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The Social Organisation and Ecology of the Japanese sika deer (*Cervus nippon*) in Southern England

VOLUME ONE

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by

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To

my future wife, Elaine

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UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE, DEPARTMENT OF BIOLOGY

DOCTOR OF PHILOSOPHY

The Social Organisation and Ecology of Sika deer (*Cervus nippon*) in Southern England

by James Christopher Edward Mann

1. A variety of field survey techniques, supported by material from culled animals were used to investigate habitat occupation and use, feeding ecology, social structure and behaviour of sika deer in deciduous woodland in Hampshire and amongst coniferous plantations in Dorset.

2. Seasonally changing patterns of habitat occupation were found in the New Forest associated with the seasonally changing nature of the habitat. In Dorset the pattern is seasonally unchanging.

3. The majority of observations were of deer feeding; the choice of habitat coincides not only with feeding requirements, but also shelter. Animals were found lying up for longer and in less exposed sites in the winter.

4. The New Forest deer feed opportunistically and have a varied diet being mainly grazers in the spring and summer and taking coniferous browse in the winter. The diet of the Dorset animals is constant; containing equal and major portions of grass and *Calluna*.

5. The sex ratio in both areas is four hinds per stag. Fecundity in the New Forest is less than 84%; in Dorset 90%. Calf mortality in Hampshire is 30%.

6. Group size in each forest is affected by vegetation type; smaller groups are found in closed habitats.

7. New Forest stag sightings were plotted and home ranges found to overlap during the rut. No evidence is offered for territorial defence. The structure of the rutting groups seems to be flexible.

8. Severe competition from New Forest ponies is blamed for the lower fecundity and nutritional stress in the Hampshire sika deer.

CHAPTER ONE

Introduction

INTRODUCTION

1 The origin of the sika deer: *Cervus nippon*

Sika deer are members of the Cervidae, a family within the Artiodactyla which also includes the genera *Dama* (fallow deer), *Rangifer* (Reindeer), *Alces* (moose), *Capreolus* (roe deer), as well as red deer as fellow members of the genus *Cervus*.

In the natural state sika come from eastern Asia, including the south-eastern corner of Russia, the mainland of China, the Island of Taiwan (Formosa) and various Japanese islands. Over this area they were thought to have developed into a number of races of which Formosan, Manchurian and Japanese are the best known. Other races have been described from the mainland (and are still being reported: Zhuopu et al. 1970), but these may in fact be only one race which varies gradually from one end of its range to another (Horwood and Masters 1981). An alternative hypothesis produced after some more recent research suggests that some, if not all, of the sub-species of sika deer may be entirely of hybrid origin (Lowe and Gardiner 1975).

2 Introduction and spread in Britain

It is generally accepted that sika deer were introduced into Britain around 1860. At that time specimens from two races, Cervus nippon nippon and C. n. hortulorum were presented to the Zoological Society and some C. n. nippon were purchased by Viscount Powerscourt for his park at Enniskerry, County Wicklow, Ireland. These bred very successfully and by 1884 Powerscourt wrote that he had "...upwards of 100 of them, besides having shot two or three yearly and also having given away a great many and sold others...".

The Zoological Society acquired specimens of another race of the species, C. n. taionanus in 1861, and the Manchurian form of C. n. hortulorum in 1864 but, with the exception of Woburn private parks were all stocked with C. n. nippon (Gray 1861, Powerscourt 1884, Sclater 1862, Swinhoe 1864 - all quoted in Lowe and Gardiner 1975).

There have been a few deliberate releases of sika deer into the wild, and inevitable escapes, so that sika are now established in the feral state in several parts of Britain and Ireland (see figure 1:1)

The introduction of sika to the west of Scotland follows a similar pattern with escapes from Carradale (in the south of the Kintyre Peninsular) in 1896. These deer spread gradually northwards, were halted briefly by the

Crinan Canal, but have now dispersed as far north and west as Oban where a couple was shot in 1980 (D.Henderson pers. comm.). The sika deer are known in Strathlachan and Glendaruel although whether they walked round Loch Fyne, or swam across the narrow strait between Lochgilphead and Ballimore is unknown. A very few have been shot in Eredine Forest on the east bank of Loch Awe.

In the north of Scotland the present distribution reports major populations at Farigaig (on the east bank of Loch Ness), Torrachilty (near Dingwall), Ardross and Shin (near Lairg in Sutherland) (A.Hinde pers. comm.).

The numbers of sika are increasing rapidly in these areas and an indication is given (assuming a constant shooting policy) by the number culled each year (figure 1:2).

Sika deer were introduced into the New Forest when a pair was given to John, second Baron Montagu of Beaulieu, by King Edward VII from his Windsor estate in the early 1900's. The precise date is unknown and there is some debate as to whether this was in 1902, 1903 or 1904 (Rowland 1967). This first pair was penned at the Old Bungalow at Thorns Beach but escaped into Sowley Wood (Grid reference: SU 375965) in the same year. A second pair arrived a year later and was released in Ashen Wood (Purnell Firs: Grid reference: SZ 393004). The present stock has bred from these, and so successful were they that by 1930 steps had to be taken to reduce the population. Since then they have spread through Hawkhill Inclosure, Frame Heath Inclosure and New Copse Inclosure at least as far as the Brockenhurst Manor in the west. It is in this area (Grid reference: SZ 340025) that the Hampshire part of the study has been based.

Sika deer arrived in Dorset through two separate introductions; one in 1896 to Brownsea Island in the middle of Poole Harbour (Grid reference: SZ 020880), and the second a few years later to Hyde House Deer Park about four miles north west of Wareham (Grid reference: SY 871905).

It is claimed (Whitehead 1964) that some of the Brownsea Island introduction swam ashore; presumably to the Goathorn Peninsular (via Furzey Island), on the night of their release. It was not long before they spread onto the Rempstone Estate and by 1909 they were a common sight on the heaths around there (Horwood 1971).

The first record of an escape from Hyde House comes from the neighbouring Trigan Estate where sika were seen in 1926 or 1927. Whether or not there were other escapes is unclear, but the whole herd was freed during the Second World War while the estate was in the hands of the Government (Horwood 1971). These animals were present in sufficient numbers by 1947 to have created permanent tracks around and across Morden Bog as Horwood (loc. cit.) reports from an inspection of aerial photographs taken at that time.

3 The red:sika hybrid

Of considerable interest, not merely because of the taxonomic challenge it presents, but also because of the conservation and management implications, is the fact that sika deer hybridise successfully with the native red deer (*Cervus elaphus L*). Early reports were made of this phenomenon by Powerscourt (1884) and Brooke (1898) in County Wicklow in Ireland, and it has also been reported more recently in at least four separate areas of Britain (Whitehead 1964, Delap 1967, MacNally 1969, Blair 1972).

Recent studies (Harrington 1973, 1974) have shown that sika, red and wapiti (*Cervus elaphus canadensis*) can be successfully interbred and electrophoretic separation of blood proteins is now used to distinguish hybrid from pure stock.

Conditions for hybridisation are stringent; a red stag (mechanical problems are thought to inhibit the sika male from covering the much taller red hind) of less than three years of age (irreparable damage is caused to the hind's reproductive tract by the vigorous thrusting of the older male) can mate successfully with sika hinds during their overlapping rutting seasons (R. Harrington in a paper to the Ungulate Research Group meeting at Southampton

University; December 1981). Despite these rigorous conditions it is believed that the phenomenen is widespread and "...is an insidious invasion which leads to the complete destruction of the genetic integrity of at least the red deer population and possibly of the sika population..." (Harrington 1973). It is now believed that the only native stocks of red deer persisting in Britain and Ireland are in County Kerry (where although sympatric, the native red deer may have evolved in greater geographical isolation than other herds and may be less compatible with the sika), and Scotland (where sika deer are not yet thoroughly dispersed) and north-west England (Lowe and Gardiner 1975). Hybridisation has also been reported between these species where their ranges overlap in north-eastern China (Corbett 1966 - in Lowe and Gardiner 1975) a detail which caused Lowe and Gardiner to suggest that maybe the mainland subspecies are in fact variations on the hybrid stock and perhaps the only true subspecies are found on the islands where they have evolved in geographical isolation.

It is unclear whether the sika deer in the New Forest are hybrid or pure bred. It is generally agreed that the main concentration of the sika in the New Forest is in an area bounded by the Southampton to Bournemouth railway line in the north, the Lymington River in the west, the Beaulieu River in the east and the sea in the south. The main herd of red deer is known to be several miles away in the north half of the forest although there is a smaller herd centred on the Brockenhurst Woods. There have been occasional sightings of red deer in Frame Heath Inclosure (H.K.Hill pers. comm. and self).

Before the Second World War Hartford was reported "full" of red deer and by 1949 there were a few in King's Copse, Exbury, Ladycross and King's Hat areas (Rowland 1967). It is certain therefore that the New Forest red and sika deer have at least been sympatric for part of the last 50 years; it is thus probable, although not certain, that either or both herds are hybrid. No information is available as to whether the Dorset animals are pure bred or not, but the presence of hybrids in either instance would be difficult to determine from observations as sika-like hybrids are difficult to distinguish from pure bred sika (Harrington 1973).

Hybrids are becoming increasingly common in Scotland where the unusual characteristics of the first generation crosses have aroused many comments from the stalkers (D.Henderson pers. comm.). Hybrids have also been reported in New Zealand (Davidson 1973).

4 Literature review

There has been very little information published on the Japanese sika deer in Britain since its introduction in

1860 and the majority of that refers more to descriptions of the animal (Whitehead 1964, Harris and Duff 1969) and to speculative reports on hybridisation (Delap 1972).

The majority of published work comes from abroad; particularly from New Zealand and Japan, and the information in these articles is reviewed below.

a. Diet

Using criteria obtained from a study of East African ruminants and their rumen morphology (Hofmann and Stewart 1972), Hofmann (1981) suggested that the sika deer should be classified as an "opportunustic feeder"; the rumen being typical of bulk and forage eaters. The animals are, he reports, particularly efficient at breaking down fibrous food (even food of poor quality) and in building up fat reserves.

This classification supports the work of Takatsuki (1980) working on sika deer on the Kinkazan Island off Japan. He used faecal and feeding site examination to describe the diet and suggests that although the food composition varies considerably in composition between different vegetation types, the main component is always of grass. This latter conclusion is duplicated in work by Robinson (1973) on sika deer in Bowland (Lake District), and also by Prisyazhnyuk and Prisyazhnyuk (1974) working on Askolod Island. They found that the bulk of the food was grassy in origin and that fallen leaves are also taken; 97 species were consumed in all. Furubayashi and Maruyama (1977) reporting on sika in Fudakake (Tanzawa Mts Japan) state that 106 species were taken of which only 34 are forbs and grasses. That the remaining 72 are trees suggests that these animals are more browsers than grazers. Horwood and Masters (1970) report a similar finding from macroscopic examination of the rumen contents from 200 sika shot at Wareham in Dorset and from 6 shot in the New Forest in Hampshire. In the latter case the presence of pine needles led these to suggest that the New Forest deer are browsers, but they classified the Wareham deer as grazers.

b. Habitat Selection

Very little information has been published on habitat selection or use by sika deer.

Dzieciolowski (1979) reports that sika deer have a marked preference for two types of habitat; moist, mixed coniferous forest and grassy meadows. This is supported by Horwood and Masters (1970) who extend the details to propose a daily migration between feeding grounds (fields) at night and shelter in coniferous plantations during the daytime.

On a broader scale, seasonal movements of sika deer were investigated by foot print counts in the snow on the south slope of Mt. Nycho (2464 m) in Japan (Maruyama and Totake 1976). In the latter part of the winter the animals are concentrated at an altitude of between 1200m and 1500 m, probably because of the deep snow. As the snow melts they move higher but are soon attracted downwards by the growth of fresh plants. During the calving season these sika deer are widely scattered but by the middle of November they are forced up to shelter in the evergreen coniferous forest in the sub-alpine zone by the abrupt defoliation below.

Miura (1974) also found that the animals occupy a small winter range (based mainly on bamboo), whereas during the summer, the animals were widely dispersed and exploiting predominantly grassy areas.

Davidson (1979) working with self-attaching collars in New Zealand showed a low rate of dispersal of the sika deer (mean of 2.2 km in 16 months) and suggested that this is partly due to the annual return of the hinds to feeding grounds although the stags tend to disperse further.

c. Social Structure

Dzieciolowski (1979) reports a male to female sex ratio of 1:1.63, which is quite different to that offered by Prisyazhynuk and Prisyazhnyuk (1974) who suggest the male:female:calf ratio is 1:3.6:1.3.

d. Social Organisation

Miura (1974) writes that in the summer the mean group size of sika deer is less than 3 and most groups contain a hind and a calf; larger groups containing between 5 and 11 individuals are sometimes seen in the winter. This general finding is supported by Prisyazhnyuk and Prisyazhnyuk (1974) who report that the most frequent herds contain between two and ten animals but that herds of up to 40 animals are occasionally found.

