At Park 'B' in 1986, for example, most successful bucks confined their rutting activities to two or three stands. Temporary stands still predominated in 1988, but were held for briefer periods and many bucks also roamed widely, tending towards the non-territorial systems (see also Multiple stand - 5.2.1).

Discriminant analyses

Thus far the ecological parameters have only been considered in isolation. However, it is more likely that any influence on the population mating system will reflect an interaction of these various factors. The discriminant analysis introduced above was used to explore the ability of various combinations of the variables in Table 5.2 to allocate 18 'park-years'(using two years per site) correctly to the three mating system categories observed.

Total herd size, doe-number, and buck-number were strongly correlated with each other (Pooled within-group correlation >+/- 0.6), as were buck-density and sex ratio; only one variable from each of these correlated groups was included in any discriminant variable combination together with doe density, total park area, and cover. Several combinations of five variables entered step-wise into the analysis produced discriminant functions giving no misclassification of any park years and their mating systems. 100 % correct classification of our cases, that is 67 % better than would be expected by chance, could still be retained even when limiting the analysis to three variables; that is by using buck-density and cover together with doe numbers or doe-density. Greatest separation of mating systems using only three variables, avoiding any highly correlated parameters, was achieved by using the combination of buck-density, doe numbers, and cover, where the first discriminant function (Fig. 5.3) accounted for 86 % of the discrimination. The strong influence of density, and especially that of adult bucks on the mating system adopted, was already indicated by our univariate comparisons above. The combination of this with cover availability is less well proven at this stage, as our sample provides park sites with high cover availability only in conjunction with intermediate deer densities. However, the high level of accuracy in allocating correct group membership for our sample emphasises the level of significant difference between mating systems in relation to their associated buck and doe density, population size, and cover. The derived functions provide us with a good basis for predicting the likely type of mating system in unknown parks given only limited information on their character, although they remain to be tested for such cases not included in deriving the model.

The adult buck and doe numbers and densities (mean ± SD) associated with each major mating system category are summarised in Figure 5.4.

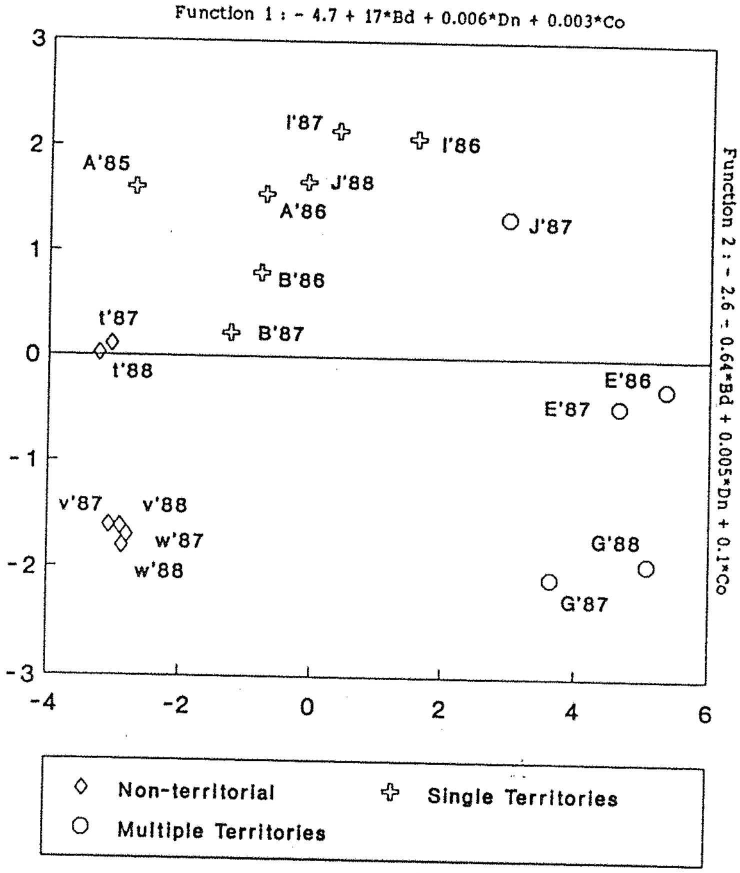


Figure 5.3 : Linear discriminant-function analysis using buck-density (Bd), doe-numbers (Dn), and cover-availability (Co) to separate mating system types. Lables show park codes and study years.

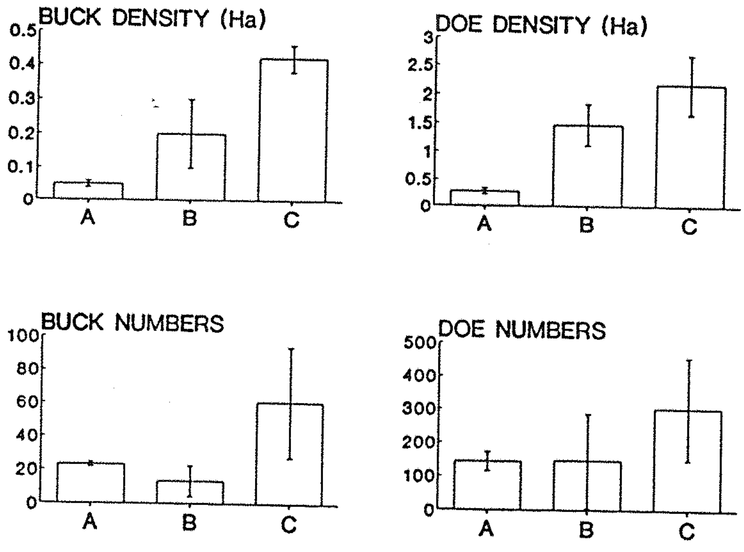


Figure 5.4 : Summary of ecological characteristics of mating system categories (x ± SD) from 9 parks over a 2-year period.
A: no territories, n= 6; B: single territories, n= 7; C: multiple territories, n= 5 .

5.2.3 Courtship, mating strategies, and costs and benefits associated with variation in mating behaviour.

Distribution of mating success amongst males

The success or benefit associated with different mating systems was considered firstly in terms of the distribution of successful copulations among mature males adopting the same or different mating strategies. Fallow bucks will usually attempt to mount a doe several times before successful intromission and ejaculation occurs; the final copulatory mount is however, very distinctive (see below) and only such copulations were recorded as 'successful'. Although only a proportion of all matings occurring during the rut were observed at each site, amongst these a single mating strategy clearly predominated, and must be assumed to have been the most productive in terms of achieving mating success there.

Only a small proportion of the adult bucks at each site achieved the majority of matings in any one population studied. Despite the occurrence of different mating systems between parks, however, this skew of mating success among successful males was very similar in all populations (eg. Table 5.3). Thus in the 1988 lek at park 'G', 34/51 observed matings were achieved by two bucks, although 19 mature bucks defended reproductive territories. Similarly, in a Temporary stand system at Park 'B', and a Dominance system at Park 't', a single buck was responsible for the majority of the matings observed (Table 5.3). In general, we may thus conclude that for bucks to maximise their individual reproductive success and attain a high rank in the skewed distribution of matings, different mating strategies are most appropriate under different environmental conditions.

Effects of female age on date of mating

A relatively high number of matings were observed in 1987 and in 1988 on the lek in Park 'G', where the great majority of females were also individually tagged and hence of known age. Even when the actual number embossed on an ear-tags could not be read during observations, does could nevertheless still be classified as being one-, two-, three-years or older, as tags fitted were colour coded for the year of birth. Matings observed during 1988 in Park 'G' are tabulated in Table 5.4, and show that of the first 24 matings seen only one involved a yearling female, while amongst the following 24 matings 10 involved yearlings (X^2=7.6, p=0.006).

Table 5.3: Reproductive success of bucks exhibiting alternative mating strategies within three different park years.

Buck name	No. of days observed on territory or in dominance group	Dates seen mating (Oct)	Highest mating rate achieved in 4 consecutive h	Total matings seen
Park 'G' 1988 (lek)				
C3	5	19	11	21
M1	6	15,16	7	13
W1	7	19	4	5
C4	7	15,22	2	4
B1	7	15,16	2	3
B92	4	19,20	2	3
C2	4	15	1	1
Yearling	?	19	1	1
(plus 12 bucks active on lek for 3+ days for which no matings seen and 16 bucks nonactive)				
Park 'B' 1987 (temporary stands)				
W63	6	21,25,28	5	7
W40	4	25	2	2
CC2	1	21	2	2
(plus 25 bucks for which no matings seen)				
Park 't' 1988 (dominance)				
MDL	6	21,24,28	1	3
CDL	6	26	1	1
MDB	6	31	1	1
CCB	6	8 (nov)	1	1
(plus 18 bucks for which no matings seen)				

Table 5.4 :

Details of matings observed on a lek in park 'G' during October 1988.
The number of pre-copulatory mount attempts observed, and the number of complete minutes which elapsed between the first mount and actual copulation are shown where available as indices of the duration of courtship. Ages of does were known in most cases from ear-tags, colour coded for the year of birth.

Buck name	Age of doe mated (years)	No. of Pre-Cop. mounts	Time from 1st to final mount (mins)	Time (GMT)	Date (Oct)	Time observed from
M1	2	6	4	10:03	15th	06:00
BL1	2	11	21	11:13	15th	06:00
M1	3	19	5	11:19	15th	06:00
BL1	2	3	2	11:24	15th	06:00
C2	>2		2	11:54	15th	06:00
C4	3	13	4	12:10	15th	06:00
C4	2			14:05	15th	06:00
M1	3			14:18	15th	06:00
M1	2	8	4	14:30	15th	06:00
M1	>2	9	7	15:57	15th	06:00
M1	>2	1	0	16:03	15th	06:00
C4	>4	6		16:29	15th	06:00
M1	2	38	28	16:38	15th	06:00
M1	>4	3	1	16:44	15th	06:00
M1	2			17:10	15th	06:00
M1	3	7	4	07:30	16th	06:30
M1	3		4	08:19	16th	06:30
BL1	3		6	08:33	16th	06:30
M1	2		6	09:35	16th	06:30
M1	3			11:22	16th	06:30
C3	3			06:35	19th	06:30
PR	>2	1	0	06:39	19th	06:30
C3	3		3	06:54	19th	06:30
W1	1	2	2	07:25	19th	06:30
C3	>4	1	0	08:09	19th	06:30
C3	>4	7	2	08:25	19th	06:30
W1	1	4	1	08:35	19th	06:30
C3	2		2	08:39	19th	06:30
W1	1		9	08:46	19th	06:30
W1	3	4	1	08:53	19th	06:30
C3	?		2	09:50	19th	06:30
C3	>2	4	0	09:56	19th	06:30
C3	1		3	10:41	19th	06:30
C3	>2		9	11:02	19th	06:30
B92	>4			11:20	19th	06:30
C3	1	1	0	12:09	19th	06:30
C3	1	8	6	12:27	19th	06:30
C3	3	7	3	12:40	19th	06:30
C3	1	1	0	12:49	19th	06:30
W1	?		3	13:15	19th	06:30
C3	1	6	5	13:18	19th	06:30
C3	>4		3	14:53	19th	06:30
B92	>4	13	5	14:56	19th	06:30
C3	3	19	6	15:13	19th	06:30
C3	?	3	3	15:28	19th	06:30
C3	1	5	1	15:34	19th	06:30
C3	3	28	17	15:50	19th	06:30
C3	1		5	16:06	19th	06:30
C3	?	24	8	16:46	19th	06:30
B92	3		9	15:06	20th	06:30
C4	1		2	17:17	22nd	13:30

(no matings seen on 5 other observation days [1, 6, 7, 11 & 23 Oct]

A similar result was obtained in 1987, when 6 out of 9 matings observed of yearlings occurred after the median observation. Results presented in Chapter Four demonstrate that does yearlings generally have lower fawning rates than older does, and tend to produce lighter offspring with on average later birth dates. This illustrates that bucks achieving matings early on in the rut are likely to attain additional fitness benefits to those associated with the advanced birth dates of their progeny (see Chapter 4) alone. Thus of the 13 copulations observed by Buck 'M1' (15 & 16th October) all were with 'adult' does, and although buck 'C3' became dominant and displaced 'M1' from the lek thereafter, at least 33% of his 21 matings involved yearling females (Table 5.4). Similarly, does should also obtain benefits by being amongst the first to conceive, and hence dominant females might be expected to compete for access to preferred males against sub-ordinate does in oestrus at the same time; agonistic behaviour amongst females in mating groups were, however, only very rarely observed.

Only on two occasions were does conclusively observed to have mated with more than one buck, both cases occurring on the lek in Park 'G'. Nevertheless, as the actual identity (i.e. tag colour + number) of females could only be recorded in 22 of the 51 matings seen there, these multiple matings in fact represent 10% of those females identified. Interestingly both does were mated first by the most successful buck (Buck 'C3') , and then by Buck 'B92' on an adjacent lek territory (one at 3 and the other 6 hours later). Furthermore, both the does concerned were known to have been a minimum of four years old at the time.

Does the type of mating system influence reproductive success of the population ?

Fawning success rates recorded in the summer were discussed in detail in Chapter 4. These data were re-evaluated here with respect to the mating systems observed, using (as in 5.2.2) non-parametric analysis of variance to examine variation in fawning success between the 9 sites exhibiting either single- , multiple- , or no-territories during the rut. Although two of the three parks where non-territorial mating systems were observed showed rather lower fawning success than the remainder, these comparisons proved not to be statistically significant (Kruskal-Wallis Anova, $n=9$, $p>0.1$). Thus while the most appropriate mating strategies may vary with changes in male or female density, the mating system does not seem be associated with significant variation in fawning rates. Indeed if such an association had been found here, one might in any case expect that changes in numbers of receptive females would influence the mating system adopted, rather than vice versa.