Dzieciolowski (1979) reports sika deer forming groups containing between 2 and 6 individuals; the largest recorded being of 12.

Ito (1968) classified the groups of deer found on Kinkazan Island into three categories and showed that the herd size varies with season, topography and vegetation type. Autumn herds are the largest and the mean group size found in fields is 5.8 whereas in forests it is only 1.7.

e. Reproductive Behaviour

Horwood and Masters (1970) maintain that in the Poole Basin the stags mark out and defend a territory that the hinds have to cross on their nightly migration to the feeding grounds. The practice of defending a territory is also noted for the Bowland site (Mitchell and Robinson - quoted in Horwood and Masters 1981). Miura (1974) on the other hand, shows 7 males occupying a definite area throughout the season but saw no territorial defense.

The reproductive similarity between the sika deer and the red deer has been commented on by Davidson (1976). She gives the median parturition date, the spread of the birth season and the calving percentage from a small sample from a wide population and indicates the close similarity in the reproductive cycles of red and sika deer which doubtless contributes substantially to the apparent ease with which hybridisation occurs.

A step has been taken to improve research on sika deer and to consolidate current knowledge, with the formation of the International Sika Association. This year, at the annual conference, papers were very varied, ranging from "Systematic description using antler characteristics" (Meunier 1982) to "The evaluation of sika trophies" (Rumohr - Rundhof 1982).

5. Behaviour and ecology of sika deer in Britain

The most extensive British study, which ended thirteen years ago, was carried out on a marked population of sika deer on the Rempstone Estate to the west of Poole Harbour in Dorset (Grid reference: SY 985845) and has been variously reported in Horwood (1966, 1971 and 1973) and in Horwood and Masters (1970 and 1981). Field work was carried out between May 1965 and March 1969 and its aim was to "acquire as much information as possible" on the habits of sika deer (Horwood 1971). Several avenues of research were employed including the collection of measurements and specimens from culled animals, night observation from a vehicle and the capture, marking and releasing of the deer.

The reports give much valuable descriptive information on the appearance of the sika, on the annual cycle of the hinds, calves and stags, on some details of the rut and also on the home ranges of marked animals. A brief description of seasonal changes in group structure and composition is offered and a nocturnal feeding pattern is discussed.

During the rut Horwood suggests that the stags at Purbeck maintain a forest territory and mate with receptive hinds as they cross these areas on their way out to feed in the fields at night, or on their return in the morning. The stags seem to remain in the plantations, rarely emerging to feed until the rut is over. After that large mixed-sex groups are found but after a couple of months unisex parties form and the males move away.

The diet of the sika at Wareham (very close to Purbeck) was investigated using macroscopic examination of rumen contents and assessments of over 200 samples were carried out. The results suggested that the animals are predominantly grazers, rarely taking coniferous browse. This result has also been reported for sika deer in the

Lake District (Robinson 1973) and in Japan itself (Takatsuki 1980). However, on the (admittedly) shaky evidence from six animals shot in the New Forest in February, Horwood and Masters (1970) proposed that the Hampshire sika are mainly browsers and therefore contrast sharply with the Dorset animals.

The rationale behind the present study

As a result of their recent introduction, very little work has been carried out on the sika deer in Britain although a lot of anecdotal information is available (eg: Milner Bennetts 1981), but because of its rapid spread in Scotland, and its successful hybridisation with the native red deer (*Cervus elaphus*) (Harrington 1973), there is a real need for a management policy based on a knowledge of the behaviour and ecology of these animals.

Two successful herds were studied here: one in the mainly deciduous New Forest in Hampshire and the other in the coniferous forests of the Poole Basin. It is likely that a comparison between these two herds will reveal differences in ecology, social organisation and social structure which could be attributed to their different environments (Jarman 1974).

Working on East African *Bovidae*, Jarman suggests that differences are found in the behavioural ecology of antelope from areas where food supplies are exploited by different strategies. Working with 31 species, Jarman investigated the relationships between body size and many ecological parameters, notably feeding style, social organisation, habitat use and predator defense strategy. On the basis of these relationships a five-point classification was proposed extending between the small, territorial browsing antelope to the large, social, non-selective grazing animal.

Between these extremes lies a variety of mixed feeding styles which are matched by the appropriate social order. The argument gains weight from considerations of the differences within a species; where two populations occur under different environmental conditions. Jarman himself worked on buffalo, Estes (1967) on gazelle and Hirth (1977) on white-tailed deer, but apart from these, almost all ungulates in which social organisation has been studied have occurred in a single habitat and there has been little evidence of intra-specific variation eg. Leuthold (1966).

Horwood and Masters (1970) report dietary differences between New Forest and Poole Basin sika deer and also propose that differences in social structure, social organisation and ecology may exist.

The current project has attempted to collect information on each of the following main points:

1. Use of habitat; use of different vegetation types at different times of the day; diurnal and seasonal changes in habitat use; circadian cycles of specific activities and use of different vegetation types for particular activities.

2. Food and feeding ecology; important food plants and changes in diet throughout the year.

3. Social structure and organisation; total population structure in terms of age and sex, group sizes and their relation to habitat, group age and sex structure.

4. Social behaviour; behaviour within the group, dominance, interactions between individuals, reproductive behaviour.

7. The Study site

a) The New Forest: Hampshire

The New Forest is an extensive area of semi-natural woodland, partly commercially managed, occupying a central position on the Eocene and Oligocene strata in the downfold of chalk known as the Hampshire Basin. Rising to just over 400 feet above sea level in the north, the area consists of various levels of sedimentary sands and gravels covered by an impoverished soil colonised by heather and acid-tolerant grassland (Tubbs 1968).

The area was designated a Royal Forest around the eleventh century; a peculiar legal status it holds until this day. Within this area successive Acts of Parliament since 1698 provided for the enclosure of land by the Crown for the growth of timber and there are now about 18,000 areas of statutory silvicultural enclosures (see Tubbs 1968 for further details). It is in a small group of the enclosures, near Brockenhurst in the south of the forest, that much of the field work in this study was performed.

Frame Heath Inclosure (Grid reference: SU 3204) is an area of mixed and deciduous woodland with several pockets of coniferous cultivation reported (with the neighbouring enclosures of Stockley, New Copse and Hawkhill) to hold a population of about 170 sika deer. These seem to be limited in their distribution by the Southampton to Bournemouth railway line in the north, the Beaulieu river in the east, the Lymington River in the west and the sea in the south. The area also holds small, transient populations of fallow deer (_Dama dama_) and roe deer (_Capreolus capreolus_). The New Forest pony, although officially excluded from the enclosures, is free-roaming through much of the study area.

The variety of vegetation types in the area is wide, even more so since recent felling, thinning and planting created representative zones of all the commercially recognised forest stages. The enclosure is bordered on two sides by acid heath.

The area is well-provided with gravel rides and there is also an observation tower that may be hired for deer watching. A Forestry Commission campsite (Roundhill) is near Frame and provides a steady stream of visitors, so with these, the traffic from local residents, railway maintenance personnel and the Forestry Commission keepers, the area is fairly disturbed.

The 300ha of woods centred on the observation tower is designated a "deer sanctuary" in which no shooting occurs and where the highest density of deer is usually found. It was in this particular area that the study began.

b) Wareham Forest: Dorset

Situated to the west of Poole Harbour, between the A35 and the A352, the main block of Wareham Forest (Grid reference:ST 8594) consists of about 3,000ha of coniferous woodland in various stages of management.

The area is based on tertiary deposits of sands and gravels with an impoverished, locally poorly drained soil above. This has led to the formation of Morden Bog in the middle of the main forest block which was designated a National Nature Reserve several years ago.

This area, unlike the New Forest, is not tourist-oriented, and has a high annual production of timber. As a direct result the forest has a wide variety of vegetation types although because of the poor soil many of the trees are stunted; much smaller than would be expected from their ages.

Surrounding the plantations are extensive tracts of agricultural land and smaller reaches of acid heath. There are a few roe deer resident in these woods and they compete with a population of sika deer estimated at several hundreds. Despite the extensive forestry and the winter shooting of wildfowl, the area remains relatively undisturbed.

c. Purbeck Forest: Dorset

A subsidiary field site was established at Purbeck late in 1980. Slightly smaller than the main block at Wareham, the forest at Purbeck is situated to the south of Poole Harbour (Grid reference: ST 9885) and is about 2,000ha in area.

The Rempstone Estate is privately owned and is leased to the Forestry Commission who manage the forest. Part of the area is also being explored by the Southern Gas Company with a gathering station and several pumping stations at Wytch Farm. With the pine plantations as a nucleus the estate forms an island bordered by acid heathland to the east, a chalk ridge to the south, farmland to the west and Poole Harbour to the north.

The plantations were installed between 1949 and 1958 and since little timber has been extracted as yet, the region contains a relatively low diversity of habitat. The population of sika deer is thriving and this area was the site of much of the previous British fieldwork on sika deer (Horwood 1969, 1971) although the area was probably mostly in a prethicket stage then; much more open than the dense thickets of today.

Having a very similar geology and an identical climate to Wareham this area was ideal for use as a third study site when animal numbers at Wareham were found to be inadequate, and fieldwork there supplied insufficient data.

CHAPTER TWO

Habitat occupation

HABITAT OCCUPATION

INTRODUCTION

Details of the pattern of habitat occupation and within that, information regarding patterns of habitat utilization, are fundamental to an understanding of the ecology of any animal. This information provides the basis from which an explanation of feeding habits, social structure, social organisation and ecology may be developed.

METHODS

In order to obtain data on habitat use and on circadian activity cycles which can be subjected to precise analysis, data has been collected by a restricted observational method which records animals found on a repetitively surveyed area, thus lending as much importance to "animal absences" as to "animal presences". These restricted methods, walked and driven transects, have been supplemented by further observations collected on a "free format" system of walkabouts which have yielded supportive, if anecdotal, details of many aspects of the animals' behaviour. The observations are further supplemented by indirect data from permanent dung accumulation plots placed in several habitat types in both the New Forest and Wareham.

1. Direct observations

Walked transects: New Forest

A circuit was planned in the deer sanctuary at the centre of Frame Heath Inclosure (see figure 2:1) to sample areas representative of the main vegetation types in the region. The route was 1½ miles long and could be walked in about forty minutes. The habitats surveyed were mixed woodland, prethicket, polestage, rides (both grassed and gravelled) and some recently clear-felled plots. To collect information on habitat occupation the route was walked every hour between 04.00 and 20.00 GMT, and during the night at 22.00, 00.00 and 02.00. This pattern was repeated every week for a year from September 1979 to September 1980. The survey had been started the previous year but was suspended in February so data was also available from October 1978 to January 1979.

At predetermined sites along the route the following details were noted:

i The number of deer visible in each habitat
ii The age and sex structure of each group of animals
iii The activity of each animal
iv If conditions allowed, anecdotal details on behavioural interactions were also recorded as were the prevailing weather conditions.

At night a powerful hand-held spotlamp was used to illuminate the deer; animals could be detected up to 200 m away in open habitats.

b. Driven transects: New Forest

Data collected along a walked transect route is relatively detailed but by necessity the area covered is only a small part of the sika's range. In order to supplement this information and to obtain complementary data from a wider area; perhaps from a more representative selection of habitat types, a second set of transects was patrolled by car. These covered nine miles of forest rides and the route was traversed at alternate hours throughout the 24 hour period once per week from January 1980 to November 1981 (see figure 2:2 for the route). The 24 hours was split into two twelve hour survey blocks.

These driven transects were conducted in exactly the same way as were the walks and identical records were collected.

The aim was to produce data that could be compared to that collected from the walked route and to that obtained from similar surveys in other forests, or from other studies on other species.

At the start of each transect (whether walked or driven) the prevailing weather conditions were noted and subsequent changes recorded.

At night a very powerful marine searchlight, mounted on the roof of the car and powered by the car battery, was used and animals over ¼ mile away could be located.

c. Driven transects: Wareham and Purbeck

In order to collect details of habitat occupation from a different population living in a different array of habitats, a series of driven transects was undertaken at Wareham; a commercial coniferous forest in south-east Dorset (see figure 2:3 for route).

These transects were started in October 1980 and initially covered a 24 hour period per week (in 12 hour blocks) in exactly the same way as was described for the New Forest. The route was 14 miles long and included extensive reaches of the forest as well as surrounding areas of farm and heathland.

Unfortunately , after three months of transects it became apparent that the population of sika deer at Wareham was too small (bearing in mind the denseness of the undergrowth and the small areas sampled) to yield sufficient data, so another study site was used, the Rempstone Estate near Corfe Castle (hereafter referred to as Purbeck) some seven miles east of Wareham.

Purbeck survey transects were started in January 1981 (see figure 2:4 for route) and in order not to sacrifice previous work at Wareham alternate weeks were worked in each of these coniferous forests. Unlike the New Forest, several of the rides used here were grassed or sand, and repeated use by the author and by heavy forest vehicles reduced some areas to a morass and in bad weather they were impassable.

The deer population at Purbeck seems to be much larger than that at Wareham and the records collected were adequate. Unfortunately the poor state of the rides worsened during October 1981, so regretfully the survey was halted. Thus, although a year of transects had been carried out at Wareham, relatively few animal observations were obtained; work at Purbeck (the site of previous fieldwork on sika deer in Southern England - Horwood 1966, 1971, 1973 and Horwood and Masters 1970) was stopped after only 8 months.

2. Indirect observations

a) Dung accumulation: New Forest.

To supplement the observational data a series of dung assessment transects were established in five different habitats in Frame Heath Inclosure. The habitats were selected on a Forestry Commission stock map and the longest line drawn through the biggest compartment of each habitat was converted to a compass bearing. Using a convenient landmark as a starting point, this bearing was followed in the field and a 7m by 7m quadrat established every 60 paces. Small wooden pegs were used to mark the quadrat corners to ensure accurate replacement of the boundaries on successive visits.

At the start of the assessment all the dung in each quadrat was removed; thereafter dung groups were counted and removed at the end of each month. A dung group was defined as an accumulation of ten or more pellets of which more than half had to lie within the quadrat boundaries.

Eight quadrats were set up on each transect, one through each of the following habitats:

- i Mixed woodland
- ii Scrub
- iii Oak woodland
- iv Prethicket
- v Polestage

Definitions and descriptions of these are given in the next section.

The quadrats were assessed every month from September 1979 to October 1981. Several small samples of pellets were saved from each transect and were stored in 10% formalin. These were required for diet determination as it was hoped that microhistological examination of the epidermal fragments in the pellets would yield information on food habits during months when rumina from culled animals were not available.

b. Dung accumulation: Wareham

An equivalent set of dung transects, each with eight quadrats, were laid out at Wareham in the following vegetation types:

i Plantation

ii Prethicket

iii Thicket

iv Polestage

These were cleared at monthly intervals between September 1980 and October 1981. The numbers of pellet groups found were very small (reinforcing the impression gained from the driven transects on the size of the resident sika deer population) but clearances were maintained as samples of faeces were required for diet determination.

c. Vegetation Surveys

A vegetation assessment was carried out at each of the dung quadrats every three months to reinforce the habitat classifications and to locate likely food supplies. To this end the Braun-Blanquet scales of cover and sociability were employed to describe the status of each species in each quadrat. The scales are

Cover	Sociability
1. 1 - 5%	1. Isolated
2. 6 - 25%	2. Tufts
3. 26 - 50%	3. Patches
4. 51 - 70%	4. Carpet with holes
5. 71 - 100%	5. Pure carpet

3. Habitat definitions

To avoid confusion the habitats discussed throughout this thesis are described here and in future will be referred to by their designated names only.

a. Oak Woodlands

This is by far the largest and the most continuous single habitat within the boundaries of Frame Heath, New Copse and Hawkhill Inclosures. It is poorly represented at Wareham and Purbeck and could be defined as "any area of woodland with a substantial part of the canopy consisting of mature oak and beech trees." In practice this is inadequate as forestry policy in the New Forest requires the preservation of hardwood trees so there are ocasional standard oaks to be found in all the wooded New Forest habitats.

These oakwood areas are mainly deciduous with a mixed canopy usually of oak (Quercus robur) and beech (Fagus sylvatica), but occasionally Scot s Pine (Pinus sylvestris) and Douglas Fir (Pseudotsuga menziesii). A secondary canopy of holly (Ilex aquifolium), yew (Taxus baccata), hawthorn (Crataegus monogyna) and blackthorn (Prunus spinosa) is common, and there are extensive patches of birch scrub (Betula spp). Below this one finds an extensive carpet of slowly decaying leaves broken up by small patches of grass (Agrostis tenuis, Agrostis setacea) with smaller areas of Molinia. There are also local patches of bramble (Rubus agg), bracken (Pteridium aquilinum) and rose (Rosa canina) as well as many forbs.

b Plantation

This is defined as an area containing coniferous trees, planted in rows in or after 1975. No tree is higher than 1.5m and there is an extensive and varied ground cover containing several species of grass and many forbs. Bracken may hide the trees in the summer but in the winter the area is effectively an open one. There is no plantation at Purbeck.

c. Prethicket

Defined as containing coniferous trees planted around 1965, this vegetation type holds trees of about 4.5m in height. Their lower branches may meet, but do not interlock and thus the area provides a lot of shelter. These areas are extensively grassed but Calluna, Ulex and Rubus are also found here; particularly at Wareham.

d. Thicket

Trees in the thicket stage were planted around 1950, exceed 6m in height and have needleless, interlocking lower branches. These areas are therefore very dense and the ground cover is almost non-existent due to poor light levels.

e. Polestage

These trees were planted around 1935 and this stage constitutes the climax of the commercial forest. Trees have been brashed and the areas extensively thinned so a secondary canopy of birch and holly may be developing. There may also be some ground cover of forbs, grasses and bracken.

f. Clear-felled

After maturation the polestage areas are felled and large areas are opened up to recolonisation by herbs and grasses - before being planted with the next tree crop. There is frequently a large amount of brash left behind (a valuable food resource whilst fresh) but the area is open, exposed and bare for several months after felling. No compartments at Purbeck have been recently cleared.

g. Rides

Both grass and gravel-covered rides are found in all three forests and these form not only the main access routes to the compartments but are also the boundaries between the compartments, and frequently between habitat types. By virtue of being drained, ditched and shaded they support a rich growth of grasses (A.tenuis, A.setacea, Luzula, Holcus, Festuca) and many forbs. In this respect they are treated as a separate habitat except when completely overhung and overgrown by surrounding vegetation, in which case they are treated as part of that area.

h. Fields

Most of the fields are bordered on at least one side by forest compartments and despite being fenced, are often found to contain many deer. Most of the fields at Wareham and Purbeck are grassed and may hold cattle and sheep. Field areas at Frame are poorly represented and hold a small number of horses.

i. Marsh

Unique to Purbeck is an expanse of saltmarsh. This floods at every high tide, but dries out between and supports an extensive sward of halophytic plants. The marsh is surrounded by extensive reed beds in which the deer are invisible; the entire area is dissected by ditches and channels.

j. Heath

Characterised by an 85% covering of Calluna, this habitat is found in all three study sites and is colonised by "acid soil" plants; Ulex, Molinia, Vaccinium and some sphagnum moss. The Calluna at Purbeck is tall enough to hide deer lying down as, unlike that in the New Forest, it is neither cut nor burned.

RESULTS

1. The New Forest

a. Field observations.

At each stopping point on the driven or walked transect route the number of deer visible was noted, as was their sex, age class, and if possible their activity. This chapter is restricted to consideration of occupation patterns irrespective of activity. As the driven transects yield a more extensive set of observations from a wider range of vegetation types, the presentation of results will stem from these and will be supported, where appropriate, by data from the walked route.

The simplest analysis is to calculate the number of animals found each month in a particular habitat, and to express this as a percentage of the total number of animals found in all the habitats. Results are presented to show patterns of habitat occupance displayed by the deer, and the changes in this between months. Data is given in figure 2:5 for the driven transects and in figure 2:6 for the walks.

If the main vegetation types in the survey could have been sampled in roughly the same relative proportions as they occur in the study area then direct field results would give a clear impression of habitat use; these results are described briefly here.

i. Patterns of habitat occupation considered per month

In all months except one (July 1981) the majority of sightings, (up to 75%), is supported by the oakwoods and the fewest are consistently provided by the heath and plantation areas; occasionally holding no sika deer at all. During the winter months, rides, polestage areas and oakwoods contribute between 70% and 80% of the sightings between them; a situation that changes in the summer when the same three contribute between 45% and 65% of the results. The habitats which supply the fewest sightings each month, apart from heath and plantation, are felled areas and the prethicket. The contribution from the felled areas varies from 3% (November 1980) to 26% (September 1981) and in the prethicket an equivalent summer to winter difference is found (2.3% in December 1980 and 13.5% in July 1981). The precise relationship of these minor habitats to the major ones changes frequently and inconsistently, probably as a result of their relatively small sample areas and the density of the vegetation.

ii. Patterns of habitat occupation considered by vegetation type

Clearer presentation of yearly trends in the proportion of sightings in the habitats is achieved by plotting a series of graphs showing the percentage of the total number of animals found each month in each habitat. These, with equivalent details from the walked route, are plotted in figue 2:7.

Occupation of the oakwoods seems to follow an annual cycle with a high proportion of the sightings collected here in the winter and a low proportion in the summer. The walked data overlaps the driven by six months (extending the survey to 26 months) and clearly shows the same pattern.

The reciprocal relationship is evident from the prethicket areas where a higher fraction of the sightings is contributed in the summer than the winter, although the scale of numbers is much lower than in the oakwoods. This too is most effectively supported by the walked data.

This "summer high - winter low" pattern is shown by data relating to field occupation although here there is no supportive result from the walked route. The contribution by felled areas when assessed by driven transect also follows this trend, but not when assessed by the walks. The reason is that felling was carried out during the walked transect survey but on the driven route was completed 18 months ago. Thus deer located on the shorter route were exploiting the fresh supplies of brash and bark during the winter and continued to do so until felling stopped and the supplies were exhausted in May. After a brief respite colonising herbs and grasses provide a new food supply and the deer are attracted back to the area; hence the late summer increase in occupation.

The progressive attraction afforded by this recolonisation is clearly demonstrated by the histogram of felled areas sampled on the driven circuit (figure 2:7), the sharp decline in sightings in the autumn coincides with the onset of colder weather and the fall of acorns and leaves which provide an attractive food source elsewhere.

Polestage areas seem, with few exceptions, to be fairly constant in their contributions to the results. The huge increase in sightings here in October 1979 in the walked data is undoubtedly due to the search for acorns, and is reflected again in driven data for October 1981. It was reported that many standard oak trees are left standing in the coniferous blocks.

The results presented and discussed above may be interpreted as true reflections of habitat use only if the vegetation types are sampled in direct proportion to their availability.

Unfortunately this is not the case and these "raw" results are biased very heavily in favour of those habitats that by virtue of their abundance, or superior visibility (by day or at night), contribute a disproportionate amount to the total area surveyed. This is clearly shown in figures 2:8 and 2:9 which give the area of each habitat sampled by each method and express it both as a percentage of the total habitat available to the deer, and as a percentage of the area sampled. In both cases the oakwoods contribute the major part so it is not surprising that more animals are found here than in the other habitats.

The ideal situation is almost achieved by the walked circuit where the areas of oakwoods, prethicket and polestage contribute 2.8%, 2.5% and 2.4% of the total habitats respectively. Unfortunately these proportions vary considerably on the driven circuit and it is proposed to correct for this. To assist evaluation of the validity of the correction and to interpret the real value of the modified results, the field data were described above in more detail than perhaps seems necessary.

b. Modification of transect results: calculation of "occupance".

To reduce the bias caused by the majority of the survey being of one or two major habitat types and therefore allowing realistic comparisons to be made between the habitats, the deer found could be expressed as "numbers seen per unit area surveyed" (npua). These values only relate to the animals found, though, so fail to report on the status of the entire population. They are also prone to bias themselves as shifts in animals from small to large areas will produce large changes in the npua of the smaller area and no appreciable alteration of the npua of the larger.

Assuming that each portion of the habitats used in the survey is representative of the habitat as a whole, the npua values can be used to calculate the theoretical population held in the habitat merely by multiplying by the total area of the habitat that is available to the deer. This calculation can be carried out using a npua obtained over any time scale desired; here 24 hours and later, "day" and "night" are used.

The resulting theoretical populations are often large and by the nature of the modification employed, may "vary" from month to month. To reduce these values to a form in which they may be compared between months, they are expressed as the percentage of the total theoretical population per habitat; a quantity labelled as the "occupance" of the habitat.