General pattern of courtship

While much variation occurred in the frequency and time spent in various elements of courtship behaviour before actual mating took place, the basic pattern of courtship observed in territorial and non-territorial fallow mating systems was very similar. Courtship behaviours observed also closely resembled the pattern described by Asher (1986) for fallow in single-sire systems on fallow deer farms. A generalised outline of the behaviours observed is given below, together with a series of photographs illustrating a single courtship sequence (Plate 11 a-j) :

Self-advertisement by the adult males through emitting loud rutting calls or 'groans' is perhaps the most obvious sign of the fallow deer rut. Such groaning is likely to serve not only to attract and signal to the females, but also warn other males in the population of his presence. While the frequency of groaning was highly variable between individuals as well as populations, most other courtship behaviours exhibited by adult males (≥ 4 yrs) were usually accompanied by some such calls.

Already in the early stages of the rut, adult as well as yearling males were seen to spend much time checking individual does for scent. This would either take the form of walking slowly amongst groups of females, swaying their heads from side to side, nuzzling lying does along their flanks, or 'flehmen'. Flehmen (testing the air for scent) involves curling-up of the lips,and usually was exhibited while the buck stood still with his head arched slightly backwards.

The first indication that a mating was about to occur, was more persistent pursuit of an individual doe by the buck, usually accompanied by attempts to nuzzle her vulval region (Pl.11b). While closely pursuing a doe, bucks would often walk along with the head tilted to one side; the buck often continued to groan while following a doe in this way, although this tended to become less frequent as the courtship progressed. In response the doe usually walked slowly around within the territory or harem for several minutes, or lay down. The buck at that stage would switch his attention to another doe, or to other activities such as chasing out yearling males, or encouraged the doe to stand again by continual nuzzling of her flanks.

Plate 11 : Sequence of typical behaviours exhibited during fallow deer courtship.

a) b) c) d) e)

f) g) h) i) j)

If during such consort the doe stood still, sometimes the buck would stand over the doe with his chin across back or neck (Pl. 11d,g). Does occasionally responded by grooming the buck, usually around his head or neck region (Pl. 11c). Progressively the doe would stand still for longer periods (ca. 3-10 secs) during which the buck attempted to mount her (Pl.11f). Courtship activity sometimes also stimulated mount attempts by other females (Pl.11h) or even fawns. Numerous mount attempts were normally made by the buck without intromission, which were easily distinguished from actual successful copulation and ejaculation; during the final mount the buck thrusts forward very forcefully with his hind legs leaving the ground.

After copulation does would usually stand still for some time, alternately straining and relaxing their abdomen. The buck immediately after copulation always emitted a number of rapid, loud groans, before briefly grooming himself (Pl.11j). Another courtship sequence not infrequently commenced within only one or two minutes.

Factors affecting duration of courtship

As the exact onset of a courtship sequence was difficult to define, the time (to the nearest minute) between the first attempted mount and ejaculation, and the total number of precopulatory mounts were used as indices of the duration of courtship. Similar measures have also been recorded for fallow by Asher (1986) and Wallis (unpublished). Both these indices were highly variable within all populations. The interval from first mounting to ejaculation lay mostly between 2 to 8 minutes (range 0 to 48 mins., n= 112; cf. Asher [1986]: 4 to 50 mins). Distribution of number of precopulatory mounts was also highly skewed with a median of 7 (range 0 to 68, n=112); Asher's records of this measure in single sire pens on deer farms lie considerably higher with a median of 15 mounts per courtship (range 8 to 31, n=22).

Again using data on all copulations observed of known aged does in park 'G' (Table 5.4), the number of mounts per courtship was found to be lower when mating with yearlings than with older does (Mann-Whitney U-test : yearlings < three year olds, n=7,7 , $p < 0.02$; yearlings < over 2 years old, n=7,22, $p < 0.05$). As most yearlings tended to be mated later on in the rut, this rather unexpected result might be thought to be caused by differences between bucks. However, no significant differences were found between lek-bucks in the number of attempted mounts per courtship ($p > 0.1$). Differences between yearlings and adult does in the length of the courtship interval were not significant. The higher number of precopulatory mounts of adult does may be due to a greater tendency for them to walk off during such attempts.

No precopulatory mounts occurred in five observed matings (Table 5.4). In four of these courtship had been interrupted in some way immediately before copulation: thus, in one case a yearling male mated successfully (without precopulatory mounts or any form of courtship) on a lek territory, while the territory owner was fighting off another male; on two other occasions buck 'C3' mated immediately after a fight with another buck; and a doe, which had run to another territory during courtship, was mated with immediately without precopulatory mounts when she returned. Final copulatory mounts during longer courtships, were also often directly preceded by chases of young males off the territory, suggesting that the duration of courtship may generally be reduced when interference from other males (and hence risk of losing does) is high.

Differences in duration of courtship between the most successful bucks in different mating system types (Table 5.4) were not significant, although sample sizes available for such comparisons were rather small.

Does sometimes rested on lek territories for several hours while the buck only showed occasional overt interest in them. Once the buck had mated with one doe, however, several further matings often followed in quick succession. Figure 5.5 shows the temporal distribution of matings over several hours of observation of the lek. The most successful bucks are seen to have achieved up to 5 matings in some hours (Table 5.4, Figure 5.5) with distinct lulls at various other times of the day. Similarly, during four hours of observation of a temporary stand in Park 'B', where Buck 'W63' was seen to mate with a total of five does, all his copulations also occurred in less than one hour (Table 5.5).

Costs of Defence and Display behaviour

While the defence of a territory against other males may be envisaged to have quite different costs associated with it than the defence and gathering of a harem of females, exactly what these costs are will be determined by how often the defending male is challenged. Thus defence of a single stand, for example, is likely to be rather more costly in a population where most other males are also trying to obtain

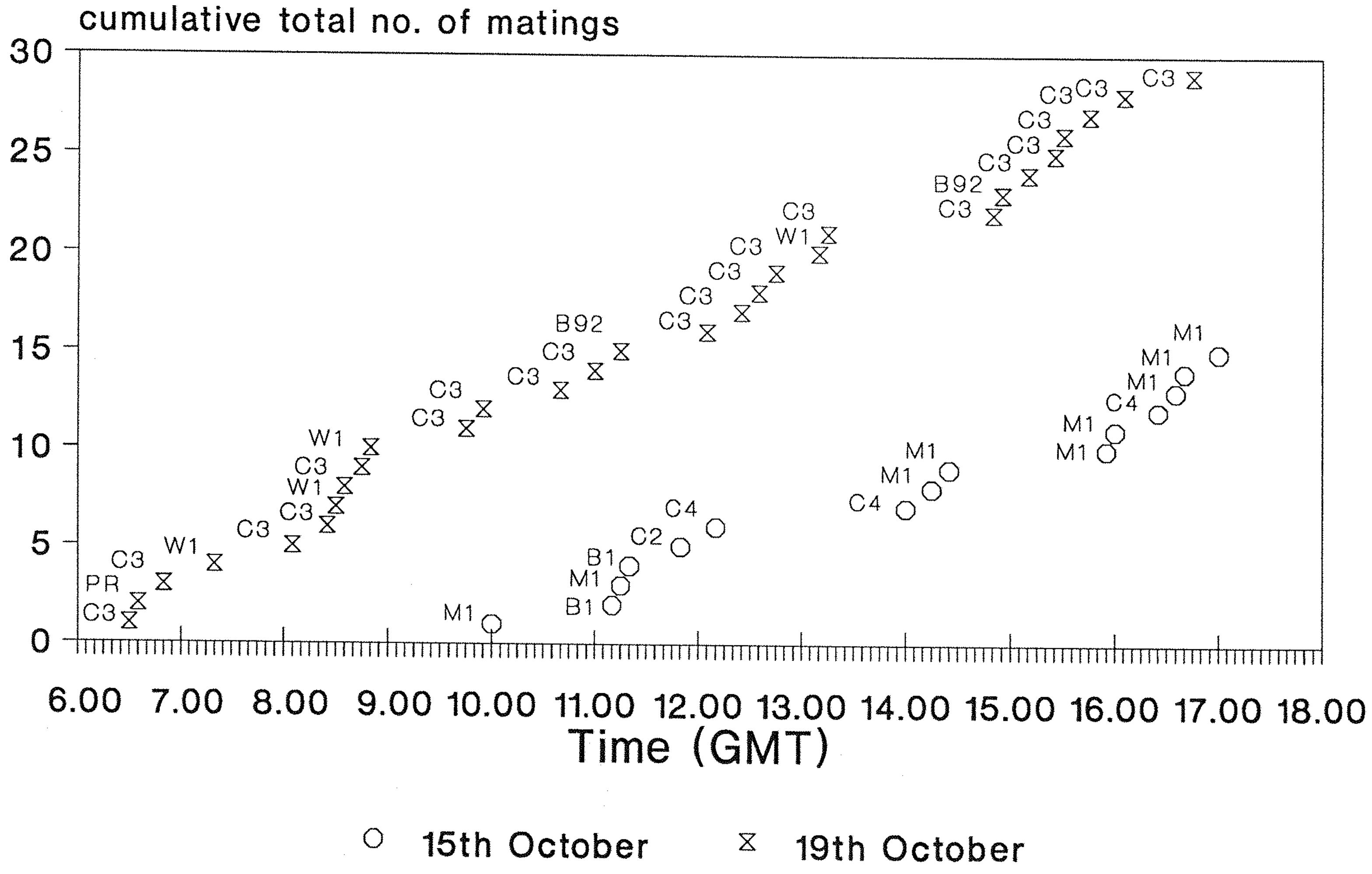


Figure 5.5 : Temporal distribution of copulations observed on a fallow deer lek in park 'G' during 2 different days in October 1988. Every data point relates to a different copulation, while labels indentify the particular buck responsible in each case.

such stands, than in populations where the majority of competitors are engaged on a lek. Comparisons of the costs involved in becoming the most successful buck within different systems are thus likely to be more useful here.

The most successful buck (in terms of numbers of observed matings) on the lek in park 'G' during 1988 (Table 5.3, 5.4) was seen to mate on only one of the 10 days for which the lek was watched that year, but he nevertheless accounted for more matings than any of his competitors during the rut. That tenure of territories on fallow leks is relatively short has also been shown by Schaal (1986) in Jaegersborg Park, Denmark, where individual bucks remained on the lek only one and a half days on average. In contrast the most successful bucks in the Temporary Stand system in park 'B' and in the Dominance system in park 't' were seen to mate throughout a full week. Although the relatively few days on which matings were seen is likely to underestimate the actual period of mating success for each buck, a longer spread of mating success in the less territorial systems is further supported by the period for which bucks in the different systems actively defended territories or groups of females against other males. Buck 'MDL' for example, was assessed to have maintained the top rank in the Dominance group at Park 't' from early on in October right through into late winter, as well as demonstrating clear interest in the females and exhibiting rutting calls throughout this period. The same buck was also observed to achieve a further mating outside of the main rut, on the 19th December.

As observations during this study were carried out on my own, other priorities of data collection during the rut (see 2.5) prevented recording of continuous time-budgets for individual focal males over extensive periods on a regular basis. Nevertheless a few focal watches were made during 1987, results of which may serve here to give some indication of differences in time allocated by bucks to attraction and defence of females on a Lek, a Temporary Stand, and in a Multi-male Dominance group. In order to allow direct comparisons between sites, results for the most successful buck in each of three parks are shown for the day on which each achieved his highest mating rate; records made during four consecutive hours have been selected, commencing with the hour leading up to the first mating observed that day (Table 5.5).

Table 5.5 :
Summary of various activities exhibited by the most successful buck during 1987 in each of three populations of differing mating system type. Data shown relate to the day on which the highest number of matings were recorded for each of the bucks, commencing with the hour leading up to his first mating observed on that day (see text).

	Hour of observation				average over 4 hours
	1st	2nd	3rd	4th	
Dominance group - Park ’t’: [Buck-M1 (0700-1100 hrs)]					
% of minutes ’Inactive’	20	10	47	23	25
% of minutes ’Active’	80	90	53	77	75
ejaculations /h	1	1	0	0	0.5
% mins. with ’close courtship	18	55	18	20	28
no. of herding attempts/h	3	1	1	3	2
chases of other bucks /h	0	0	1	1	0.5
chases of young males(<4yrs old) /h	2	6	6	3	4.25
% of minutes with chases	3	10	7	5	6.25
% of minutes spent away from territory / group	0	0	18	0	7.5
Temporary Stand - Park ’B’: [Buck-W63 [1250-1650 hrs)]					
% of minutes ’Inactive’	13	12	68	25	30
% of minutes ’Active’	87	88	32	75	70
ejaculations /h	1	4	0	0	1.25
% mins. with ’close courtship’	48	63	0	15	32
no. of herding attempts/h	4	1	0	0	1.25
chases of other adult bucks /h	1	0	1	1(#)	1
chases of young males(<4yrs old) /h	22	16	4	6	12.5
% of minutes with chases	32	18	3	7	15
% of minutes spent away from territory / group	0	0	7*	60*	-
Lek - Park ’G’ : [Buck-M4 (1245-1645 hrs)]					
% of minutes ’Inactive’	40	7	7	13	17
% of minutes ’Active’	60	93	93	87	83
ejaculations /h	1	3	2	0	1.5
% mins. with ’close courtship’	12	62	32	13	30
no. of herding attempts/h	0	0	2	0	0.5
chases of other adult bucks /h	1	0	0	0	0.25
chases of young males (<4yrs old) /h	2	5	4	9	5
% of minutes with chases	2	8	7	12	7
% of minutes spent away from territory / group	2	2	0	5	2

’Inactive’ = (lying or standing quietly); ’Active’ = Groaning and/or involved in close, persistent, courtship behaviours with female, or herding, chasing, or fighting.
= involved in a fight; * = left territory, but observed mating in another area within 500m.