The walked transect results will be used to supplement the driven results and the values used are given in figure 2:10 (driven data) and in figure 2:11 (walked data). These are also plotted in histogram form in figures 2:16 and 2:16a.

As with the field data two avenues of inspection of the results are possible; habitat occupance considered by month across vegetation types (monthly status) and considered by vegetation type across months (yearly trends).

i. Monthly status of habitat occupation

The modification of the numbers has had a considerable effect on the original results and the prethicket areas are now revealed, with the oakwoods, as one of the most important vegetation types. The overall status of the other habitats is little changed; fields, heath and plantation are little used and the apparent level of use of polestage is reduced.

Statistical analysis of these results is now possible by comparing the monthly theoretical population in each habitat using a chi-squared test. Neighbouring months are compared and successive comparisons were carried out until the required significance (in this case p=0.01) was achieved. This high level was chosen so as to avoid attaching too much significance to the inevitable fluctuations in results derived from some of the minor habitats. The comparisons and their significance values are shown in figure 2:12.

These results suggest that the habitat occupation patterns change more rapidly in spring and autumn than they do in summer and winter. In the former instance a narrower span of months is required in the comparison before the required significance level is reached.

The period covered by these driven transects is sufficiently long to allow paired comparison of a few months from consecutive years. Five such comparisons are possible but in only one was the situation in each year the same; June.

Modification of the walked transect field data by the occupance calculation causes the same re-emphasis of results; an inflation of the relative importance of prethicket areas to the population as a whole. However, the statistical comparison of the situation in adjacent months only partly supports the conclusions sustained from the driven data. This is probably because the areas utilised here are fairly small and so are less representative of the region as a whole; nevertheless even on this scale the winter occupation pattern is relatively unchanging whereas that in the spring and summer alters rapidly (figure 2:13).

Statistical comparisons (by Spearman Rank correlation) are possible between the 5 months surveyed by both methods but because of the relatively small number of habitats common to each method, the correlation is not very successful. A close similarity is shown between July 1980 in both surveys, an exact agreement in August and a clear difference in the two other months (May and June).

Pairwise comparisons are also possible between months in the two winters surveyed on foot: 1978 - 1979 and 1979 - 1980. December and January occupance patterns are not significantly different (p=0.01) but November is, perhaps due to differences in the acorn crop in the two years (see Diet, chapter 4) causing different exploitation of the habitats.

ii. Faecal accumulation results

The results above are all derived from "instant" records made from animals found in predetermined survey sites. As such they are liable to distortion by human disturbance and weather effects and thus may or may not be representative of the month as a whole, even though each month is assessed from eight or ten 12-hour survey periods. It was to reinforce (or to refute) these results that the dung accumulation plots were established.

The advantage of data from these dung quadrats is that they are less prone to disturbance and to short-term influence of weather effects than are the observed details. Further, they are cumulative, representing "animal presences" throughout the period between successive clearances and so sample more days in a month than the observer can.

Initially 5 dung transects were established in the Frame area and these were thought to survey the main habitats available. Subsequent inspection of the Braun-Blanquet records (made every three months) revealed that in fact only three distinct habitats were adequately represented; the differences between scrub, mixed woodland and oakwoods were so minor that the results were combined. Therefore the three habitats assessed were polestage Scot s Pine (Pinus sylvestris), prethicket Corsican Pine (P. nigra) and oak woodland. The number of dung groups found on each transect on each clearance are given in figure 2:14. When expressed as a percentage of the total number of piles found, the results indicate perpetual domination by prethicket with oakwood areas subordinate and polestage last.

These results are really only densities and take no account of the total level of use sustained by the habitat type in question. There is no adequate weighting given to a habitat which may hold a large number of animals but because of its surface area displays a low dung density and so is represented by a few pellet groups in the quadrat.

To compensate for this the mean number of pellet groups per square metre of ground searched was calculated for each habitat. Multiplying this value by the total area of the habitat available produces the theoretical total deposition of dung over the month. The assumption that the areas sampled are entirely representative of the vegetation type has to be made (which may be a problem if dunging is clumped) but if this is accepted, the total occupation of these areas can be represented by the percentage of the total thoeretical dung deposition each month; this is plotted in figure 2:15.

These modifications change the original result substantially and it now coincides very closely with that gained from the total occupation results (compare figures 2:15, 2:16 and 2:16a). Oak woodland is shown as having a high level of use each winter (1979 - 1980 and 1980 - 1981) and yet it is exceeded by prethicket in the summer. Polestage areas are never very highly utilised, but the results do show a lower level of use in winter than in spring or summer - contrary to the total occupance results.

The agreement between the results from the dung plots and the driven transects was investigated using a chi-squared test to compare the monthly theoretical population in each habitat with the theoretical dung deposited there. All months except two (June and September 1981) were shown to be in close agreement (p=0.05).

iii. Yearly trends in habitat occupation

As the same manipulation has been carried out on the raw data from each month, the annual trends in habitat occupation described from the field records will be found here even though the figures are now expressed as a percentage of the total theoretical population.

Histograms are presented drawn for both walked and driven transects (figures 2:16 and 2:16a) and the close correspondence of the results, particularly in the inverse relationship between the use of prethicket and oakwoods, is very clear. This is further supported by the occupance figures derived from the dung accumulation plots which are shown in figure 2:15.

iv. Day and night occupation

So far the occupation results have been presented bulked up and thus display a "monthly summary" for each habitat. Clearly this is an over-simplification. Previous data has shown a monthly change in the occupation of some habitats and this could be due to different use of the areas during day and nighttime. Seasonal differences in habitat use would therefore be attributed to seasonal changes in the length of the night and not to biological factors.

To investigate this possibility the occupation figures have been recalculated for each month, representing day and night separately. The values are given in figure 2:17 (from driven data) and in figure 2:18 (from the walked data). These are plotted in histograms in figures 2:19 and 2:20 respectively.

The same annual trends in habitat use and the same inter-relationship between the habitats are evident although slightly more exaggerated due to the greater fluctuations derived from smaller sample sizes.

The most obvious feature of this revised presentation is that there is indeed a difference between day and night occupation of some of the habitats. This is not a difference that coincides with the changing length of day as some habitats (oakwoods, for instance) show a consistently higher level of use at night all the year round. Prethicket use is higher in daytime than at night and rides seem to sustain approximately the same amount of use irrespective of day or night; except in the winter when daytime use is greater. Polestage areas, minor contributors to the total pattern, seem to be night-dominated; particularly in the late summer of 1980 and during the latter part of the winter 1980 - 1981. The figures for clear-felled areas and fields are so low when reduced in this way that no consistent pattern is apparent. This analysis shows a more varied use of habitats under day and night regimes which is not reflected in the data from the walked transects. However, there is a relatively even day and night use of rides indicated (as in the driven results), but major differences occur in the portrayal of oakwoods and prethicket. Use of oakwoods fluctuates widely, and prethicket is shown as day-dominated in winter and night-dominated in the early spring and late summer.

This difference in result may be because the areas sampled by the walked route at night are very small and must therefore produce a varied result. However, it could also be that the more intimate nature of the walked transect route, revealing details from the interior of compartments, shows that these areas are less influenced by changes between night and day than are the edge regions sampled by the driven route.

The results obtained from the clear-felled area on the walked route are considerably influenced by the presence of the workmen. They were present during the daytime so the deer were forced to exploit the fresh supplies of brash and bark at night. The felling ceased in April and by May the brash supplies were exhausted so the area supported a smaller proportion of the animals, but they were then able to feed in daylight as there was little or no human interference. Use of these areas increased towards the end of the summer as new grass and forbs colonised the area.

V. Circadian habitat occupation pattern

Some of these results are derived from samples sufficiently large that they can be broken down, meaningfully, to give an even more detailed description of habitat occupation. At this level the situation every two hours (on each survey occasion) is assessed.

These bi-hourly figures are calculated from the observed npua in each habitat at a particular time, multiplied by the total area of that habitat available to the deer. This value represents the theoretical population held by that habitat at that time and is better represented as an hourly percentage of the total in all the habitats.

The observed npua in each hour in each habitat can change more substantially in smaller areas than in larger ones and thus there is a considerable fluctuation in the derived population for each time period. The result of this is that comparisons between successive hours cannot be made directly unless the total theoretical population is the same on each occasion. In reality the graphs submitted (figure 2:21) are bi-hourly declarations of the status quo and each occasion should really be treated as a separate entity. That an area is shown as holding 20% fewer deer than it did on the previous occasion may be because the theoretical population in another habitat has increased dramatically, and may not be because deer have actually departed. There are no occasions when the total theoretical population in successive hours is the same; on a few occasions some figures are similar but these are so unevenly distributed that they are not discussed.

One graph is plotted per month and each has the results from all habitats superimposed. These figures are obtained from the driven transects; the supportive nature of results from the walked route was adequately described earlier. The smaller areas surveyed on the walks and the smaller array of habitats used will inevitably produce a more widely fluctuating set of results which would not yield so effectively to this more detailed examination.

The figures are all plotted with midnight at the centre of the x-axis to enhance the presentation of the night-based data collected at Purbeck. In order that diurnal patterns may be related to the hours of light and dark, the period of night is also shown on the x-axis.

The earlier analysis has shown that the main contributors to the pattern of habitat occupation were prethicket and oakwood areas and despite the considerable reduction in sample size here, this is unchanged. The other habitats; polestage, fields and rides sustain very low levels of use and have been excluded from the graphs for clarity.

The pattern plotted on the graphs (figures 2:21) show high levels of prethicket occupation throughout the daylight hours, and high levels of oakwood use during the night for many of the summer months, as was proposed earlier. Of the minor habitats, polestage areas sustain the most use.

This pattern persists with few variations from May to August (1980) when the use of oakwoods and prethicket becomes more fragmented so that by October the situation has changed considerably and the oakwoods sustain the most use throughout the 24 hours.

Daytime use of prethicket by the animals remains low until January when it again exceeds oakwoods. Throughout this time use of polestage exceeds that of the minor habitats, with the possible exception of the rides, which are well-used around dawn and dusk.

Daytime use of prethicket is unchallenged by April although the majority of nighttime occupation is still centred upon the oakwoods; the changeover occurring around dawn and dusk. It is at this time of year that use of the fields (negligible until now), becomes more substantial and occasionally exceeds that of the other minor habitats.

The supremacy of the prethicket use continues with few interruptions throughout the summer. Amongst the smaller areas polestage, felled areas and rides are all dominant for brief periods.

Towards the end of the summer of 1981 the separation of use of these two main areas breaks down again with rapid switching between use of oakwoods and prethicket. This has stabilised by the middle of the autumn when the levels of use of these two are very similar but oakwoods are dominant.

Emphasis amongst the lesser vegetation types changes frequently with the rides superior around dawn and dusk throughout the survey and felled areas receiving more use in the early mornings and evenings. Polestage regions become the dominant habitat amongst these in October and use of the fields, which gradually declined during the summer, remains low throughout the 24 hours.

C.Habitat preferences

i.Total preferences

Results so far have described where the deer are to be found, albeit in some detail, but have given no indication as to whether a particular habitat has been selected or whether its level of occupation is merely the result of a finite area of woodland containing an evenly distributed population.

To investigate the "preferences" expressed for each habitat, a ratio has been calculated for each habitat every month thus:

$$\frac{\text{Number of deer seen in vegetation type H}}{\text{Number of deer seen overall}}$$

This takes no account of the different areas surveyed in each habitat, and on the assumption that the deer are randomly distributed, without expressing a preference for a particular area this ratio would equal

$$\frac{\text{Area of habitat H surveyed}}{\text{total area surveyed}}$$

This can be simplified to:

$$\frac{\text{npua deer found in habitat H}}{\text{total npua found overall}}$$

A ratio in excess of one will demonstrate choice of an area; a ratio less than one, avoidance.

These values do not bear any relation to the actual occupance values discussed earlier and large preference indices, or large changes in index, do not necessarily indicate changes in occupance although the actual patterns of habitat use displayed may be very similar.

Indices are calculated for each habitat each month with data collected throughout the 24 hour period, the values are listed in figure 2:22.

The annual patterns suggested by the occupance values are neatly shown here although because of the enormous differences between the areas sampled in each habitat (see figure 2:8) indices cannot be compared directly between habitats as the effect on the observed npua in a small area (and thus on the index) of the arrival or departure of a small number of animals is exaggerated, whereas in a larger area the effect of this is negligible.

Important points to note are whether the indices are more or less than unity and whether, within a habitat, they are greater or smaller than in the previous month. Oakwoods show a very smooth cycle of active selection in the autumn and winter gradually declining to avoidance in the summer; the smoothness of the trend and the scale of the indices is the direct result of the large numbers of animals found and the large area of oakwoods sampled. The opposite cycle is shown by most of the other habitats; the areas being selected more in the summer than in the winter. The violence of the fluctuations in index is entirely the result of the small area of land surveyed, particularly in the case of fields and prethicket.

ii. Day and night preferences

Coinciding with the separation of the total occupation results into day and night, is the same split (for the same reasons) of the preference ratings. These are expected to fluctuate more widely as a result of the smaller sample sizes involved; the values are given in figure 2:23.

Obviously the overall trends described above will be unchanged, but the balance between day and night does alter during the year. Oak woodland has a night preference greater than daytime for all but two months (February and June 1981)and the smooth pattern discussed earlier is preserved. Polestage areas, always below one in index value, show a very confused pattern; probably because of the very small numbers of deer found there. Field day and night preferences fluctuate widely with winter values very low indeed and the majority of the months displaying a superior daytime index. This may be because these areas are occupied at dawn and dusk and so are included in "daytime data".

Prethicket results are susceptible to small sample vagaries, nonetheless, the similarity between day and night preferences in summer 1980 and autumn 1980 and the enormous differences between day and night indices in the winter of 1980 - 1981 is striking. The pattern deteriorates in the second summer of the study (1981).

Rides, shown earlier as being fairly consistent in rating, are depicted here as being more preferred in the daytime in every month and often avoided at night, although not consistently so. Use of the rides by the deer may not be governed by details like shelter or food supply, but may merely be because the animals need to cross in order to pass from one compartment to another, irrespective of time of day or season.

Felled areas also show a seasonal shift, not only in overall preferences but also in day and night domination. In the late spring, summer and early autumn, daylight use of these areas is preferred (probably corresponding to early morning and late evening). In the winter this preference switches to day with night avoidance but night yields a higher rating. In the spring or summer of the following year the daylight preferences are again highest.

Walked data preferences have also been calculated in this way (figure 2:24) and the overall results are very similar to those described above. Polestage is more preferred at night in the winter, as are the recently cleared felled areas. Rides are more day-selected in winter and night-selected in summer, but oakwoods show little difference. The prethicket results are inconsistent, again because of the small sample collected there.

These results have all been presented "in vacuo". Changes in habitat occupation shown here will be discussed, and explanations will be offered in the next few chapters when habitat utilisation and diet have been examined.

2. Purbeck

The second part of this chapter presents data equivalent to that collected in the New Forest, but now obtained from the coniferous plantations of the Rempstone Estate in Dorset. An identical presentation of data as was used in the New Forest section will be employed, giving the direct field results first and then modifying them to compensate for the biases discussed earlier.

Data collected on transects driven in the main forest block at Wareham had proved too sparse for worthwhile analysis, hence the Purbeck survey was begun. Wareham and Purbeck forests are very similar; they are close together so have similar climates and they have a similar geology (being based on Tertiary deposits). Further, by being managed on a commercial basis they are similar vegetationally, except that Wareham is longer established so contains a wider range of habitats than Purbeck. The observed results discussed here are from transects driven at Purbeck, but the indirect data was collected from dung accummulation plots established at Wareham.

There was no fieldwork carried out in March 1981 due to foot and mouth restrictions.

The Purbeck plantations form a continuum, (quite distinct from the more open areas) so all the plantation sightings have been amalgamated and the vegetation type - despite slight local differences - is described as thicket.

a. Field Observations

The field data is expressed first as the total number of deer found in each habitat each month and then as a percentage of the monthly total and is given in figure 2:25.

i. Patterns of habitat occupation considered per month

In every month the majority of the observations (Between 60% in May 1980 and 38% in July 1981) was collected in the fields with the other areas; marsh, heath and rides all contributing much smaller portions to the total. Almost invariably, the fewest observations are derived from the dense thickets of the compartments (between 2% and 9%) except during the summer when no deer were found in the small area of deciduous woodland sampled. This general pattern changes little each month except that the contributon made by marshy areas approaches that of the fields at the end of the summer.

ii. Patterns of habitat occupation considered by vegetation type

Yearly trends in these data are not clearly displayed because the work at Purbeck was started too late, was inhibited by foot and mouth restrictions and was halted prematurely by impassable rides caused by bad weather. Only eight months of transects were possible.

Use of the oakwoods is confined to autumn and winter when it seems likely that the deer are harvesting the crop of acorns and falling leaves (much as they do in the New Forest); deer were not found there at any other time. The use of rides and heaths fluctuates very widely as few animals were found there (between 8% and 16%, and 3% and 30% of the sightings respectively), and no consistent pattern emerges. The use of the saltmarsh is low in the winter and this increases gradually throughout the summer but this is a small area and its availability is governed by the state of the tide. The number of sightings recorded in the thickets is consistently low (directly as a result of the dense vegetation) and again follows no consistent pattern. Fields regularly provide the majority of observations showing a gradual increase during the spring, a decline during the summer, and a second increase in the early autumn.

b. Modification of transect results, calculation of occupance

Had the areas of each habitat been sampled in the same relative proportions as they occur in the study site, the direct results described above would give a valid picture of the patterns of habitat use by the sika deer at Purbeck. As in the New Forest though, this is not the case. Figure 2:26 shows the areas of each habitat sampled and expresses it both as a percentage of the total area surveyed and as a percentage of the total habitat available to the deer. Vastly differing portions of each habitat are used, so one can expect a different contribution from each habitat to the direct results.

The same compensating calculations have been carried out as before, deriving the theoretical population of each habitat and expressing this as a percentage of the monthly total; the values are given in figure 2:27.

i. Monthly status of habitat occupation

Considering the situation in each month in turn it is clear that the occupance calculations have brought about a considerable change in the overall result. The thicket areas were depicted by the original data as very minor contributors to the results but now assume the major role in habitat occupation, followed by fields. In relation to other habitats, the heath areas appear unchanged in the amount of use they sustain, but the smaller vegetation types, the rides and the saltmarsh, are now shown to accommodate a smaller part of the total population than was suggested by the original numbers.

These occupation figures have been compared between successive months using a chi-squared test on the theoretical populations held in each habitat. The significance values of these comparisons are given in figure 2:28 where significant differences are frequently encountered. There is insufficient information to suggest any general trends.

ii. Faecal accumulation results

The dung accumulation plots at Wareham were established to supply figures to either confirm or refute the occupation results which would have been collected on the Wareham driven transects. As was stated earlier the paucity of the Wareham data made analysis worthless, but as the dung transects were established several months before the Purbeck work began, they were continued. To have moved them would have resulted in a short span of months from both areas (which would not be particularly useful) so the transect clearances were maintained even though the observational data proved inadequate. The scarcity of deer sightings at Wareham may have been due to a small population or it could have been the result of dense undergrowth concealing many of the animals. The continuation of the dung transect assessments would answer this question as well as providing indirect information on the levels of habitat occupation; some of the habitats not being represented at Purbeck. The climatic, geological and vegetational similarities of the areas have been discussed and although the population of sika in the Wareham main block does seem to be small, relative use of the habitats will be revealed by this method and can be applied to the Purbeck deer.

Plantation, prethicket, thicket and polestage areas were assessed in this way and the number of pellet groups found on the transects each month and expressed as a pecentage of the monthly total, is given in figure 2:29.

These values were modified to derive the total theoretical dung deposition each month in each habitat, thus weighting the results in relation to the area of each vegetation type available. The habitat totals are expressed as a percentage of the monthly total and the results are given in figure 2:30. Both sets of values reveal thicket as the habitat with the highest occupance and plantation is shown to support a low level of use. Prethicket and polestage use fluctuates from month to month.

As far as is possible these results support the idea obtained from the occupance calculations (and not produced directly by observation) that thickets are much used, adding to the confidence with which the occupance calculations are presented. Further, the scarcity of dung groups supports the decision to work at Purbeck and to reduce the level of committment at Wareham for even if the deer cannot be seen, they do defaecate and that so few dung groups are found suggests that the population is indeed small.

iii. Yearly trends in habitat occupation

The yearly trends plotted in figure 2:32, displayed by examining the occupation level of a habitat month by month, must be the same as given by the original data although the actual values are considerably different. Occupation of oakwoods is seasonal, coinciding with autumn and winter, and there is a gradual increase in the use of the saltmarsh during the summer. Those areas supporting the most use, the fields and thickets, show a lot of variation in the level of use sustained each month (the source of the significant differences from the monthly occupance comparisons given above) which are probably due as much to sample variation and weather effects as to changes in the behaviour of the animals.

iv. Day and night occupation

Greater detail is available when the total occupance figures are divided to portray day and night periods separately. Given in figure 2:31, these values show that the major levels of daytime occupation are in the thickets and although very few animals are found on which to base this result (relatively few being found in daylight anywhere) this result is strengthened by the fact that the deer were not found in any open habitats at the same time. The main concentration of occupation at night is in the fields although this general pattern is less clear in the summer than in the winter. Then the deer often emerge to feed in the open areas an hour or so before dusk, and may not return to the thickets until an hour or so after dawn, so these observations are included in the "daytime" section of the records. Use of rides follows this trend even more markedly as the deer are found there on their way out to, and on their return from, the fields.

v. Circadian pattern

Although derived from fewer circuits than in the New Forest, most of the Purbeck data are numerous enough to allow a more detailed analysis and so bi-hourly occupance values have been calculated and are plotted in figure 2:33.(For clarity only three habitats have been plotted; fields, thicket and heath.)

There is, however, a slight irregularity in the presentation of the graphs. The line depicting the occupance of the thickets terminates in "mid-air" on all the graphs whereas the others are returned to the x-axis. During almost all the daytime circuits no deer were found, this is therefore expressed as "zero occupance" for all areas. However, the animals must be somewhere and as the areas of open habitats sampled are a much larger proportion of those available and are much easier to survey, it is less likely that significant numbers of animals would be missed here. Therefore, as no deer are found in the open habitats they must be in the thickets; areas which are by their very nature impossible to survey adequately. Thus for biological reasons this occupance line cannot be brought to zero nor for logistic reasons may it be extended to 100%, so it has been halted at the point where concrete data ends.

At Purbeck there are fewer habitats available than in the New Forest yet again only two make major contributions to the pattern; thickets and fields. Each month's plot displays a very similar pattern; thickets are the dominant habitat between dawn and dusk and the night is dominated by the use of the fields.

There are variations on this theme. In January 1981 the survey coincided with some nights of particularly foul weather which is shown by the domination of the thickets from midnight until dawn as the animals returned to shelter. Use of the rides exceeds all but thicket before dusk and oakwoods sustain significant (but seasonal) use in the middle of the night. In February no animals were found in the thickets after 20:00hrs GMT, and like January, use of the heath is shown as substantial during the latter part of the night.

This pattern repeats for March, April and May when the shorter nights seem to induce an even higher use of the fields, apparently achieved more rapidly than in earlier months.

Several months have shown heath areas to be dominant around dusk and again at, or just after dawn (eg February, April and June). This may be because the animals move out a long way into these areas and so are found returning to the thickets later than they are from other less distant feeding grounds.

September, like January, shows field domination extending only to midnight with the occupance of fields and thickets being equivalent after that time. The survey conditions were again hampered by poor weather which has obviously influenced these results by forcing the deer to shelter. Use of the saltmarsh, increasing slowly through the latter part of the summer, is higher than that of most other minor vegetation types throughout the night and use of the oakwoods is now significant in the middle of the night; the habitat having been totally unused during the spring and summer.

c. Habitat preferences

The preceeding section has suggested that the sika deer at Purbeck have a circadian migration from daytime occupation of thickets to nighttime exploitation of fields. It is certain therefore that some considerable measure of habitat selection operates and this has been investigated using the same preference "rating" employed with the New Forest data.

The table of preference indices, calculated for the full 24 hours (derived from the ratio of the observed npua in a particular habitat to the total observed npua) shows quite simply that all habitats, except heaths and thickets, are selected (figure 2:34).

This interpretation changes when day and night values are calculated separately (figure 2:35) for now the index for thickets (although rarely exceeding unity) is always higher in daytime than at night, a situation duplicated on the rides whereas fields show a very strong night selection and a minimal daytime preference.

DISCUSSION

1. The New Forest and Purbeck compared

The data above, whether in its "raw" state, or after modification to the occupance figures, reveal considerable differences between the patterns of habitat occupation in the two study areas. Each forest contains a different array of habitats though, so differences in habitat use would be expected and direct comparisons are limited.