A clear distinction is possible between minutes during which the bucks were 'Active' (that is minutes during which groaning, fighting, chasing, herding or courtship behaviour was recorded at least once), and those spent entirely 'Inactive' (lying or standing still). The proportion of minutes spent 'Inactive' was less than 30 % for all three bucks, and only exceeded 40 % during one of the four hours for each, with least inactivity shown by the buck on the lek (Table 5.5).

All three bucks left their group or territory for relatively short periods; thus for example the lek buck 'M4' twice left to drink at a pond over 300 m from his territory, and once during a prolonged chase of another male; the Dominance buck 'M1' at one stage went to lie-up about 500m away from his group for 18 minutes before rejoining, but no other matings took place in his absence.

The frequency of chasing young males (predominantly yearlings in most instances) away from the mating group usually rose noticeably in hours when a buck was involved in courtship sequences, and was highest in the Temporary Stand system. The chasing out of young males by other bucks on adjacent territories may result in a relatively low rate of intrusion by young males on the lek; however, the numbers of chases of yearlings were also quite low in the Dominance group, where such behaviour was generally confined to the alpha-male.

Fights or chases with adult bucks were rare in all systems during the periods shown; in both Park 't' and Park 'B' on approach of the dominant male sub-ordinate males usually simply moved out of the way or turned quickly to 'displacement' feeding behaviour. On the lek occasional clashes between adult bucks did occur near the boundaries of territories, although bucks involved in courtship sequences were very rarely interrupted by other adult males.

Herding of females was quite infrequent in all systems; while herding attempts by males on territories were usually aimed at a specific doe which was leaving or approaching the territory, in dominance systems the male would occasionally trot or 'goose-step' with his tail raised around the periphery of the whole group.

The proportion of time allocated to courtship of females was not surprisingly highest in hours when matings were also observed. However, even though the overall mating rate achieved ranged from 0.5 to 1.5 per hour amongst the three bucks, a near equal amount of time was allocated to courtship (i.e. actively pursuing or in making contact with females) by each (Table 5.5).

The relatively low amount of time allocated to active defence of territories or females suggests that ownership is reinforced to a great extent through display behaviours such as groaning and pacing around the areas. Being restricted to periods of high mating success, the above comparison may also underestimate the costs of maintaining a territory or high dominance rank, as most matings may occur during relatively quiet periods of the day, while dominance may already have been established earlier in the day. Evidence for this comes from very active periods of fighting involving most bucks holding territories on the lek in park 'G', which were observed around dawn on two occasions in 1988 during the main rut. Both times around 15 bucks came together shortly before first daylight in a peripheral lek territory of approximately 0.1 hectares in size. Although due to poor light conditions not all fights could be seen clearly, most bucks were certainly involved in several fights in close succession. These periods of heightened fighting activity lasted for around one hour, after which most bucks returned to take up lek territories.

On a day when buck 'M1' achieved 10 out of a total of 15 matings seen on the lek in Park 'G' he was observed to fight twice before 0830 hrs, but not again throughout a further 9 hours of observation. Similarly, when buck 'C3' achieved 21 out of 24 of all matings observed on the lek on one later day during the rut (Tab. 5.4), he was involved in fights with three different bucks before 0830 hrs, and a further three brief clashes (all with 'B11' on an adjacent territory) during the rest of the day. It thus seems likely that a dominance hierarchy is re-established at certain intervals even in the highly territorial systems, with the consequence that bucks are only rarely engaged in long escalated fights during periods when oestrous females have accumulated on their territories.

5.3 DISCUSSION

The comparative approach adopted in this study clearly demonstrates the wide intra-specific variation of fallow deer mating systems. These systems may be broadly characterised by the degree and type of territoriality exhibited by the mature sexually active males. The range observed during the main autumn rut encompasses non-territorial mating strategies such as following, harem defence, and multi-male dominance groups; through temporary and permanent single reproductive territories; to the development of multiple territories and leks. Several of these strategies have previously been individually described for fallow populations, however a lack of uniformity in defining such terms as "rutting stands" and "harems" make interpretation of the differences between populations difficult. Systems based on single non-contiguous reproductive territories ("rutting stands") have long been accepted as typical for the species (Cadman 1966, Chapman & Chapman 1975), while the significance of subtle variation in territorial reproductive behaviour as earlier reported by Heidemann (1973) and Espmark & Brunner (1974) has tended to be overlooked. "Rutting stands" are also described by Braza et.al. (1986) for a wild population in Donana, SW Spain, however they also refer to the same population as exhibiting a harem-based mating system. An earlier publication by these workers (Alvarez et.al. 1975) is often quoted in the literature citing evidence for non-territorial breeding in fallow deer (eg. Schaal 1987, Clutton-Brock et.al 1988). More recently lek-breeding in fallow deer has been reported (Schaal 1986, Schaal & Bradbury 1987, Pemberton & Balmford 1987), and more detailed investigations of the functioning of fallow leks have been provided (Schaal 1987, Clutton-Brock et.al. 1988, Apollonio et.al. 1989).

The present observations on park populations, together with comparison to observations of wild fallow made concurrently by Simon Thirgood (1990) have enabled the definition of different mating strategies, which can be arranged along a continuum on the basis of degree and type of territoriality. Such definitions serve merely to characterise specific points along this continuum, and considerable overlap may exist between reproductive strategies. Such overlap is, for example, demonstrated by the gradual change from a dominance group to harem defence (5.2.1). Nevertheless, the described continuum of mating strategies provides a useful framework for evaluation of the interaction of mating systems and ecology, and earlier observations recorded in the literature may easily be located along this gradient. The previous lack of such an overall perspective has contributed to much of the current misunderstanding in the literature.

Schaal (1985, 1987) first systematically described variation of mating strategies within a single population of fallow deer relating this to habitat and "reproductive phase". During the main autumn rut in continuous woodland he described a loosely territorial system with small rutting stands, while in more open habitats adult males were non-territorial and defended harems. In the secondary winter reproductive phase he observed temporary "pair-bonds" in woodland habitats, whereas multi-male mixed sex dominance groups occurred in more open areas. Schaal speculated that this variation was due to differences in the spatiotemporal distribution and abundance of food and mature females, and nonbiotic habitat features.

Here, using data from parks varying widely in their population and habitat parameters, it has been possible to make quantitative comparisons between these parameters and the type of mating systems observed. Buck density, defined as the number of adult males above the age of 4 years per unit area, consistently emerged as the best predictor of the type of mating system adopted in park populations. Low buck density was associated with non-territorial mating systems, and the degree of territoriality progressively increased with buck density. In those parks in which leks were observed, both buck density per unit area as well as the actual numbers of adult bucks were relatively high, in agreement with the only other described lekking park population not included in this study at Jaegersborg (Schaal 1986, 1987). Previous workers have attempted to explain the occurrence of lek-breeding in fallow populations in terms of overall population density (Schaal 1987, Clutton-Brock et.al. 1988), however in the present study separation of all park mating systems was not as clear using this variable in place of buck density. Additionally, overall densities for some reported lekking populations (e.g.Jaegersborg [Denmark] and San Rossari [Italy]) are lower than densities of several non-lekking populations included in this study. Nevertheless, doe density is an additional factor which, acting in conjunction with buck density, refines the exact mating system adopted in a particular population.

Park populations may perhaps be considered somewhat artificial, as the deer are confined within a limited area of restricted vegetational diversity. Indeed, these limitations have enabled very accurate measurement of population parameters such as density, sex ratio, and age structure of these herds. Comparisons with Thirgood's concurrent work on wild fallow populations, however, support the wider applicability of these results (Langbein and Thirgood, 1989; Thirgood, 1990):

While population parameters such as density are by necessity estimates for most wild herds, the degree of female aggregation in relation to density seems to be of considerable importance. Thus in low density, but highly aggregated wild populations Thirgood most frequently observed bucks to be to establish a temporary territories and 'following' strategies, which may be a response to the reduced probability of the territories being visited subsequently by another female group. In high density, less aggregated wild populations, there was a range of both territorial and non-territorial strategies within a 'mixed' population mating system. However, within this mixed system density again appeared to influence the composition of the system. Thus in one population at very high density in the New Forest, England, Thirgood describes a complex mixed system containing a small lek, as well as additional single stands, temporary stands, and following strategies. A significant reduction in the number of does using the area during the rut in the following year resulted in a reduction of the size of the lek, and similar decreases in the numbers of bucks active in other strategies in the area.

It therefore appears that density has a similar effect on mating systems in wild populations as in shown here for parks, with high densities being a pre-requisite for, but not necessarily the cause of the formation of leks, and low density populations showing least sign of permanent mating territories.

A functional explanation for the effects of density is complicated by the difficulty in isolating the effects of density from those of total numbers. At low population numbers, dominant males are able to successfully monopolise a high proportion of the population in a harem and density effects are minimal. When both buck and doe numbers are high, it is increasingly difficult for bucks to monopolise large proportions of the does using harem-type strategies as harems become too large to be economically defendable in the increased inter-male competition. Defence of a reproductive territory becomes more viable with increasing doe density, as the likelihood of these territories being repeatedly visited increases.

The same processes may explain the changes in mating strategies of fallow deer observed after the peak autumn rutting period, reflecting temporal changes in the density of receptive does in the population. For example, after the peak of the mating season bucks were often observed to leave their territories in persistent fast chases of oestrous females. When the proportion of receptive females in the population declines, the benefits of pursuing oestrous does may outweigh those of permanently defending a reproductive territory. As the actual numbers of females synchronised in oestrus must be a major factor in the cost-benefit trade-off for males, the use of density figures including all mature does, or in the case of total density even the non-reproductive fawns, provides only a simplified index of what is a dynamic density situation over the reproductive period. Differences in the degree of oestrus synchrony between populations, if these could be assessed accurately, would most likely provide an important component in refining analyses of mating systems.

Results presented in the following Chapter show that most does conceived significantly earlier on the lek at park 'G' than in all other parks for which comparable data were available. While other factors such as body condition and day-length are also likely to affect oestrus synchrony, the large numbers of bucks and high degree of reproductive activity associated with leks may also act to accelerate the onset of oestrus. Evidence for this is provided by the fact that does translocated 100 km from park 'G' to a new park conceived significantly later in future years (E.Graves, pers.comm.). The influence of olfactory cues provided by the presence of males in stimulating onset and synchrony of oestrus is well established for mice (Whitten, 1956; 1958; 1959; Vandenbergh, 1973), and has also been shown to occur in sheep (Thibault et al., 1966; Knight and Lynch, 1980), while cervical mucus from oestrous cows acts as a priming odour involved in synchronisation of oestrus in heifers (Izard and Vandenbergh, 1982).

With increasing buck densities, does in oestrus may avoid the consequent heightened male harassment by congregating on defended areas. Clutton-Brock et.al. (1988) suggest that such safety from harassment by young males provided by clusters of territories, is one possible explanation for the formation of fallow leks. The degree of protection gained by oestrous does staying in the vicinity of a dominant male may be in fact be an important criteria used by does in choosing males in any of the mating systems, as young males are also (though perhaps to a lesser degree) chased off by the dominant buck in large non-territorial mating groups.

Results of the present study did not show the ratio of adult to young bucks in the population to be an important factor influencing mating systems. It seems more likely that the total number of young and mature bucks not defending reproductive territories or groups of females, which are likely to harass oestrous does, is more important in influencing the degree of territoriality and development of lekking.

Individual bucks on leks have been shown to hold territories and achieve high mating success for only a few days during each year (Schaal, 1986; Clutton-Brock et al.,1988; Thirgood, 1990; and this study; but see also Apollonio et al. 1989). In mating systems with a lower degree of territoriality, however, results of this study show that some bucks stayed dominant for most of the rut, and in park 'B' the same buck even accounted for the majority of matings in three successive years. This result is not entirely surprising as less-territorial systems generally occurred at lower buck density and total numbers of competing bucks in the population.

During this, as well as in other studies of the fallow rut (Apollonio et al. 1989, Clutton-Brock et al. 1988), territorial males were rarely observed directly to disrupt each other's copulations. The relatively low amount of time allocated to active defence of territories or females suggests that ownership is reinforced to a great extent through display behaviours such as groaning and pacing around the areas. Gosling (1986) on reviewing mating systems of various species of antelopes suggests that territory 'owners' have more to lose than intruders have to gain, and they should therefore be prepared to escalate contests further. He goes on to suggest that *"multiple references for dominance are probably the norm: a territorial male may depend mainly on advertising its identity as an owner to win contests, but it may also be individually known to many intruders who remember the outcome of past encounters in male groups"*. During the present study periods of intense fighting at intervals of several days, involving a high proportion of all rutting males, was observed in one lekking park population. Thirgood (1990) also describes a number of distinct peak days for fighting activity in his studies of free-ranging fallow. Apollonio et al. (1989) suggest that social relationships between lek males are established well before the rut and continue to be respected throughout the mating season. This perhaps rather overstates the situation if applied to many of our populations, where dominance hierarchies (especially at high population density) clearly alter during the rut as successful bucks tire. They are then often displaced from their mating groups or territories by other males which have previously been less active and are presumably then, as a consequence, in superior physical condition. Some limited data available from catch-ups held during this study, indicate that the most successful bucks are often lighter after the rut than those who achieved fewer matings. Such differential weight loss may strongly influence changes in dominance relationships and fighting ability through the rut. Future studies incorporating the weighing of all males before and after the rut should clarify the importance of this factor.