The New Forest sika deer, living in a more diverse habitat, have a seasonally changing pattern of habitat use, whereas the sika at Purbeck, occupying a less varied habitat seem to be less varied in their exploitation of the vegetation types. Further, there are some data suggesting that the deer at Purbeck are predominately nocturnal whilst those in the New Forest maintain a significant level of activity throughout the 24 hours.

Winter preferences for oakwoods are shown in both forests although the small amount of this habitat available at Purbeck means that only a small part of the population can use it. In the New Forest this habitat dominates the total occupance results for most months each year. Both forests also show a high level of use for thicket-like vegetation. This is highest in use in daytime throughout the year at Purbeck whereas in Frame, although still diurnal, the dominance is limited to spring and summer. In both sites the patterns of habitat use are centred upon two main vegetation types; prethicket and oakwoods at Frame, thicket and fields at Purbeck. All the other habitats, by virtue of the low number of deer recorded there or by their limited availability, contain a minor proportion of the total theoretical population and so play a subordinate role to the major habitats.

Dominance amongst these smaller habitats changes frequently and at Purbeck a pattern is very indistinct. In both forests the use of rides is often highest at dawn and dusk though this is less limited in the New Forest; there they are exploited throughout the day. Use of polestage areas (a vegetation type not found at Purbeck where the plantations are too young) is night-oriented, particularly in the winter.

The biological implications of the results presented here are not discussed fully in this chapter. More information is required (and will become available) as knowledge of the animals' location is not as valuable as that coupled to information on what they are doing. Without these details reasons for the patterns of habitat occupation presented here must be purely speculative and not very useful. The activity patterns will be analysed in Chapter 3, the diet in Chapter 4 and all these details will be discussed together in Chapter 7.

2. Sexual differences in habitat occupation?

Comparison between habitat usage by males and females in this study is desirable; for during the majority of the year (i.e. outside the rut) the stags and hinds are found to occupy different parts of the study sites. In the New Forest the males move away from the deer sanctuary in the middle of Frame Heath Inclosure after the rut and are rarely found during the spring and summer (and then only at the west end of New Copse Inclosure). It is thought that they move out to the Beaulieu Estate and onto Brockenhurst Manor to the east and west of Frame respectively (H.Cutler, pers. comm.). At Wareham and Purbeck stags and hinds are also reported to occupy separate regions (Horwood 1966, 1971), but unfortunately so few stag sightings were collected outside the rut in either of the study areas that comparisons between the sexes are pointless. During the rut the sample size (particularly in the New Forest) is adequate, but now the lives of the two sexes are intimately linked and thus no significant differences are found. It is for these reasons that hinds and stags have been treated together when deriving all the ecological data. Possible reasons for this separate lifestyle, with a review of current literature, will be given in Chapter 7.

3. The validity of the "occupance" calculation

Patterns of habitat occupation in these two forests have been discovered using a repetitive, restricted survey method and the data collected were submitted in two forms. Firstly the original data, presented as collected, were listed as the number of animals located in each habitat and this was then reduced to the percentage of the total number of deer found each month.

If these figures are to be used to compare the level of use sustained by each habitat some correction is required because they are distorted. Each habitat is sampled differently, either because it occurs on the route in different amounts, or because within each the visibility is affected by the denseness of the undergrowth. These differences affect comparisons between day and night as much as between seasons.

Had the habitats been surveyed in the same relative proportions as they are available to the deer, the original results would have been acceptable and the bias would not exist. Unfortunately the difference between day and night visibilities is sufficient to remove this possibility.

A simple and logical correction for this would be to express the observations as the number of deer found per unit area of habitat surveyed. However, this "density" is really only an indication of the intensity of use supported by the vegetation types and does not reflect the importance of each habitat to the population as a whole.

If one assumes that each habitat is representatively sampled, one can then describe the location of the population as a whole using the npua values to calculate the number of animals in each habitat. This is derived by multiplying the relevant npua by the total area of each vegetation type that is available to the deer. Thus valid comparisons can be made between the habitats in terms of the numbers of animals supported there, but a direct comparison between two successive months is not valid unless the total theoretical populations are the same. To reduce these values to a more manageable scale they are given as percentages of the total calculated population. Occasionally this total is absurdly large but when expressed in percentages, the actual values are not important.

This calculation avoids one major bias but substitutes another. The main assumption is that each habitat is sampled representatively, but this is really only valid for areas where a reasonable depth of view is possible. The very nature of the driven transects introduces bias for the centres of the compartments are not accessible to the vehicle and in some cases only a narrow strip along the edge of a block is surveyed. This defect was partly compensated for by the walked transects whose supportive data were described earlier.

Assessment of the faecal "standing crop" along the edges of compartments has shown a much higher level of use here than is sustained by the middle of either of the adjoining areas; particularly if the edge is the interface between a dense stand of timber and an open expanse of hill or young plantation (Ratcliffe and Mann, unpubl). It is in this edge region that deer wait before emerging to feed and it is to these places that they retreat when disturbed. In the New Forest these border areas are likely to be susceptible to human disturbance and to be less sheltered from bad weather, but they may also be selected because of the superior grass and herb growth encouraged by higher light levels. Thus, for whichever reason, these border areas may not be totally representative giving in one case a low result, and in the other an inflated one. This problem applies more to the closed habitats than to the open areas where an adequate survey may be achieved.

Considerable though these objections are they cannot be overcome and at least the modifications to the data allow a meaningful comparison to be made between the use of habitats within a month. The modification also allows comparisons to be undertaken between forests for the biases outlined here, unlike those in the simple presentation of the original numbers, are equivalent in each area.

4. Methodological discussion

The technique of taking regular records of animals in particular locations together with their activities is an obvious one, but it is open to as many biases as it has advantages. The walked transects surveyed small areas of woodland over a comparatively minor section of the total forest. Later because extensive forestry operations along 1/5 of the route were thought to affect the deer, driven transects were started to assess a larger total area from a wider range of habitats. Also it was likely that a greater proportion of the animal population would be encountered.

Trials with a concealed observer showed that disturbance by the author, on both walked and driven transects, was comparatively slight; deer resumed their previous activity if not their precise location within 10 minutes of the passing of a pedestrian and they frequently failed even to acknowledge the passing of the car.

Areas of woodland surveyed by either technique are necessarily small and seasonal variation in the visibility in these areas is considerable, mostly due to the emergence of tree leaves and to the state of the bracken. Areas surveyed at night are much smaller than those used in the daytime, but to an extent all this can be taken into account when analysing the data.

Various workers have used spotlights to count deer at night and to observe their preferences for different feeding areas (eg: Montgomery 1963, Progulske and Duerre 1974, Ahlen 1965, Horwood 1966 and 1971) and some report problems with the technique (eg: Jackson 1974). Jackson states that the method "...proved unreliable as the deer became very wary and often moved away before their numbers, age, sex or feeding site could be determined..". Progulske and Duerre (1964) working in Dakota on white-tailed deer and mule deer, found that although the animals did not seem to be frightened by the lights, they tended to move away to the edge of their feeding grounds. The sika in this study also appeared unconcerned by the lights (although the few fallow deer seen were alarmed) but more were frightened away by a pedestrian with a handlamp than by a car and a searchlight. No information was collected to suggest that an undesirable influence was exerted by the surveys which were spaced two hours, and one week apart. This spacing was thought to allow the deer adequate opportunity to recover from any disturbance and as there is a considerable volume of traffic through the area anyway, they may have been accustomed to cars even before this work was started.

The main problem with the transects, particularly at night, is accurate identification of the animals. Purbeck and Wareham support populations of roe deer and there are many fallow deer in the New Forest. Confusion can easily arise between these three deer species and the cattle, ponies and sheep that may be encountered anywhere along the routes. Simultaneous use of binoculars and spotlamp assisted considerably (especially over the greater distances used at Purbeck) and any animal of doubtful origin was excluded from the records. Ahlen (1965) claims that it is possible to distinguish between red, fallow and roe deer by the colours reflected in their eyes when they are caught in the light; this was found to be unreliable for any animal except the fox in this work.

If more than a dozen or so deer were found in any area it was frequently impossible to record more detail than the size of the group as movement of the animals increased the chances of counting one twice. Records were required on age class, sex, group size and activity for each assembly of deer, but any doubts caused the exclusion of the observation. Very large groups were counted at least twice and the lower figure recorded.

The ease of finding deer varies enormously with the structure of the habitat and their activity. Deer feeding in fields or heathland may be visible from ¼ mile away, but might be invisible within 10m if lying up in dense Calluna or long grass. It oculd be suggested, therefore, that some of the results are biased towards those open areas where the proportion of animals missed is lowest.

The advantages of these techniques are that they are easy to apply and rely on no complicated equipment. Observer efficiency is improved by using a car, particularly in bad weather, and the enormously increased sample covering a more representative section of the animal's range is of considerable benefit. The extraneous influences due to bad weather and disturbance from other persons (observer disturbance being constant) are, it is hoped, reduced by the fairly large size of the sample. Progulske and Duerre (1964) find a significant correlation between various weather conditions and the numbers of deer recorded; in this report it will be shown that the periods sampled are representative of each month's weather as a whole and hence "correction" of the data to accommodate climatic effects is unnecessary.

The walked transects, despite being much shorter and therefore less representative of the areas, or of the population as a whole, are able to offer data from parts not accessible by car. Small tracks and paths leading through the middle of the compartments can be used and the impression gained from these, reinforced by the dung accumulation results supplements the "edge oriented" driven data.

The assessment of dung accumulation has been used on many occasions to lead to information on habitat occupation (eg: Jackson 1974, Dzieciolowski 1976, Loudon 1979, Henry 1981, Bailey and Putman 1981), and has been the subject of much discussion, criticism and comment. An excellent review of current methods is given by Neff (1968) and a review of the problems, disadvantages and advantages is given by Bailey and Putman (1981).

In this study the technique has been used because it is cumulative, does not require observer presence and is unaffected (as far as one can tell) by disturbance and weather conditions (degradation of the pellets excluded).

The actual rate of faecal accumulation in a particular vegetation type is not useful in itself; without knowledge of animal defaecation rates, or dung decomposition rates, the actual population of deer in an area cannot be assessed accurately (Dzieciolowski 1976). However by comparing the rates of faecal accumulation between vegetation types and the changes which occur in this rate, (whether monthly or, less reliably, seasonally) the relative intensity of use in each habitat can be deduced.

The main sources of inaccuracy which affect the validity of the results include the non-random use of the environment caused by differential mobility of the animals within the habitat, irregular defaecation by the animal, different defaecation rates of individuals, and differential search efficiency combined with differential decay rates.

Decay rates in the habitats are extremely variable and are affected by site features (soil richness, itself influencing the invertebrate fauna, season, weather sequences and drainage.) Some pellet groups persist almost two years on dry Calluna sites but only about three weeks on herb-rich, moist grassland in the summer. (B.Mitchell, pers. comm.) It is for these reasons that the accumulation plots were cleared each month and the standing crop of dung (determined when the plots were established) was discarded.

Jackson (1974) has noted that fallow deer frequently defaecate when rising after a period of rest; a habit observed in the sika deer. Thus groupings of pellets may occur in favoured resting places, leading to bias in the counts obtained. Henry (1981) assessed dung accumulation in a large number of quadrats and using a dispersal coefficient revealed a clumped distribution of faecal groups in the study site as a whole, but a random distribution of groups within a habitat.

Assessing red deer faecal standing crop in Scotland, Ratcliffe and Mann (unpubl.) showed, by calculating a running mean, that no significant changes occurred to the mean after the assessment of eight quadrats. Obviously neither of these details cancels the possibility of a habitat being a preferred "latrine area" as shown in the New Forest ponies (Putman et al. 1982), particularly in the New Forest where some blocks of vegetation are quite small, but to reduce this possibility, no quadrats were established within 50m of the edge of a compartment, the largest representative block of woodland available was used and the quadrats were spaced as far apart as was practical.

Another problem in the use of this technique is that it relies upon accurate identification of the dung. In the areas assessed in this study roe deer and fallow deer also occur and confusion can arise, paricularly between roe and sika pellets. Whilst every effort was made to identify pellets by features of shape and size, mistakes must occur and one can only hope that as the resident populations are thought to be small, the proportion of wrongly identified pellet groups is also small.

Dung deposited by fallow deer, roe deer and ponies in the quadrats was recorded to indicate use of the habitats by these animals and perhaps to give some indication of competition, but the amount of information collected was small.

A investigation of the different levels of use sustained by each habitat by males and females was attempted, but sexing pellets from culled animals proved impossible, so identification of those in the field was felt to be even more unreliable and was abandoned.

5. Corroboration of habitat occupation results from walked transects

Originally the driven transects were started to extend the walked route as local forestry operations were thought to be influencing the behaviour of the deer. It rapidly became apparent that the longer route, greater areas surveyed and the more extensive range of habitats included would reverse the situation, with supportive data derived from the walks.

The walked route was 1/6 of the length of the driven one, included five main habitats, and although about the same number of sightings were recorded each month by each method, the walked route was considered to be unrepresentative of the Inclosure as a whole. The main advantage of the shorter transect was that the centres of compartments and other areas not accessible to the car, were included. When coupled with the driven survey, 26 months of data were available including all, or part of, four winters.

The overall results produced by these methods were in close agreement which validates the use of the walked route, on its own if necessary. There would certainly be less correspondence between the results if the areas of forest sampled were less varied (as at Purbeck for example) as it would be even more difficult to survey representatively. The disagreement caused by splitting the data into night and day may be merely the result of the greater disturbance caused by the walker at night frightening the deer away, or it might be due to deer feeding elsewhere at night in regions not included on this route.

6. Corroboration of occupation results by cumulative dung assessment

In an extensive review of the uses and drawbacks of the faecal accumulation technique Neff (1968) states:

> "...a major problem requiring future research attention concerns the use of pellet group patterns as an index to habitat preferences. Pellet group counts are widely used for this purpose yet the relationship between defaecation and other animal activities remains conjectural. It is commonly assumed that the numbers of pellet groups counted in an area is closely related to the number of animal hours or days spent in that area, or that the pellet group count is an indication of the importance of the animal population.
>
> Neither assumption appears entirely trustworthy but in a few cases it has been possible to directly observe animal activity in corroboration or contradiction to pellet group distribution..."

The submission of the number of pellet groups found in each transect each month, however expressed, is not very useful as it only indicates the comparative levels of use of those particular cases. To derive an index that describes the animal use of the habitats as a whole the theoretical dung deposition was calculated for each habitat and each was expressed as a percentage of the monthly total. This treatment weights the results and compensates for the habitat that contains more animals than the others but appears to hold fewer as the dung is more thinly distributed due to the size of the habitat. It does assume that the dung is randomly distributed in each habitat (Henry 1981) but the results produced do agree very closely wth those obtained directly using the driven or walked transects.

The possible inflation of the number of dung deposits due to preferential use of the compartment edges was considered when laying out the transect and no quadrats were established within 50m of such a boundary. The dung results therefore really do refer to the habitat types as a whole and the close agreement between these and the occupance figures from the New Forest transects suggests that maybe areas sampled on these circuits are more representative than was stated above.

In neither forest were sample plots established in the open areas as it was felt that human interference (an occasional nuisance in the closed habitats) would destroy the quadrats.

Too few habitats were assessed both by dung accumulation and by observation in the Dorset forests for a statistical comparison to be undertaken. Inspection of the results suggests, as far as is possible, that they are very similar. The thickets, too dense to yield many observations, are shown by dung accumulation to be the most extensively used habitat in the forest. Thus not only do the results support each other, they supplement each other by supplying information on occasions when use of one or other method is inappropriate.

Charles et al. (1977) investigated the selection of upland swards by red deer on the Island of Rhum (in the Inner Hebrides) using both faecal counts and direct observation. They report a close agreement between the two techniques during the summer, when observations were collected for 18 hours a day, but a poorer agreement in the winter when observations could only span 8 hours a day.

7. Disturbance and weather

In a survey relying upon instant records of animals to yield data on habitat use and feeding ecology, the danger of results distorted by external influences is very real.

This is particularly relevant when records are collected over a small portion of the study period and from a small section of the habitats available.

It is hoped that observer disturbance is constant and that all the data will be affected equally. Trials with a concealed observer for both walked and driven techniques showed that within ten minutes of the passing of a pedestrian all the deer had resumed their previous occupation, if not their precise location . When a car was used , as in the longer transects, animals frequently failed to acknowledge the vehicle's presence and it was felt that the sample spacing of two hours was sufficient to allow disturbed animals time to settle. The car was never driven faster than 5mph and as there is much traffic passing along the rides in Frame the sika were accustomed to cars.

Observer effects apart, the main potential problem in the New Forest stems from tourist disturbance.

To maintain part of Frame Heath Inclosure as a deer sanctuary and to reduce disturbance around a public observation tower, Forestry Commission signs have been erected requesting that walkers remain on the gravel rides, or more simply, "Keep Out". Naturally not everyone follows these instructions but the proportion of visitors who do not is small so the walked transect (routed through this area) remains fairly undisturbed.

During the summer months and the height of the tourist season, few deer were found between 08.00 hours and 20.00 hours GMT whether visitors were present or not. Thus the portion of the data that could be affected is small and the main influence is confined to the few months which coincide with school holidays at Easter and in the summer. The area received a lot of visitors at the weekend throughout the year, but no data were collected between 08.00 on Saturday and 10.00 on Monday mornings. Some parts of the driven transect were away from the main public access points and the usual range of visitors, so disturbance in these areas was not increased above that created by normal forest traffic.

At Wareham and Purbeck forestry and farming operations create more disturbance than do tourists, but as this occurs throughout the year, and as the majority of sightings are collected here during the nights, no particular month will be affected more or less than any other. Tourism is not a major industry in these commercially managed forests and thus disturbance from the occasional walker or rider is considered negligible.

The other influence exerted on the data is from the weather. In order to reduce observer selection of pleasanter working conditions (not necessarily optimum for the deer) transects were carried out regularly on the same day each week; yet this is no guarantee that an even representation of weather types with their attendant animal sightings and activities will be achieved. Daily weather records were collected by Mr. and Mrs. H.K. Hill, residents of Frame Heath Inclosure, who noted the following details:

a. Maximum and minimum temperature; frosts.

b. Precipitation; whether hail, rain or snow, and heavy, light, steady or occasional.

c. Wind conditions, direction and strength (using the Beaufort wind scale).

Comparisons between the monthly means of these details and the mean of conditions encountered on survey days yielded no significant differences in any month so the conditions under which survey information was collected are representative of the conditions in the New Forest during the time of this study. As a result one can suggest that the habitat occupation patterns discussed here, and the behaviour and activity patterns to be discussed later (Chapter 3), are accurate representations of the situation encountered each month.

At Purbeck the survey days are not representative of the month as a whole, but of fairer conditions as circuits became impossible in foul weather (due to heavy mud trapping the car, or to absorption of the searchlight by fog, mist or rain). This visibility influence is more important here as much greater survey distances are involved in the open areas where observations may be collected over ¼ of a mile or more; under the trees (as in Frame) obstruction by the vegetation is a more serious problem than absorpton of the light beam. Considerable variation was encountered in the numbers of animals found on each circuit in either study area and insufficient replication of particular conditions occurred to allow evaluation of the effects of the weather. It did appear as if animals avoid exposed areas in high winds and also in rain, but deer at Purbeck were found to spend the majority of the daylight hours in the thickets regardless of the weather and some animals could always be found feeding in the fields at night.

In his report on the feeding ecology of fallow deer in the New Forest, Jackson (1974) decided that no statistical assessment of the influence of weather conditions on his data was appropriate and he gave anecdotal reports on the effects of various weather types on the feeding behaviour of the deer. The present study, based on repeated surveys, is better designed for statistical evaluation of weather influences and comparisons were attempted between circuits carried out under opposite conditions, ie. rain - dry, windy - still etc. at the same time of day in a month. The variation in the numbers of deer found on these circuits was no more than was found on circuits conducted under identical conditions. Thus no evaluation of these influences was possible and brief notes, along the same lines as Jackson's, are offered.

At the onset of rain sika feeding in the open were observed to seek shelter under trees and were frequently seen lying up ruminating. If this rain persisted for more than an hour or so the animals would emerge and resume feeding. During periods of heavy rain, high winds or both, animal sightings in exposed habitats (rides, felled areas, fields) seem to be reduced, but one cannot report a corresponding increase in the deer found in sheltered areas.

Fewer observations were recorded during the hot sunny periods in the summer when it seems as if the deer are hidden away in the thickets; perhaps to avoid insects. The greatest numbers of sightings, although usually collected around dawn and dusk, also seem to be gathered in cool, overcast, almost windless conditions (in total agreement with, amongst others, Dasmann and Taber 1956 and Harper 1962) although this last feature is less important in the New Forest where the sheltering effect of the trees considerably reduces the windspeed at ground level.

These ideas are supported by Staines (1970, 1976) who, from his work on the dispersion of red deer in Scotland, concluded that the most important weather factor inducing them to seek shelter was wind. This was expressed more quantitively by Grace and Easterbee (1979) who showed that windspeed over tall vegetation (1.0m) is half that over short (0.1m) and also that heat loss from animals in exposed conditions is more than twice that which is experienced by animals in sheltered (woodland) sites. The importance of an insulating layer on the ground was described by Gatenby (1977) who stated that heat loss to the ground from sheep bedded on short grass is much higher than when they are on long grass. Thus, in periods of high winds and low temperatures one would expect a reduction of animals in open areas and if lying up, the deer are more likely to be in areas of long grass or deep litter; entirely as suggested above.

Effects on feeding behaviour (to be discussed in Chapter 3) are not so clear-cut. Hammerstrom and Blake (1939) writing about white-tailed deer and Robertson (1967) writing about roe deer, suggest that the animals feed upon less palatable species when inadequate shelter influences areas of superior forage, a viewpoint extended by Staines (1970) who suggests that red deer will tolerate worse conditions when feeding than when at rest. Certainly sika deer were found feeding in all weathers and in most habitats, but whether reduced use of open areas in winter time was due to unpleasant weather effects or to inferior resources one can only speculate.

Short-term effects like those outlined earlier will certainly affect the data, particularly at Purbeck where the feeding areas are very exposed and the sample size is too small to yield a representative result for the month. In the New Forest it is hoped that the size of the sample and the representative nature of the survey will yield a realistic result.

CHAPTER THREE

Habitat utilisation
and
activity rhythms

HABITAT UTILISATION AND ACTIVITY RHYTHMS

INTRODUCTION

So far information has been presented describing the occupation of different vegetation types by sika deer in the New Forest in Hampshire and at Purbeck in Dorset.

Significant seasonal differences in the level of use sustained by these habitats have been described but as yet no attempt has been made to define this use.

In this chapter an effort is made to determine whether the pattern of habitat use described earlier is the result of the selection of a vegetation type for a particular activity and further, to investigate the relationship between patterns of habitat use and the activity patterns and rhythms of the animals.

METHODS

Data for this analysis were collected on the driven transects as described in Chapter 2, and the detail extracted from these more extensive records is that of the number of animals in each habitat each hour, performing each activity.

Three main behaviours are recognised for this analysis; feeding, walking , and lying and ruminating. Occasionally animals were found grooming, scratching, running, defaecating or just standing still, but as none of these activities is likely to be influenced by the habitat in which they are observed, they are considered too minor to yield to worthwhile analysis.

"Feeding" included deer browsing from trees or shrubs, grazing, or quartering. The latter activity is characterized by an apparently aimless, head-down slow progress through an area, with the animal pausing briefly to select an item from the ground; this was observed particularly frequently in the autumn and winter when acorns and fallen leaves were being exploited (see Diet, Chapter 4).

Deer "lying" are prone, legs tucked beneath, and are almost always chewing. Whilst it is unclear whether these animals are asleep, they appear very unresponsive and particularly at night show no signs of alarm at the presence of the observer.

Animals recorded as "walking" are moving purposefully, head up, through an area and should not be confused with animals quartering (who have their heads down). Obviously no habitat is likely to be selected for a walk, nevertheless the detail that more animals are found moving around in a particular area, or at a particular time, than are feeding, may prove useful. On occasions these contribute a fair part of the observations, on others they are included for completeness' sake.

Certain observations made in the field are not included in this analysis either because the deer were behaving oddly, or because they had been startled by the observer or some other agent. These, designated "disturbed", would contribute nothing to the subsequent analysis so are excluded from these records; they represent less than 5% of the total data.

RESULTS

1. Utilisation

As a summary of the original observations, data are presented describing the behaviour of the animals in the sample. The figures are subsequently modified (as in Chapter 2) to represent the behaviour of the population as a whole using the "occupance" calculations described earlier.

A. New Forest field data

i. Total values for 24 hours

Only results from the driven transects will be given as the supportive nature of the walked transect results has already been adequately described.

The simplest presentation gives the number of animals seen in each habitat each month, performing each activity.

These can then be expressed as the percentage of all the animals per habitat found performing each activity; pinpointing the use of a particular habitat for a specific activity.

a. Feeding

The percentage of all the animals feeding that was found in each habitat each month is given in figure 3:1.