Differences in habitat have frequently been proposed as a second set of factors affecting reproductive behaviour in cervids (eg Schaal 1987: fallow deer; Hirth 1977: white-tailed deer; Lent 1965, Bergerud 1963: caribou), and several authors have attempted to categorize cervid mating systems within this framework (e.g. Clutton-brock et.al. 1982, Bubenik 1985). In this study, non-territorial reproductive strategies which rely on maintaining a cohesive group of females, such as harems or dominance groups, occurred only in open habitats where cohesion was most feasible. High cover availability was particularly associated with single territorial systems, however, high percentage tree cover in the available sample of parks was always associated with medium buck densities. Additionally, single rutting territories are often observed in entirely open areas as well as in open and closed canopy woodlands and do not appear to be restricted to particular habitat types as suggested by Chapman & Chapman (1975) and Ueckermann & Hansen (1983). Fallow leks have also been observed to form in both open and closed canopy woodland (Apollonio et al., 1989; Thirgood 1990; this study) as well as in open permanent pasture (Schaal 1986, this study), whereas leks reported in other ungulates all occur in open areas [Uganda kob *Adenota kob* (Buechner 1961); white-eared kob *Kobus kob* (Fryxell 1987); topi *Damaliscus korrigum* (Montfort-Braham 1975); Kafue lechwe *Kobus leche* (Schuster 1976)]. An obvious contrast between wild and park populations was the greater range of concurrent mating strategies observed within single wild populations (Langbein and Thirgood, 1989; Thirgood, 1990; 1991), while in parks a single strategy could usually be discerned as the most productive in terms of male mating success. A similar flexibility within wild fallow populations has been documented by Schaal (1985,1987) in Alsace, NE France. The principle cause of such intra-population variation is likely to be the increased diversity of habitat, in terms of composition and structure, with its subsequent effects upon the distribution and localised density of the deer. In conclusion, while habitat is an important factor acting upon mating systems of fallow, its effects seems to be largely indirect, acting through influences on female density and dispersion.

The great variation in mating systems exhibited by fallow deer is mirrored by the general plasticity of their social organisation (Putman 1981,1988; Schaal 1982; Thirgood, 1990). Intra-specific variation of social organisation has also been demonstrated for many other cervids (eg. white-tailed deer (Hirth 1977), red deer (Mitchell et.al. 1977), sika deer (Takatsuki 1983), roe deer (Putman 1988)). Although to this date little research has been reported on intraspecific variation in mating systems of other cervids, the general conclusions drawn here on the variability of mating systems in fallow deer in relation to ecological parameters, may well apply to other deer species if studied over a similar range of environmental conditions.

Chapter Six

FACTORS AFFECTING MORTALITY IN PARK DEER

6.1 INTRODUCTION

Results presented in the previous chapters show body condition (at least as indicated by body weights) and fecundity in fallow deer to be closely associated with climatic conditions, as well as with population or management parameters, such as stocking density in relation to natural forage and supplementary feed availability. Other effects shown included measures of public access and presence or absence of competing livestock species in addition to fallow. The aim in this chapter is to reinvestigate these factors in relation to levels of mortality sustained in a range of deer parks over a number of years.

Among northern-temperate deer populations, and particularly in those occurring in areas devoid of large predators, mortality tends to be highly seasonal. Substantial losses of juveniles are not uncommon soon after birth in summer (Clutton-Brock et al. 1982; Skogland 1985; Asher and Adam 1985), although overall the majority of deaths tend to occur towards the end of winter (Mitchell et al. 1971, 1986; Guiness et al. 1978; Goldspink 1987; Bergerud 1971). In common with most mammal populations (Caughley 1966), mortality is also very unevenly distributed among different age classes. Thus during the juvenile phase mortality rates among deer of either sex are relatively high, but rapidly decline as the animals mature, followed by a more gradual increase with age (Houston 1982; Sauer and Boyce 1983; Clutton-Brock et al. 1985b; Mitchell et al. 1986). Furthermore, in strongly dimorphic mammals, which includes the majority of extant species of deer, mortality tends to be skewed with respect to sex, with juvenile and adult males having significantly lower chances of survival than females (reviews by Ralls, Brownwell and Ballou 1980; Clutton-Brock et al. 1982; 1985a).

Aside from predation, increases in natural mortality in deer have mostly been linked to the reduced food availability associated with changes of population density and/or climatic conditions. Food limitation in the late stages of pregnancy may affect the growth of foetuses and therefore the chances of survival of neonates (Verme 1963, 1977; Skogland 1985; Albon et al. 1987). Skogland showed density-dependent effects on such juvenile mortality in the summer for Norwegian reindeer populations, manifested through winter food limitation. Albon et al., in contrast, found juvenile mortality of red deer calves on Rhum to be independent of population density, but related to the climate in spring; this climatic effect is again thought to arise due to differences in nutritional status of hinds, which varies annually depending on the timing of the first flush of new grass growth.

The lower survival of juveniles through winter is likely to be related to their high metabolic requirements compared to adults, associated with their smaller body sizes and fat reserves (Mitchell et al 1976; Albon 1983). Variation in mortality of adult females are thought to arise due to differences in the depletion of body condition (e.g. due to lactation, pregnancy) at the beginning of winter, depending on whether the animals raised offspring in the previous summer (Mitchell et al. 1976; Clutton-Brock et al. 1985a). The higher metabolic and growth rates of males in dimorphic species (reviewed Glucksmann 1974; Clutton-Brock et al. 1985a), and in the case of adults, the reduced food intake and high energetic costs during the rut (Simpson 1976; Kay 1978; Mitchell et al. 1976; Clutton-Brock et al. 1982) makes males more prone than females to the effects of low food availability and harsh weather. Furthermore, Illius and Gordon (1990) show that juvenile red deer experience a reduction in incisor breadth in relation to body size during the transition to adult dentition, and predict that yearlings, male calves and stags will suffer the greatest reduction in foraging efficiency due to differences in the incisor development when feeding on depleted resources.

Adult females thus tend to be most resilient to the various factors which may reduce survival. Hanks (1981), on reviewing current research on large mammal populations, notes that a rise in adult female mortality is in fact usually the last of a number of sequential events which occur in a population as demographic vigour declines, being preceded by increased ages at first reproduction and reduced adult fecundity. Increased juvenile mortality in contrast is often the first sign of a declining population, and has been shown to be the key factor in natural regulation of various ungulate populations (e.g. african buffalo, *Syncerus caffer*, : Podoler and Rogers 1975; Sinclair 1979; red deer: Clutton-Brock et al. 1985b; reindeer: Skogland 1985). Adult mortality, which tends to be relatively low in comparison to other classes even in the wild situation, might be expected to be even lower in park populations, as these are usually subject to a high and selective annual cull, amongst which animals in visibly poor condition should be included. The highly complex relationships governing natural mortality illustrated by the examples above, with variable effects of different factors depending on the age and sex class of individuals, suggest that mortality rates might nevertheless continue to exert significant regulatory influences in park populations.

During the current investigation, natural mortality rates recorded among the 8 main study populations where most intensive field work was carried out, were extremely low. The average natural mortality rate (Sep. to May) over the four years of study did not exceed 4.5 % of numbers present before winter in any of these populations, and in five of the sites in fact lay under 2.5 % in every year of study. Early neonatal losses of fawns, discussed previously in Chapter 4 (see Tab. 4.1), were also rather low (<5%) in most of these sites. This narrow range of variation in mortality rates and the small number of actual deaths involved, provides only limited scope for investigation of these results with respect to environmental conditions or the age-distribution of the animals affected. The present thesis on the population ecology of fallow deer in parks, however, would seem rather incomplete without some further evaluation of mortality. Analyses presented below have therefore been extended to include data for a number of additional park populations, at least some of which were known to have suffered more substantial natural losses in recent years.

Such an extension of the database was made possible, when as a result of a sudden and unexpectedly heavy mortality among the deer herds in a Richmond Park, London, the Department of the Environment commissioned a study into the possible causes of such losses[1]. The park in question had lost 42 red deer (13%) and 52 fallow (10%) during the 1985/6 winter; mortality rates far above those recorded in any of the initial 'core' parks during the study period. Nevertheless, such sudden 'die-offs' in parks, without any known link to disease, are not as uncommon as might be thought. Thus, during the course of investigations for the D.o.E. we accumulated data on seven other cases of similar heavy losses, which had occurred in various parks at some time in the past.

A preliminary analysis (Putman and Langbein 1989) suggested that the factors implicated when escalated mortalities or 'die-offs' are recorded (> 7% of the population) are no different from those affecting more 'normal' variation in levels of natural mortality; that is in the year when a die-off occurred the response to the same factors influencing mortality in other years is merely more extreme. The factors found to influence levels of natural mortality in general were stocking density in relation to available grazing area and productivity of natural forage, percentage of a park providing good cover from adverse weather conditions (winter and summer), and the regime of supplementary feeding practised overwinter (quantity, quality and timing of supplementation). Degree of public access and disturbance to a park for recreation was also found to affect mortality, but only indirectly, acting in combination with some other predisposing factors, except where deer mortality was high due to road-traffic and fence accidents (Putman and Langbein 1989).

The above analysis was, however, based on incomplete and perhaps unreliable data: firstly, we were at that time relying heavily on records maintained by the estates themselves in an unstandardised fashion. Furthermore, not all parks considered were equally represented in the analyses, as the number of years of data each could provide differed widely.

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[1] This study formed the basis of two contracts awarded to the University of Southampton from Sep'87-Feb'88 and Oct'88-90, to which I was appointed as research assistant. The initial pilot contract enabled study of factors affecting mortality based on past herd records maintained by a sample of 21 different deer parks. The longer-term study that followed involved extensive observational work to investigate patterns of temporal and spatial habitat use and behaviour of the deer in two parks, together with consolidation of data on mortality, body condition and reproduction for 15 parks across for the last four years (1985-9).

Results of these contracts have been reported to the Department of the Environment (PECD 7/2/44 and 7/2/65). Data on mortality are re-examined here in the context of the other findings of this thesis.

That preliminary study also did not consider climatic variation between parks, which in the earlier chapters of this thesis has been shown to have major effects on variation in deer body condition between parks. Analyses presented below reassess the relationships between mortality, population parameters and management practices, based on data on deer populations where performance was monitored by ourselves since 1985, providing a more consistent and complete set of data than was available for the earlier work.

Methodology

The 14 fallow deer parks studied in relation to mortality are widely dispersed throughout England and Wales (50°30' - 53°30'), and all occurred between 20-400 metres above sea level; park sizes vary from 5.7 - 820 ha. Figures for stocking densities were calculated as the mean daily number of stock units (to take account for any variation in timing of culling or live sales) supported per hectare between November and March, and ranged between 0.5 - 8.2. Nine parks contained only fallow deer, and five had mixed populations of red and fallow; results discussed below pertain in the main to these 14 sites where fallow deer were present, while a further site containing only red deer is also considered for comparison.

Individual methods of assessment and definition of population and management parameters are described fully in Chapter 2. Population data used in this section derive from direct censuses carried out in each park in September and March each year. Mean weights of fallow deer are based, either on whole carcase weights (total weight less bleedable blood) or, where available, live-weights obtained during our live capture operations between November and February. Weights of adult females and yearling males are chosen as indicators of population condition in general, as offering high sample size and lowest variance. Mortality figures are minimum estimates based on the number of animals found dead overwinter up until the end of March of each year. Meteorological data are based on published monthly records from the nearest weather station to each park (Meteorological Office - HMSO).

Analysis

Relationships between the level of mortality sustained within a park and the different population or management parameters were investigated individually by correlation analysis [or, where appropriate Student's t-tests] and in step-wise multiple regression. Mortality (always assessed excluding culled deer) was considered separately as a) *natural* fallow deer mortality and b.) the level of mortality including *accidental* deaths (e.g. road traffic or fence casualties). Analyses were undertaken at three distinct levels.

i) Data sets were explored using each year's records separately for all parks (offering a total of 56 fallow park/years). Mortality levels vary markedly within a park between years, and analysis at this level of all park years allows discrimination of those factors characteristic to a particular park in a particular year in relation to a given level of mortality.

ii) No bias is introduced in the above analyses by over-representation of one park or one year, since data are presented for all 14 parks considered in the same 4 years. However, analysis at the level of park-years (above) may overemphasise, by replication in successive years, those features of a park or population that are unchanged between years, or are not-independent of previous values. Analysis was thus repeated across all 14 fallow parks for which data were available, but using a) data for single years, b) mean values over the period 1985-89 in each park.

iii) In three of the parks included in the study, total winter deer mortality in one or more years between 1985-9 exceeded 7% of the total population. Data on similar high levels of mortality were also available for another three of the parks having occurred in earlier years. Wilcoxon's matched pairs tests were used to compare population and management characteristics in such years of heavy mortality (total n=8) with average values in the same park over three years when 'normal' levels of mortality occurred.

6.2 RESULTS

6.2.1 'Overwinter' (September to May) mortality

Table 6.1 provides information on the range and mean values of population and park parameters of interest, across the 14 fallow populations and 4 years included in analyses of mortality. The level of natural mortality sustained overwinter within the different populations in each year of study is illustrated in Figure 6.1, showing this to have stayed below 4% for most parks and years. However, variation in mortality within some populations between years was high, with for example, Park 't' experiencing deer mortality of 11.3% in 1985/6 but only 0.5% in 1988/9. Variation between populations was also notable, average mortality over four years ranging from 0.5 - 6.2 % between different parks.

A breakdown of mortality into different age/sex categories was not possible in many cases, as we relied on records available from herd books (where mortalities tended to be lumped), and indeed would be unhelpful in many other cases where numbers involved were very low. Data on age/sex of the deer concerned in the high losses sustained in Park 't' in 1985/6 were available, breaking down into 25 fawns, 3 does, and 21 bucks in the case of fallow deer. These results are in line with findings from other studies of mammal populations, which have generally shown mortality to be highest amongst juveniles of either sex, followed by a period of low mortality before a further increase in later life; a higher rate of mortality amongst males than females has also often been noted among dimorphic species (e.g. mammals in general: Caughley 1966; wapiti: Houston 1982; whitetailed deer: Eberhardt 1969, red deer: Clutton-Brock et al. 1982).

Table 6.1:

Summary of population and management characteristics of the deer populations included in analyses of mortality rates. Maximum, minimum and mean values of the various parameters are shown where appropriate.

	Min.	**Max.**	**Mean**
Total park area in ha.	5.7	820.0	217.0
Winter stocking density (SSD)	0.5	8.2	3.3
Mean winter density over previous 3 years	0.6	7.6	3.3
*Winter Grazing density (GAD)	0.8	11.5	5.3
Mean grazing density over previous 3 years	0.8	9.6	5.2
*Proportion of park providing tree cover	0	0.5	0.2
Date winter feeding commenced [before/after end November]			
Daily ration of supplementary food over winter			
* as metabolisable energy [MJ per animal d^{-1}]	0.1	26.7	5.8
and crude Protein [g per animal d^{-1}]	1.2	394.	466.1
and Average winter supplement per animal in previous year			
Mean weight (within a park) of			
* adult fallow doe (liveweight:kg)	34.7	48.9	42.1
yearling fallow buck (liveweight:kg)	35.3	55.9	44.5
*Mean monthly temperature (°C: Nov-March)	1.7	6.9	4.9
*Mean monthly temperature (°C: Jan, Feb)	0.8	6.5	
*Total winter precipitation (mm: Nov-March)	167	747	360.0
*Number of winter days snow on ground at 09.00	0	60	11.7
Number of winter days of groundfrost at 09.00	60	110	85.5
*Mean monthly temperature (°C: May,June)	9.7	17.5	12.8
*Total precipitation (mm : May,June)	70	306	130.0
Percentage of park area open to public	0	100	47.2
*Level of public use [scale 0-9]	1	9	4.4
Deer species [fallow only/ red + fallowdeer]			
Presence/absence other stock (cattle/sheep)			

[Asterix indicate variables carried forward for multivariate analyses]

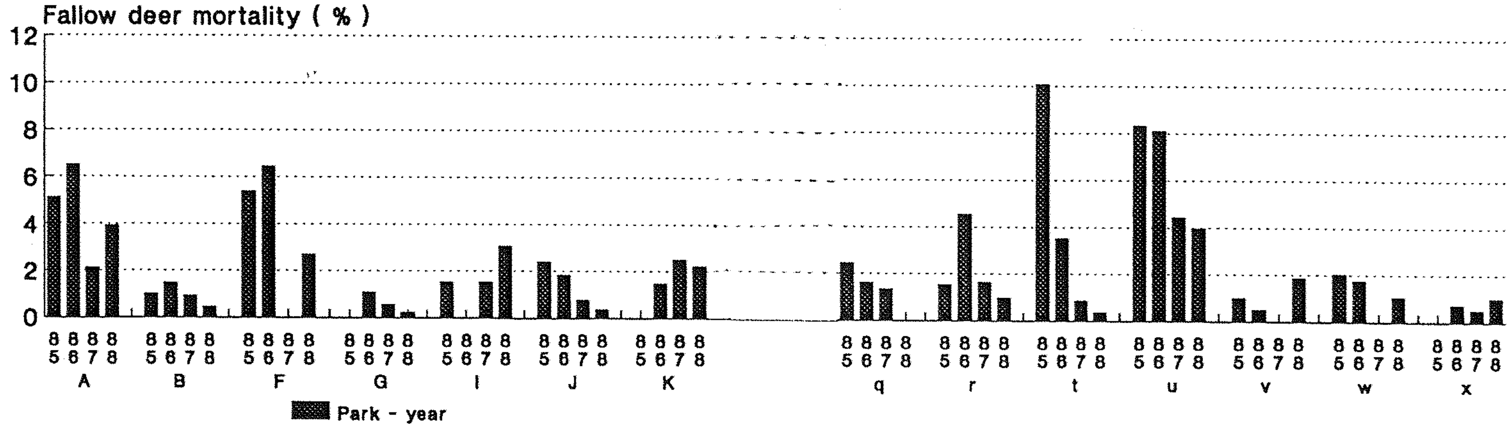


Figure 6.1 : Variation in fallow deer mortality rates (1985/6 -1988/9) in 14 British parks.
(Based on annual totals calculated April-April).

Univariate comparisons

Winter losses showed significant individual correlations ($p<0.01$) with i. the index of population body condition used here (adult female weight), ii. length of the growing season of the previous year, iii. average winter temperature (over all months: November - March) and also temperatures in January/February alone.

Weaker associations were apparent between mortality and iv. levels of supplementary feed offered overwinter (assessed as metabolisable energy [ME], and crude protein [CP] per animal), and v. time feeding commenced (early or mid-November vs. December). In Chapter 3, relationships of fallow body weights with supplementary crude protein were found to be non-linear, but to be approximately linear with metabolisable energy over the range of data available. Relationships of supplementary feed and mortality might be expected to show a greater tendency to relate in a non-linear fashion, for values in excess of certain, minimal sustenance levels. Examination of these relationships indeed showed mortality to increase in a non-linear manner with both feed variables. Square root transformations of both feed variables improved linearity of relationships with mortality, in most analyses the strongest correlations being obtained when the metabolisable energy variable was employed. In contrast to most of the other variables tested, values of supplementary feed showed strong univariate associations with mortality only in some study years (1985/6 and 1988/9: $r=<-0.45$, $p<0.05$ one-tailed), but not during the others.

Results of the main univariate comparisons are summarised in Table 6.2, providing details of analyses considering all 56 park-years together, and when repeated using four-year park averages. Where correlations missed significance in the latter analysis, trends can be seen to remain in the same direction. Example scatter plots of mortality on body weight and on winter temperature are shown in Figure 6.2a & b.

The analyses presented in Table 6.2 relate primarily to natural mortality alone. When analyses were repeated using information for <u>all</u> mortality (i.e. including accidental deaths due to dog chases, road traffic accidents etc., in addition to natural mortality), relationships with both our measures used to assess public disturbance now also became statistically significant. Public access thus tended to increase the level of overall mortality within a park, but was not associated directly with *natural* mortality rates.

Table 6.2:

Correlation coefficients between levels of mortality among park deer and population or management variables. Results shown are from analyses using i) all individual park years ii) park means over four years (1985-89).

	(i) All park years	(ii) Average per park over 4 years
Fallow mortality		
winter temperature	** (r=-0.36)	NS (r=-0.36)
days of snow	*** (r=+0.41)	NS (r=+0.41)
Jan/Feb temperature	*** (r=-0.33)	NS (r=-0.24)
adult bodyweight	* (r=-0.41)	* (r=-0.45)
Total (red +fallow) natural mortality		
winter temperature	*** (r=-0.40)	NS (r=-0.37)
days of snow	*** (r=+0.46)	* (r=+0.46)
Jan/Feb temperature	*** (r=-0.41)	** (r=-0.41)
fallow doe weight	** (r=-0.40)	* (r=-0.42)
Total mortality including accidents		
days of snow	** (r=+0.31)	NS (r=+0.23)
Jan/Feb temperature	** (r=-0.29)	NS (r=-0.06)
public access	*** (r=+0.32)	* (r=+0.43)

(* p<0.05; ** p<0.01; *** p<0.001 [one-tailed])

Fig. 6.2a: Mortality on body weight

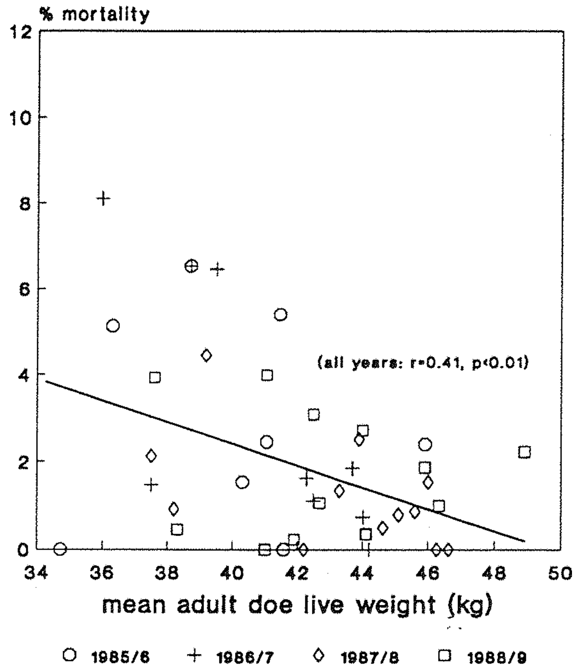
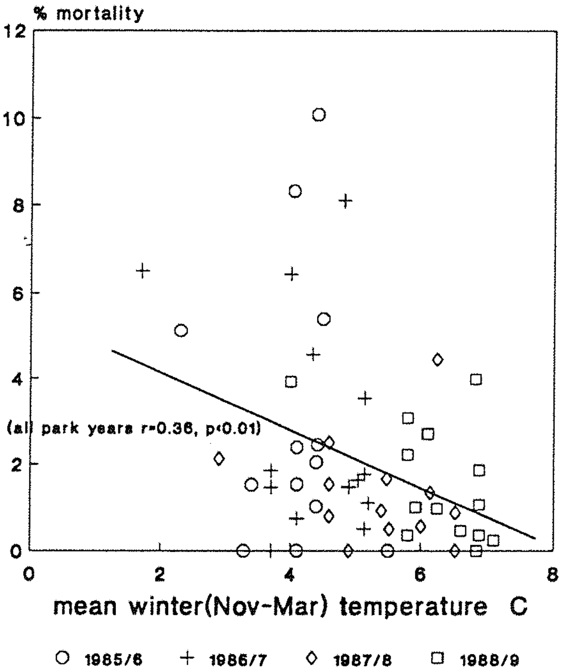


Fig. 6.2b: Mortality on Temperature



(for correlations in individual study years see text, and Table 6.3).

Matched-pairs analyses between those years within any park where high mortality levels (>7%) were recorded, and an average of those years within the same park of low or zero mortality, provide independent confirmation of relationships between high levels of mortality and :

at ($p<0.01$)
- mean winter temperature
- food supplements (ME)
- winter precipitation

at ($p<0.05$)
- days of groundfrost
- days of snow lie
- food supplements (CP)
- winter grazing density (GAD)

(Wilcoxon's test, n=8 , one-tailed; insufficient data were available for die-off years for such comparisons on body weight).

A high degree of inter-correlation was apparent among some of the independent variables considered. As discussed in detail in Chapter 3, body-weights of adult female and yearling male fallow were highly correlated within parks ($p< 0.0001$). The proportion of a park's area open to the public was highly correlated to the subjective index of levels of public use (Spearman Rank correlation, r_s =+0.85; $p <0.001$). Winter grazing density (GAD) was correlated with absolute stocking density (SSD), and perhaps not surprisingly with densities of previous years ($p< 0.001$; $r>0.8$ in all cases). Finally, a number of climatic variables showed close intercorrelations ($p< 0.001$, $r >0.7$ unless otherwise indicated): Mean winter temperature was significantly inversely related to number of days of groundfrost, days of snow and temperature in January/February; winter temperature was also significantly associated with winter precipitation ($r =-0.40$). Number of days with snow lying was highly correlated with January/February temperatures ($r=-0.80$). Length of growing season in any park year (defined as number of days a year when mean temperature was > 5°C) was highly predictable from regressions on mean winter temperature (see Chapter 3.5.1).

Multivariate comparisons

In view of the clear interactions within the independent variable sets considered above, multivariate analyses were carried out using a restricted variable list (asterix in Table 6.1). Step-wise multiple regression analyses were carried out at the level of all 56 park-years, as well as within individual study years or four-year averages. Analyses were repeated with and without the inclusion of bodyweight parameters - since while low bodyweight may indeed be a factor contributing directly to overwinter mortality, it may also merely reflect, as an indicator, pasture productivity or summer grazing pressures. [All values of R2 shown in the text below are adjusted down for the available degrees of freedom at each stage of the analyses]

Mortality was shown above to be significantly correlated with winter temperature or alternatively the number of days of snow-lie. Days of snow, as the first variable entered in multiple regression using all available park years, accounted for 21.4% of the variance in fallow mortality; inclusion of adult female bodyweight in the model increased R^2 to 25.7%, with a further increase to 32.5 % ($p<0.001$) on entering the supplementary feed parameter ($ME^{0.5}$). If climatic data are not included in the analysis, adult doe bodyweight and level of supplementary feeding alone combined to offer an adjusted R^2 of 28.3% ($p<0.001$). Treating each year of study separately, mortality was most strongly associated with doe weight in 1986,1987; but more strongly with snow days/ or winter temperatures in 1985,1988 (see Fig. 6.2a&b). In 1985 supplementary feed itself showed a direct association with mortality (see above). In each of the three other years supplementary feed explained significant amounts of the residual variance at the second step of analysis, once differences in winter climate or body weights had been taken into account. Such results support the hypothesis that, as also indicated by the univariate comparison above, supplementary feeding exerts a particularly significant influence on mortality especially during cold winters and/or when body condition at the beginning of winter is low. The best significant step-wise regression models in each separate year of study are shown in Table 6.3.

When mortality measures were extended to include all non-cull mortality, thus including accidental deaths, significant correlations occurred using either of the two measures of public access. Once these were selected none of the other independent variables showed significant partial correlations with the residual variance, and were thus not selected in the multiple analyses ($F_{in}= > 4.0$).

Table 6.3 :

Summary of main significant Multiple regression analyses of mortality. (R^2 values, adjusted for reduced degrees of freedom at each step, and two-tailed significance levels are shown).

Dependent variable	Independent variables	adj. R^2%	p<value
i.(using all 'park-years')			
Fallow mortality	adult bodyweight		
	+ $\sqrt{ME}$ suppl.per animal	28.3	0.001
OR	adult bodyweight		
	+ days of snow	25.7	0.001
OR	adult bodyweight		
	+ $\sqrt{ME}$ suppl.per animal		
	+ days of snow	32.5	0.001
Total deer mortality	adult bodyweight		
(red + fallow)	+ $\sqrt{ME}$ suppl.per animal	27.0	0.001
OR	adult bodyweight		
	+ $\sqrt{ME}$ suppl.per animal		
	+ days of snow	31.4	0.001
ii. (treating study years separately) **Fallow mortality :**			
1985/6	no significant multiple model		
1986/7	adult fem. bodyweight	54.2	
	+ $\sqrt{ME}$ suppl. per animal	64.3	0.02
1987/8	adult fem. bodyweight	20.4	
	+ $\sqrt{ME}$ suppl. per animal	22.5	
	+ days of snow	44.1	0.055
1988/9	days of snow	19.7	
	+ $\sqrt{ME}$ suppl. per animal	40.5	
	+ adult fem. bodyweight	41.8	0.029

Throughout the above results, whether based on direct relationships between mortality and individual population attributes, or in multivariate analyses, few significant associations were detected between mortality and stocking density. Only in matched pairs test between 'high' and 'low' mortality years within parks was a trend noted for mortality to have been associated with higher than usual herd sizes. This suggests that most of the park populations sampled fluctuate within relatively 'safe' levels of stocking densities in relation to the available forage and supplements provided. Only when a relaxation of culling and/or supplementary feeding coincides with extreme winter conditions do these factors seem to become implicated in significant rises in mortality.

The importance of the balance of stocking levels, supplementary feeding overwinter, and late winter weather conditions, are well illustrated by comparison of mortality levels over an eight-year period in two deer parks in London; both these parks contain mixed populations of red and fallow, and are situated within 5km of each other (Table 6.4). Only in one year were mortality levels found to be very high there, coinciding with particularly low late-winter temperatures; even in that cold winter, however, mortality was only high in that park where little or no supplementary feed was provided. However, even this park (Park 't'), where little supplementary feeding was carried out for over five years, only sustained heavy mortalities during one severe winter.

Table64 :

Mortality levels and associated characteristics in two deer parks in London, between 1981/1989.

In interpretation of the table note that both the parks are very similar in character, both have mixed populations of red and fallow deer at approximately the same densities and are subjected to similar levels of public access; because of their geographical proximity, they are also exposed to similar climate.

PARK 'v'				PARK 't'		
Total deer mortality (%)	Suppl. feed (MJ/SU)	Grazing density (SU/ha)	YEAR (Jan/Feb temp) °C	Grazing density (Su/ha)	Suppl. feed (MJ/SU)	Total deer mortality (%)
1.5	5.4	2.6	1981/82 4.6	2.6	0.1	1.7
0.2	5.2	2.7	1982/3 4.9	2.7	0.1	1.3
0.5	6.4	2.2	1983/4 4.7	2.4	0.2	1.8
1.6	6.7	2.1	1984/5 2.4	2.6	0.1	1.0
0.5	**5.9**	**2.4**	1985/6 **2.0**	**2.8**	**0.1**	**11.3**
0.8	5.7	2.5	1986/7 3.0	2.2	5.4	3.9
0.6	6.2	2.2	1987/8 5.8	2.2	1.9	1.0
1.4	7.5	1.8	1988/9 6.3	2.1	3.9	0.5

6.2.2 Juvenile mortality in the summer

Aside from mortalities occurring overwinter, most other deaths recorded were of recently born fawns during June and July (see Chapter 4). The cause of death of those animals is likely to be rather different from the causes discussed above in relation to overwinter losses. No more than 4 dead fawns were found during any summer, in any one of the eight closely monitored parks (Table 4.1), and thus no in depth analysis of the factors associated with summer mortality is possible here. In only one of these eight parks did mortality of neonates exceed 7% of those born over the entire study period (park 'H': 6/26 = 23%); the park concerned differed from all 7 others in that i. the total park area was given over to grass (no other cover available), ii. red deer were present in addition to fallow, iii. a significant proportion of does were known to be over six years old. While this evidence is far from conclusive, the generally high rates of neonatal deaths recorded on fallow farms (Asher and Adam 1985, Vigh-Larsen 1988) suggest that lack of shelter for newly born fawns may be of significance in relation to neonatal losses sustained.

Most fawns which were found dead during summer in any of the park populations were mostly well below the average birth weight recorded for live fawns, suggesting that mothers may have been in poor condition during gestation. High numbers of neonatal deaths do not, however, necessarily indicate that the population as a whole is in poor condition : for example, in one hypothetical population most yearlings may fall below critical body weight thresholds for any of them to conceive, while in another, where yearlings only just exceed such thresholds, some of these may not in the end be able to produce viable fawns. While a higher population reproductive success would be attained overall by the latter example-population, this might also be accompanied by higher numbers of dead neonates. Summer mortality has already been discussed in part in Chapter 4, and this aspect of mortality is therefore excluded from the discussion below.

6.3 DISCUSSION

Contrary to the impression which may be given by the title of this chapter, mortality due to natural causes amongst fallow within British deer parks in general was found to be low (mean < 2.5% annually). Natural mortality is thus not likely to exert a major influence on the demography of most of these deer populations, the role of controlling population numbers largely being taken on by management through means of culling.

Annual culling usually removes around 30% of both male and female deer, other than fawns, from each population, and hence has a direct influence on levels of natural mortality sustained. Amongst females, which form the majority of the population in virtually all park herds, culling is mostly unselective with respect to age; as a result of such a cull chances of survival of yearlings and adults from one year to the next are reduced to 70% and therefore the probability of any individual surviving to six years of age immediately falls below 1% (0.7^4). Ueckermann and Hansen (1983) put the upper limits of natural life expectancy for female fallow at between 15-20 years of age, although in general females are thought to show a decline in condition beyond 7 years of age (e.g. Chapman and Chapman 1975). Death of does due to old age will therefore be rare in the parks subject to high annual off-take. Culling of male deer tends to concentrate on 1 to 3 year old animals; hence chances of death due old age amongst the small numbers left to go on may be rather higher than in the case of females, although any animals showing signs of declining condition are in any case likely to be included in the annual cull. Natural mortalities amongst adult deer in parks will thus be largely confined to animals which 'slipped-the-net' or those which decline in condition rapidly after the cull.

While the age breakdown of mortalities was not available in many cases, as far as data were available these indicated that overwinter mortality amongst fallow is highly concentrated amongst juveniles, in line with results from other studies of mammal populations (e.g. mammals in general: Caughley 1966; wapiti: Houston 1982; whitetailed deer: Eberhardt 1969, red deer: Clutton-Brock et al. 1982).

Amongst most wild populations of fallow deer, as well as most other temperate deer species, overwinter losses contribute the major proportion of annual natural mortality - and losses are increased following particularly severe winters. Thus in the intensively studied red deer population of the Isle of Rhum, mortality of hinds (and particularly that of yearlings) increased in those years with particularly cold winters (Clutton-Brock et al. 1985b). The well documented dramatic crash of the reindeer population introduced to St. Matthew Island in the Bering sea, following their extremely rapid expansion for a number of years, was also associated with a particularly severe winter (Klein 1968). Mortality of mule deer and white-tailed deer in Piceance Basin was shown (Bartmann and Bowden 1987) to be significantly correlated over a 7 year period, with mean winter temperature and snow depth. Snow depth and snow compaction are themselves strongly correlated with mortality in mule deer and white-tailed deer populations within the northern United States (e.g. Severinghaus, 1947; Verme and Ozoga, 1971; Mech et al. 1987).

Similar effects might be thought to be negligible amongst deer in British parks, which as well as being largely under close management, experience very mild climatic conditions in comparison to the studies mentioned above. During the present study climatic conditions nevertheless emerged as the major factor affecting escalation of deer mortality rates. Mortality levels among fallow (as well as red deer herds, Putman and Langbein 1990) were significantly, inversely correlated with mean winter temperature (November-to-March and January-to-February) in that year, length of previous growing season and animal bodyweights (doe, hind and yearlings). With lower levels of significance, winter losses were also associated (positively) with winter precipitation and (negatively) with the amount of supplementary food provided per animal overwinter; significant differences in mortality also accompanied differences in date of commencement of such winter feeding. These same variables emerged consistently at all levels of analysis: that is, whether all years where included separately for all parks, or when restricting analysis to particular years or park averages, as well as in matched pairs analyses of high vs low mortality years within parks, offering further confidence in the relationships detected. In contrast to a preliminary analyses of factors associated with mortality in park deer (Putman and Langbein 1989), stocking density (other than through amount of supplementary feed available per animal), amounts of available tree cover or other shelter, and presence or absence of other livestock did not show direct relationships with winter mortality, and measures of potential disturbance through access by the public were implicated only in increases of accidents involving deer.

Many of these independent variables considered are, however, themselves intercorrelated: The metabolisable energy and crude protein content of food supplements were closely associated; thus wherever one measure showed correlation with levels of mortality, either or both may be implicated. In most analyses of mortality, levels of metabolisable energy were used as the more direct measure of food supplementation (after square-root transformation to account for non-linearity towards the upper end of the range of supplementation). Relationships among the different climatic variables are more difficult to resolve. Cold winter temperatures and high rainfall may be directly associated with increased levels of mortality, by depleting energy reserves more rapidly in response to windchill, or they may act indirectly through their influence depending on length of the previous growing season and consequently on build-up of fat reserves . In the event, both effects would seem indicated. Mortality was more highly correlated with days of snow and January/February temperatures than with winter temperature overall, suggesting some direct influences of cold weather. Equally, mortality is strongly negatively associated with all measures of animal bodyweight (a measure of the bodily reserves available overwinter to compensate for energy shortfall) - while autumn body weights themselves are strongly associated with the length of the previous growing season (see Chapter 3).

Multiple regression analysis highlight the most important groups of interacting influential factors: highly intercorrelated variables which contribute no additional explanation to the relationships once one of them is entered are not selected. Mortality among fallow populations related primarily to number of days of snow cover in winter, adult female bodyweight and supplementary feeding. While in years of low or 'normal' mortality, mortality levels were well predicted on female body weight alone, in years where high losses occurred in a number of populations, mortality was better predicted by late winter temperature and snowfall; in either case, but in particular during years when mortality was high, supplementary feeding levels explained significant amounts of the residual variance. It seems clear that high levels of mortality may be expected among animals of poor condition at the end of cold winters. However, while some increase in mortality seems inevitable during severe winters, park managers clearly can and for the most part do exercise some control over this, through supplementary feeding.

Animals in populations at higher densities, fed a lower level of winter supplements, or entering winter with low bodyweights, may survive equally well in relatively mild winters; thus major 'die-offs' among such susceptible populations appear only sporadically. The plots of body weights shown in Figure 6.2 may be helpful in forecasting populations which may be at risk: Annual losses of more than 4.5% (i.e. mean + 1SD) of the population were not sustained in any 'park-years' when does averaged over 42 kg at the beginning of winter, and in the only two parks which averaged over 4.5% mortality over the entire study period mean adult does weight was less than 39 kg. Likewise, none of the parks where daily winter feed provided per animal contained over 9 MJ of energy, experienced mortality levels in excess of 4.5% in any year. The other major factors implicated, that is severe winter weather conditions, are difficult to predict in advance. However, if animals culled at the beginning of winter are found to have average body weights below the levels indicated (< 41.5 kg live weight, or < 23.5 kg carcase weight, for adult does), this at least may be taken as an indication that a higher than usual amount, (and possibly an earlier start), of feeding is likely to be required to ensure that the deer are able to maintain sufficient condition to survive the winter.

Chapter Seven

FINAL DISCUSSION

Of the 200 or so British deer parks which are still in existence today, the majority have been established for several centuries and were constructed specifically to raise fallow deer for hunting, ornament, and venison (Cantor 1987). Deer parks in general might therefore be thought to offer near optimal conditions to support this species. However, the data and conclusions presented in the previous chapters demonstrate extensive variation between different fallow populations kept in parks, in terms of their reproductive performance, survival, and growth rates. These parameters, pertaining to the performance of animal populations, are generally thought to be influenced by the physical condition of its members, which in turn tends to reflect the quality of forage and suitability of the environment in general. The presence of broad variability between the performance of different park fallow populations, and also within single populations across years, has during this study allowed investigation of the influences of a number of different population parameters, climatic conditions and management regimes, on aspects of fallow deer performance and behaviour.

Emparked deer populations, in contrast to farms, present fully mixed-sex herds, which are free to range over relatively extensive areas of parkland throughout the year, and able to express their natural seasonality of social and breeding behaviours. As such, many of the population processes taking place in deer parks are likely to be comparable to those in more natural environments. Most parks, however, do differ from the wild situation by being stocked at much higher population densities, such increases being possible to sustain through the provision of supplementary feed for the deer during winter. Such feeding was found to be extremely variable from park to park, so that in some cases it barely suffices to off-set the very high stocking levels as compared to the wild, while in others it may effectively remove winter resources from importance as a major regulatory factor limiting rates of population increase.

The physical condition of fallow deer during the present study was found to vary widely between populations, and to a lesser degree between years. The range of that variability was described in some detail during earlier chapters, as only few data on live fallow deer, which have not been raised on farms, have previously been published. In summary, 'live-weight' was found to be the most useful among a range of measures made on live animals to characterise the physical condition of different populations. Greatest variation in weights was recorded amongst the juvenile age classes. Mean weights in that population where the heaviest deer were recorded, exceeded those of the lightest by, for example, 65% for male fawns (6 months old), 33% for yearling females (18 month old), and 30% for adult females (> 2 years), samples at both these parks having been weighed during November of the same year. Analyses of variance showed highly significant differences in age-specific mean body weights between most of the 11 parks in which large samples of deer could be caught. Differences shown between populations were concordant across all the different age/sex classes distinguished, so that the relative rank of parks showed little change whether based on weights of fawns, yearling, or adult animals of either sex, as long as reasonable samples were available of each. Linear morphometric measures taken to estimate the skeletal size of live fallow, as well as ratios of weight to skeletal size, again resulted in similar ranking of the study parks, to that obtained by using live weights alone.

The deer parks included in this study varied not only in their stocking densities, climate, and proportions of various habitat types available to the animals, but also in herd management and the provision of winter feeding. Single populations assessed over a range of years, provided somewhat less complex systems offering a relatively constant management regime from year to year, and only local rather than geographic variation in climate between years. Within each of a number of such populations for which a run of data for six or more consecutive years was available, significant inverse correlations could be shown between current population density and the carcase weight of yearling males (offering largest sample sizes of cull data). In one of these populations this relationship could be shown to be stronger when re-plotting yearling weights on population density in the year of their birth (change in R^2 from 69% to 85%), indicating the particular importance of conditions during early growth.

Density-independent relationships were shown between body weights and summer pasture productivity of the main grazing areas, as well as with climatic conditions (temperatures and precipitation) during winter. Strong density-dependent associations across parks were revealed between mean deer weights and the amount of supplementary winter feed (in terms of either metabolisable energy or crude protein) provided daily in relation to stock numbers. Clearly all three factors, pasture productivity, climate (through effects on primary productivity but also directly on thermoregulation) and winter feed, may influence deer body weights. Combination of these effects in multiple regression analyses produced the best models in the case of yearling female body weight, where up to 89% of the variance in weights could be accounted for by these three variables. After accounting for density-independent influences of winter climate, negative effects of increased stocking densities were also apparent. In order to demonstrate the effects of density on body weights and growth between sites as directly as they could be shown for the within site comparisons discussed above, it may be useful to compare across a sample of sites less variable in climate and feed management in the future (see further work).

Hanks (1981), on reviewing recent research on population condition, suggests that in populations of large mammals the following events may occur sequentially as physiological condition and consequently also 'demographic vigour' (Caughley 1977) declines :

1. juvenile mortality rises
2. age at first reproduction increases
3. adult fecundity declines
4. adult mortality increases.

Juvenile mortality has been proposed as the proximate expression of a downward trend in the rate of population increase in a wide range of mammalian species (see reviews by Hanks, 1981; Fowler 1987). Juvenile mortality among the 8 most intensively monitored park populations during the present study was not highly variable, and remained relatively low throughout the study. This may in part be attributable to a succession of three unusually mild winters ever since 1986, spanning much of the study. Supplementary winter feeding is practised to some extent in all the parks studied, and may act to keep some weak fawns alive, which might have succumbed to starvation in the wild. Among data recorded in additional, less closely monitored parks, some high natural winter mortalities were recorded and these indeed tended to be dominated by juvenile animals. A factor which may contribute to the high summer survival of neonates in parks, is the usually extensive availability of shelter in the form of high ground vegetation, which is often lacking on deer farms where higher rates of neonatal mortality are common.

Age at first reproduction, noted above as the second common sign of a declining rate of increase, did show wide variation within the same sample of park sites. Fawning rates of females conceiving as yearlings ranged from only 12.5% in some, to over 90% in other populations. Yearlings were consistently found to have lower fawning rates than older does at the same site, and such differences were widest in the populations exhibiting the lowest age-specific body weights. Yearlings were also shown to produce lighter offspring, with conception and birth dates on average 11 days later than adults. These results, supported by similar findings by Asher (1986) for fallow on deer farms, suggest that yearlings not only produce fewer offspring than adults, but their young in general also have reduced chances of survival. Yearling mothers may thus contribute a disproportionately high number of the offspring dying as juveniles in any one year. A winter-body weight threshold for yearlings, at which 50% produced fawns the next summer, was determined as 32 kg. It could therefore be argued that juvenile mortality may in fact be higher in some populations where many yearlings do conceive, than in others with lower rates of overall population increase, where only very few yearlings are in fact able to conceive.

Fawning rates of adult does (≥2 years old at rut) were very high (> 75 %) in all the sites where such age-specific data could be collected. The reproductive success of a number of individual females could be followed over several years, showing that up to 90% of does within certain populations successfully reared fawns in each of three consecutive years. Even in park 'A', where the lowest yearling fawning rates as well as lightest mean body weights were recorded during the present study, adult fawning and rearing success exceeded 90% in each year of study. This clearly supports Hanks' above doctrine, that adult reproductive rate is more resilient to declining body condition than that of younger does. The fact that the adult fawning success in fact lay higher in park 'A' than in several of the other monitored sites, may be attributable to the fact that the majority of does in this park had not incurred reproductive costs as yearlings. Several studies of Scottish red deer have illustrated that the probability of conception at the rut is lower for those hinds which reared young in the preceding summer than for yeld animals (e.g. Mitchell et al 1977; Clutton-Brock et al. 1982, 1985b). As a consequence of the generally high adult fecundity of fallow does throughout all of the parks monitored during the present study, only few yeld fallow females were available for comparison. It may be of interest in future studies to investigate if, where yeld does do occur, yeldness is particularly associated with two-year old does failing to conceive after a first pregnancy as yearlings. No direct relationships or threshold levels of body weight and reproductive rates could be demonstrated for adult does. However, significant direct correlations were revealed between the amount an quality of supplementary feeding provided and reproductive rate (calculated across all age classes combined); strongest associations were obtained here with the amount of crude protein provided daily per deer, which may be of particular importance in maintaining pregnancy.

Natural mortality, including adults as well as juveniles, was generally low (mean < 2.5%) in most parks and years for which data were available. Any escalations of mortality were associated with particularly low late winter temperatures and low body weights. Provision of supplementary feeding was again found to reduce the effects of low weights and cold temperatures on the mortality levels sustained. The highest level of natural fallow deer mortality in any one park was recorded in 1985/6, associated with the coldest winter over the duration of this study. The losses sustained at that park broke down into 25 fawns, 3 does, and 21 bucks, in line with Hanks's conclusion (Hanks 1981) that the last parameter to give way as a population is subjected to environmental stress, is the survival of adult females.

Management recommendations

While management of deer populations in parks is akin to that practised in the wild in as far as all age and sex classes are free to range over the entire park area, the densities of deer maintained in parks (range 0.8 - 7.7 per ha, this study) commonly represent more than a ten-fold increase over densities of wild or feral populations (ca. 0.05 to 0.4 per ha; various sources quoted in: Chapman and Chapman 1975). The upper bounds of the range of mean body weights and reproductive rates determined for British park fallow deer during the present study, are among the highest values reported for any wild or enclosed populations of this species, while mortality rates were in the main relatively low. This clearly demonstrates that fallow deer may, and often do thrive in park environments, despite the high densities which are associated with them. The broad variability in performance between populations, however, emphasises the importance of careful evaluation of the habitat in terms of its natural forage production, and consequently the requirements for supplementary feeding in relation to deer numbers.

Average body weights were found to be a good indicator of population condition in relation mortality, and also of reproductive success. Examination of relationships between mortality and body weights in Chapter 6 showed that annual mortality (calculated across all age groups) tended to remain below 4.5% (=mean mortality rate + 1SD) for those populations and years where weights of adult females averaged no less than 41.5 kg live-weight (or > 23.5 kg dressed carcass weight) at the beginning of winter. Regular annual assessment of mean weights at the annual cull or handling operation, may therefore be used to provide an early warning as to when stocking levels are becoming too high. Thus, mean weights below the threshold indicated can be taken as indicative that current stocking levels are too dense, unless supplementary feeding is increased significantly.

Pasture productivity, assessed in areas temporarily exclosed to the deer between April and May, was found to average 410 g m^2 across parks (range 115 g - 609 g), equivalent to production of 4100 kg dry weight of grass per hectare. Substituting this average value of productivity in the regression equations determined between pasture productivity in relation to stocking levels in Chapter 3 (p.90), suggests that mean adult female body weights should be possible to maintain at above 41kg at stocking levels up to 5.9 stock units *per hectare of good grazing land* offered by the park. In areas offering more productive pastures (e.g. >600 g m^2), stocking levels should be possible to increase to 8.7 stock units per ha of pasture; however, in areas of low productivity (<200 g m^2), as were recorded in this study at higher altitudes and on poorly drained land, stocking levels below 2.9 stock units per hectare of pasture would be recommended, as higher levels are likely to result in low weights and hence higher mortality.

A consistent, and perhaps rather predictable conclusion to emerge from each of the parts of the study summarised above, is that levels of supplementary feeding overwinter play an important role in determining the performance of park deer; that is, high levels of supplementary feeding were associated not only with heavier body weights, but also with faster growth rates, higher reproductive rates, and increased survival. Across our sample of study parks the amount of supplementary feed provided per fallow deer varied from just 0.1 % of daily maintenance requirements for metabolisable energy, to 130 %. A general trend was discernible across parks and years for more supplementary feed to be provided per deer the smaller the total herd size. Only a minority of park managers at present seem to work out levels of feeding based on current herd numbers, instead tending to still rely on total amounts which have 'traditionally' been given, or what is provided for in the budget. It seems clear that high levels of mortality may be expected among animals of poor condition at the end of cold winters. However, while some increase in mortality seems inevitable during severe winters, park managers clearly can, and for the most part do, exercise some control over this through provision of supplementary feeding. Animals fed at only low levels of winter supplements, or entering winter with low bodyweights may also continue to maintain high rates of survival in relatively mild winters. Major die-offs among such susceptible populations are therefore difficult to predict in advance. However, high levels of mortality, exceeding the 2.5% average level by more than one standard deviation, were only sustained in park-years were does averaged 41.5 kg or less; similarly such levels of mortality were never recorded where feeding exceeded the equivalent of 9MJ of metabolisable energy per day between mid-Nov. to March. As indicated above, lower mean weights recorded at the cull may be taken as a warning that higher than usual amounts of feed are likely to be required, to ensure that the deer are able to maintain sufficient condition to enable them to survive the winter. The clear beneficial effects of supplementary winter feeding on live and carcass weights, as well as improvements in reproductive success of the deer, illustrate that such feeding at up 9MJ (ca. 82% of maintenance) is rarely wasted from an economic point of view, even if the winter turns out to be less severe than first anticipated.

Performance of fallow deer in parks on the whole compares very favourably with body weights, reproductive rates and neonatal mortality reported for fallow farms (Asher and Adam 1985; Asher 1986; Vigh-Larsen 1988; Kerckerinck 1987). The often superior rates of performance in parks may relate not only to lower stocking rates than on farms, but also the greater diversity of habitats offered by a typical park environment; such diversity is likely to bestow benefits to the deer in providing a greater range of natural feedstuffs, often including an ephemeral supply of tree-fruit such as acorns and chestnuts (just before the autumn rut) at the time when fat reserves need to be laid down for winter, as well as natural shelter from adverse weather conditions. There is little doubt that shelter is of importance in reducing weight loss, and hence increasing survival during winter. While many farms provide artificial shelter in winter, little cover is usually available during the summer; in the case of neonates lack of shelter and consequent exposure on open pastures may be one of the factors responsible for the increased neonatal deaths on farms as compared to parks.

Results in parks show that yearling females may reach average body weights of over 42 kg; that is, levels averaging over 30% above the threshold winter live weight of 32 kg at which at which 50 % of yearlings were found to produced fawns. Asher (1986) in fact noted oestrus activity in pubertal farmed fallow does weighing only 28-30kg. The average weight of yearlings calculated across all the park populations studied exceeded 36kg (SD ± 2.5kg), illustrating that only few yearlings failed to achieve ovulation thresholds in the parks. Thus, while reproductive rate of yearlings is particularly sensitive to environmental conditions, the lower reproductive capability of yearlings females is not likely to limit rates of population increase significantly, if adequate feed levels for juvenile growth are provided. If management is aimed at achieving highest possible female reproductive success, any female cull should be directed to remove the weakest female fawns and yearlings, and thus ensure that only those animals in good condition join the breeding population as yearlings.

Future studies

The present study of deer in parks, rather than in the wild state, has enabled the close monitoring of a number of populations for which population parameters such as density, food supply, reproductive rate and survival could be relatively easily assessed in each case, and populations could be readily sampled to obtain physical measurements of live animals.

Repeated live sampling of individuals for a number of years in self-contained populations of large mammals is only rarely possible in the wild. The possibility to do so here, offers an opportunity to follow the Life-time Reproductive Success of several cohorts of animals based on individuals, rather than relying on samples of each cohort culled in successive years. Fluctuations in individual condition may also be monitored from year to year and related directly to known reproductive effort and other environmental conditions experienced. While results of such recaptures have begun to emerge from the current study, few of the known-aged animals concerned are as yet only over four years old, and the full average reproductive life-span of female fallow may well exceed ten-years. Those investigations which have been successful in determining LRS for animal species, persistently point out the need for comparative studies in other populations of the same species, or other species in the same family (see review by Clutton-Brock 1988). The large numbers of animals now individually marked in a range of British deer parks presents the basis for long-term studies of LRS not just in one, but in several populations all experiencing differing environmental conditions.

The deer parks included in this study varied not only in densities, but also climate, the proportions of various habitat types available to the animals, as well as herd management and the provision of winter feeding. Any comparisons between parks during the present study therefore generally presented rather complex systems with several variable factors. In order to illustrate, for example, the effects of density on body weights between sites, as clearly as they were possible to show for within site comparisons across years, it may be preferable to compare performace of deer across a sample of sites which is less variable with respect to management and climate. Future studies in parks should capitalise on the possibility for manipulation of these populations, by holding various management factors constant across sites, to allow testing of the various relationships indicated by the present study. For example, a series of parks owners could be asked to provide identical level of feeding, for a number of populations offering differing densities or pasture productivity. An alternative approach to follow up the present work, which has in fact now begun, is to bring together adult animals from a number of the different original study sites in new 'daughter' parks. Within such new parks all the deer now experience the same environmental conditions of current density, feeding regime and climate. It is hoped that this will enable evaluation of the separate contributions of current environmental conditions on the performance of individuals, from those they experienced during active growth as juveniles.

The continuation of the present study along the lines suggested above, by capitalising on the framework already in place, may allow exploration in greater depth of a number of remaining questions of the dynamics of fallow and other ungulate populations. The population dynamics of fallow deer, however, has by comparison to other common European deer species formed the subject of few previous population based investigations. On the basis of the far-reaching variability of fallow deer performance and behaviour demonstrated merely within the relatively favourable environmental conditions offered by British deer parks, initiation of further studies of the dynamics of fallow deer in other areas seems warranted, in particular where this species occurs close to the limits of its natural range.

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Appendix I :

Incisor measurements as an aid to age-determination

Summary: *While a number of methods are available to determine the age of deer from carcass materials, no reliable objective techniques exist for ageing live fallow deer in the field. In contrast to molariform teeth, the incisor teeth of the lower jaw are readily accessible while handling live deer. This section explores the possibility of using measurements made of incisor teeth to estimate age. Measurements of incisors were made on culled animals, whose ages were either known (due to attachment of ear-tags to the animals as juveniles), or determined by study of tooth eruption and wear patterns (Chapman and Chapman 1975). Strong linear relationships between incisor height and age were obtained for both sexes. Standard deviations around regressions of age on incisor height were, however, too great to allow confident prediction of age to the nearest year, even when using animals from within a single park population.*

Accurate assessment of the age of individuals is of importance not only in studies of the dynamics of animal populations, but also for management of livestock. Body size, for example, can only be a useful guide to the condition of a sample of animals, if it is known whether that sample contains a mixture of animals at various stages of growth, or is made up only of fully grown animals.

The majority of methods available for determining the age of deer rely on materials such as lower jaws, eye-lenses, or bones obtainable only from animals after their death. The most widely used techniques for ageing fallow deer are those based on the study of the eruption and wear of their teeth (Rieck 1965; Chapmann and Chapmann 1975; Ueckermann and Hansen 1983). Rieck (1934, 1965) also demonstrates the possibility of ageing fallow by counting 'annual zones' in the regenerative dentine of the first incisor, while Brown and Chapman (1990) have recently developed a systematic scoring system based on wear patterns of a range of cheek teeth in known aged animals.

All the above methods, however, can only be applied to the age-determination of animals after their death, as they require the lower jaw of the animals for close examination. During the present study many animals of unknown age were caught at annual live catching operations. Those individuals caught for the first time as juveniles could be readily identified as such by checking for the presence of deciduous 'milk' incisors, or inspecting the stage of eruption of their permanent incisors. However, in most fallow deer, all three pairs of permanent incisors are already fully erupted by the age of 15 month (Chapman and Chapman 1975). As the incisors are the only teeth readily accessible when handling live deer, tooth eruption patterns are thus of little use in estimating ages of live deer over one year old. The usefulness of linear measurements of incisors was therefore explored here, in the hope of developing an objective method for ageing live deer, based on the wear of these teeth with age.

While the eventual aim of this exercise concerned the ageing of live deer, materials from culled animals were used to determine regression equations of age on incisor size. 43 jaw bones containing intact incisors were obtained from animals culled in park 't' during 1987, and a further 75 jaws from animals culled or found dead in 7 of the other study parks between 1986-9. The age in years of these specimens was assessed by inspection of patterns of tooth eruption and wear of the molar and pre-molar teeth (Chapman and Chapman 1975) or, in the case of animals over the age of six years old, by counting the number of annuli visible in sections of the cementum surrounding the root of the first molar (M1). Results were adjusted to the nearest month depending on the month of death, assuming a common birth date of 15th June for all animals. The height of the central pair of incisors (I1's) was measured to the nearest 0.5 cm using vernier callipers, by measuring from the highest point on the front cutting surface of the tooth, down to the 'cemento-enamel-junction' (i.e. the line where the enamel of the crown joins with the cementum surrounding the root of the tooth).

Figures Ia & c. show plots of age on incisor height for 17 male and 26 female fallow culled at park 't' during 1987. High correlation coefficients were obtained ($r < -0.85]$, $p<0.0001$), indicating that incisors tend to wear in a linear manner with age for both sexes. However, both regression lines of age on incisor height showed high standard errors; 95% prediction limits associated with the equations obtained are given on the graphs, and indicate that the predicted age of, for example, a doe with an incisor height of 8 mm would be 64 months ± 26 months (i.e. placing the animal between 3 - 7 1/2 years).

A wide range of incisor heights was recorded already among one year old deer (range females : 10 - 12.5mm; males: 9.5 - 11mm), animals of the same sex at park 't' all having been culled during the same month. This suggests that individual size variation of newly erupted incisors, rather than differences in wear rates, may be the main cause of the wide range of incisor heights also recorded within older age-classes.

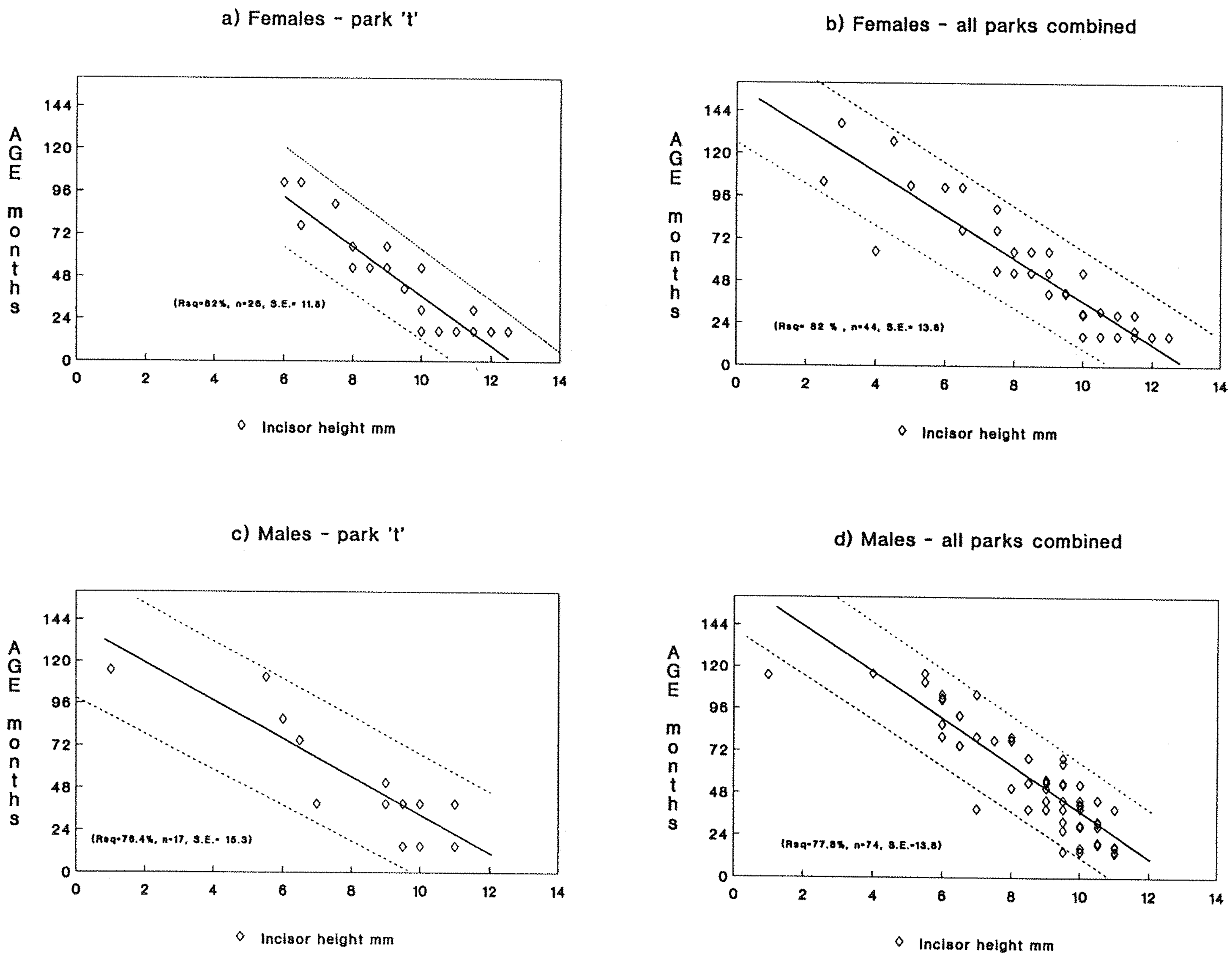

Figure I a-c: Regressions of age on incisor heights measured on culled animals, using data from park 't' only (Fig. a & c), and for pooled data from 8 British deer parks (b & d). Dotted lines show the 95% prediction limits associated with each regression.

On pooling data for all 8 parks for which specimens were available, the significant correlations with age were maintained, with only little change in the standard errors associated with the regression lines. Among these pooled data, the widest range of ages (1 to 6 years) were recorded for male deer with incisor heights of 9.5mm (Fig. Id). Nevertheless, among specimens of either sex, all those below 3 1/2 years of age had incisor heights above 9 mm; conversely all except one animal with incisors less 8.5mm was over 4 years old. Thus, while incisor sizes are generally too variable to allow confident classification of animals into separate year-classes, worn incisors measured in the field may at least allow the placing of animals as being of above certain minimal ages.

Incisor heights were routinely measured for most live deer caught at annual catching operations. Because of the high degree of variability discussed above, it was, however, decided not to use these measure to allocate animals to particular year-classes.

Appendix II :

Meteorological data at main study parks during the period of study.
Data extracted from Monthly Weather Report (HMSO 1984-9) for the nearest Weather Station to each park, located at similar altitude. (In the case of parks I, J, & K, the same weather station was used as all are located within a 15 mile radius; further details on climatic variables see section 2.8).

Park	Winter (Nov-Mar)					Summer	Growing
Code	Mean Temp. C	rainfall (mm)	days Rain	days Snow	days Frost	days Rain	season (Jan-Dec)
1984/5							
A	2.3	484	72	47	94	137	207
B	5.5	610	72	0	69	186	279
E	3.9	354	61	30	109	159	253
F	4.5	263	53	21	93	204	269
G	5.5	408	68	6	96	109	294
H	3.7	321	58	37		185	236
I	4.1	263	56	16	100	174	258
J	4.1	263	56	16	100	174	258
1985/6							
A	1.7	626	87	60	109	149	214
B	4.9	545	69	1	69	155	292
C	3.7	318	56	15	95	74	269
E	3.3	378	63	27	109	82	256
F	4.0	281	50	8	88	93	282
G	5.2	383	56	2	85	145	310
H	3.0	363	67	18		86	238
I	3.7	318	56	15	95	74	269
J	3.7	318	56	15	95	74	269
K	3.7	318	56	15	95	74	269
1986/7							
A	2.9	721	80	25	97	306	225
B	5.4	713	83	24	69	166	285
C	4.6	271	52	13	88	137	281
D						131	
E	4.1	321	52	13	107	131	251
F	4.9	240	49	12	86	135	287
G	6.0	386	54	6	88	88	297
H	4.0	406	68	13		265	265
I	4.6	271	52	13	88	137	281
J	4.6	271	52	13	88	137	281
K	4.6	271	52	13	88	137	281
1987/8							
A	4.0	747	80	9	79	117	229
B	6.6	738	80	0	73	153	366
D	5.9	296	64	2	66	80	300
E	5.6	383	63	0	66	62	288
F	6.1	277	51	3	68	92	328
G	7.1	437	68	0	68	126	361
H	4.1	458	73	4	74	109	274
I	5.8	318	49	0	68	111	301
J	5.8	318	49	0	68	111	301
K	5.8	318	49	0	68	111	301

(years shown indicate for e.g 1984/5 = winter data for Nov'84 to Mar'85, while growing season and summer data are for 1985)