A very clear seasonal pattern is displayed by the changes in the number of deer feeding in oakwoods each month and this is plotted in figure 3:2. This habitat is used by more animals for feeding in the winter than in either of the two summers studied, probably because during the winter these areas combine food resources (leaves, acorns and grass) with a high degree of shelter. In the summer the food resources in the woods are poorer than in those areas outside (due to low light levels) so then fewer animals are found feeding there.

Prethicket areas show the opposite trend; higher numbers of animals feeding there in the summer than in the winter, although the actual values (ranging from 2.9% in winter to 13.7% in the summer) are much lower than those from the oakwoods.

Clear-felled areas and fields follow the same pattern. Cleared areas contribute more to the data set than the prethicket does with 27.5% of the animals feeding located here in September 1981; this value having risen from 3.8% in the winter of 1980. These clear-felled areas are recently established, are exposed and hold a small supply of food plants which may be rapidly depleted, so do not persist as an important feeding area for very long. The fields contain up to 10% of the feeding animals during the spring and summer and less than 3% in the autumn, although the figures collected here fluctuate considerably.

Rides and polestage areas show a slightly different pattern. The proportion of feeding animals found in the rides fluctuates around an annual mean of 14.5% (st. dev. 3.7) and follows no regular pattern. It could be suggested that of those deer many are not in fact selecting rides to feed at all but are in transit between compartments, having stopped to nibble on the way. The numbers of deer in the polestage areas fluctuate as little as those found on the rides; around a mean of 8.3% (st. dev. 3.5) although there is a sharp increase in the number feeding here in the autumn of 1981 (perhaps exploiting the acorn crop from the few standard oaks left in these blocks). Otherwise, because of the dense canopy and the poor light levels, polestage areas contain few food resources and the number of deer in these habitats changes very little throughout the year, perhaps because neither is selected specifically as a feeding area.

The overall distribution of feeding animals changes with the time of year. During the summer there is a more even distribution of feeding deer amongst the habitats whereas during the winter the majority is located in the oakwoods with few anywhere else; the monthly results are plotted in figure 3:3.

b. Ruminating

The percentage of animals ruminating in each habitat is given in figure 3:1, and a histogram is plotted showing changes in the numbers lying up in oakwoods throughout the study period; figure 3:4.

In the oakwoods (as when feeding), the habitat is used by more deer during the winter than during the summer, particularly in the early winter. It could be suggested that deer are lying up here because they were feeding in the area earlier although as the habitat is very sheltered, it may be selected for lying up as well.

Very few deer were observed lying up in the prethicket areas and only then in the spring and summer of 1981. This is a trend also shown by animals in the clear-felled areas and the fields; that these habitats are not (with very few exceptions) used for ruminating in the autumn and winter.

Animals lying up in the polestage show an irregular pattern with high numbers of deer ruminating in the summer (of both 1980 and 1981) and fewer during the autumn and (of both 1980 and 1981) and fewer during the autumn and spring.

Virtually all the deer recorded lying up were in the oakwoods or polestage blocks. As polestage compartments contain limited food resources throughout the year (but particularly in the summer when there are neither acorns nor falling leaves and very little grass) it is unlikely that they are selected as feeding areas. It seems more likely that this habitat, being dry and sheltered, is selected mainly for lying up and ruminating and that animals found feeding there are in transit in much the same way as those recorded on the rides.

c. Walking

It would be absurd to suggest that a habitat was selected by an animal to walk in, nonetheless, the main habitats found to contain deer walking are the oakwoods and the rides. It was suggested earlier that the rides act as transit routes for animals moving from one compartment (or habitat type) to another. In the oakwoods, because of the diffuse nature of some of the food resources (especially in summer when gaps in the canopy encourage herb growth beneath) walking may be associated with the search for food, as indeed it may in cleared areas where deer are frequently found moving around. In polestage areas this may again apply, or it could be associated here and in oakwoods with searching for a suitable place to ruminate.

ii. Day and night separated

Data reported in Chapter 2 suggested that changes occur in the levels of occupation of various habitats on a circadian basis, so it is quite possible that some of the changes are due to selection of areas for specific activities at different times of the day. If there were day and night changes in activity, these would have been shown as day and night changes in habitat occupation.

Despite the fact that most sightings are of deer feeding, there are sufficient data recorded of deer lying up in each habitat for a worthwhile division of the results into day and night sectors; the values are given in figure 3:5.

a. Feeding

The overall seasonal trends discussed above are unchanged, but almost invariably more feeding animals are observed in the oakwoods at night than during the day; a feature also shown by data collected from animals feeding in the fields and in the polestage areas. The converse is true in the prethicket though this may be partly due to the problems associated with finding deer here at night producing an artificially low number.

Rides also contain fewer deer feeding at night, as do the cleared areas, although this may also be an artificial result as most of these sightings coincided with dawn and dusk (see Chapter 2) and were assigned to "daytime".

b. Ruminating

The majority of animals ruminating is to be found in the oakwoods at night except during the summer of 1981. Then, during June, July and August, the highest numbers were found in the polestage. Few animals are found ruminating anywhere else; those that are found are in the open areas during the spring and summer; but at night.

c. Walking

The records of animals found walking in any particular habitat are rendered too few by this division to yield any meaningful results. However, it does appear as if more deer are found crossing rides during daylight hours than at nighttime.

B. Purbeck field data

An identical analysis of data is now offered from observations collected on transects driven at Purbeck. The percentage of animals feeding, lying up or walking in each habitat is given in figure 3:6.

i. Total values for 24 hours

a. Feeding

The majority of observations of deer feeding was collected every month in the fields. This habitat holds between 59% (April 1981) and 36% (June 1981) of the feeding animals but no discernible seasonal pattern was exhibited.

More deer are found feeding in the saltmarsh at the end of the summer than during the late winter and spring but this could be an artificial result caused by the area being inaccessible because of the tides, or it may be a real result brought about by winter avoidance of an exposed habitat followed by late exploitation of food resources.

Small numbers of animals feeding were collected from the other habitats but again there is no clear pattern.

b. Ruminating

Few observations were collected of deer lying up ruminating because many are concealed by the dense undergrowth and the tall heather found in most of the habitats. The results are therefore biased towards the less overgrown areas so the scope for comparisons between the use of different habitats for this activity is limited. The only areas where deer were found lying up were marsh, heath and fields.

During the winter (January 1981) few deer were recorded lying up in these open areas but the number increased gradually as summer wore on. The contribution to the data from the marshy areas is irregular.

c. Walking

The majority of walking animals was located on the rides, (much as in the New Forest) probably because deer are found there on their way out to feed in, and on their return from, the fields.

ii. Day and night separated

Most of the observations were collected during the night at Purbeck (see Chapter 2) because the deer here seem to remain concealed in the thickets until dusk and return there just after dawn. With the shorter nights of spring and summer and several daylight hours being free of human disturbance, deer are found feeding in most habitats for a couple of hours before dusk and for an hour or so after dawn. As a result there are enough data here to allow some limited comparisons between day and night activities to be made: data are given in figure 3:7.

a. Feeding

Early in the year few records were made of animals in daylight, but by April deer are found feeding during daytime in all the habitats, the majority being on rides, in heath and in the thickets. By the middle of the summer (August 1981) the fields contain most of the deer feeding in daylight (50%) as thay always do at night, a situation repeated in September.

b. Ruminating

Animals were never found lying up and ruminating at Purbeck in the daytime. Most of the areas surveyed at this time are open and therefore relatively exposed, so greater security would be afforded by the dense thickets. Those deer already lying up under cover would be concealed by the undergrowth and are easily missed by the observer.

c. Walking

A very few deer are recorded as "walking" in any habitat during the daylight hours and those are found mainly in the heath areas or on the rides. This is consistent with the idea that they spend the days in the thickets so would be found on the rides whilst moving around before going out to, or returning from, the fields. Deer found walking, or feeding, in the heaths in daylight may be returning from more distant feeding grounds and having had further to travel, would appear later than they would had they come from more local feeding areas.

C. Behavioural occupance: New Forest

The original data, as above, gives the proportions of the total number of animals found in a habitat that were undertaking various activities, but this treatment does not allow direct comparison between the habitats as no account is taken of the areas of each habitat surveyed; those contributing most in area to the sample could be expected to yield more records (see Chapter 2). Further, the relative importance of each vegetation type to the population as a whole is not included. To supply these requirements the results have been modified to derive a "feeding population" or a "ruminating population" much as was calculated earlier when deducing the total population in a particular vegetation type (Chapter 2).

The theoretical number of animals feeding, lying or walking is calculated by finding the number of animals per unit area surveyed (over any timescale desired) engaged in each activity in each habitat. This can then be multiplied by the available area of that vegetation type (assuming that the data used is a representative sample of the habitat type as a whole) and that yields the theoretical population feeding, walking or lying there at that time. Comparisons are possible by this method between any activity and any habitat within a month, but unless the total theoretical populations are the same, a direct comparison between two months is not valid. To allow for this and to reduce the figures to a more manageable scale (some of the values are absurdly large), each "theoretical behavioural population" is expressed as a percentage of the monthly total. The results are given in figure 3:8 for the New Forest and figure 3:9 for Purbeck.

As the majority of the sigtings is of deer feeding, the overall result of this modification will resemble that given for "total occupance" very closely; as in Chapter 2. The failure of the total theoretical populations to coincide is because those animals classified as "disturbed" are excluded from this analysis but were included before as earlier measures only required "animal presence".

i. Total for 24 hours

a. Feeding

During the spring and summer a large part of the population feeds in the prethicket areas and feeding use of the oakwoods is low. During the autumn and winter, the situation is reversed and as winter progresses the oakwoods support an increasing population of feeding deer (up to 52% of the total).

The proportion of the population shown feeding in the other habitats is small; in fields, for example, this is less than 4% each month and even lower in winter. The rides occupy a mid-rank in the order of habitat use and frequently support a greater part of the feeding population (between 3% and 9%) than the polestage areas.

Felled areas are hardly used for feeding during the winter (holding less than 2% of the population) and on occasions are equal to the field areas in feeding occupance. These habitats assume more importance during the summer and by August the felled areas hold 11% of the population feeding; even more than the polestage.

b. Ruminating

Each month the greatest part of the population listed as "lying up" is found in the oakwoods (figure 3:8). This habitat holds a high proportion of the total population and of this 11.5% is lying up there in December 1980, but only 1.0% in July 1981.

Polestage areas are frequently second to oakwoods in the size of the population lying up and of the total population 4.2% is revealed ruminating there in December 1980, a value that decreases to 0.3% in April 1981.

This order of precedence, oakwoods followed by polestage, hardly changes throughout the year. Much smaller fractions of the population (frequently less than 1%) are found lying up in the open habitats (fields and felled areas), but not during the autumn and winter.

ii. Day and night separated

To confirm or to refute the suggestion that the habitats do support different activities at different times, the "behavioural occupance" data were recalculated for each habitat each month, but separated into day and night. The values obtained from this are listed in figure 3:10 for those animals feeding, in figure 3:11 for those lying up ruminating.

a. Feeding

The daytime feeding population of the prethicket, especially in the spring, is frequently greater than that of oakwoods; a situation that is reversed at night (eg May and June 1980, April and May 1981). In the autumn the domination of feeding use by oakwoods is supreme. Use of felled areas is night-dominated, perhaps to avoid disturbance from humans, but against this is the fact that more animals are found feeding on rides in daytime than at night.

b. Ruminating

The same seasonal pattern of habitat use for this activity as was found earlier is displayed, but the number of deer lying up in oakwoods at night almost always exceeds that there during the daytime. Numbers in polestage areas are invariably lower than either of these, although this area also shows more animals lying there at night.

Few other deer are found bedded down anywhere else. Some are seen in the fields but these are not limited to night-time (unlike Purbeck). Deer were also found ruminating in prethicket (but only in a few months), when, with one exception (July 1981), they were only found in the daytime. On these occasions a large proportion of the ruminating population is held here (February to May 1981 inclusive). This is consistent with anecdotal information suggesting that the sika deer spend a major part of each day lying up in the thicket (probably exploiting the extensive food supplies and shelter) but, because of the dense nature of the vegetation, they are seldom recorded as they are well concealed.

D. Behavioural occupance: Purbeck

The calculations employed earlier have been performed on data collected at Purbeck; to obtain the theoretical population of deer feeding, ruminating or walking about. As in the New Forest, these values will bear a very close resemblance to the total occupance results given in Chapter 2, for once again the majority of the records is of deer feeding. The values obtained for deer in each habitat are given in figure 3:9.

i. Total 24 hours

a. Feeding

In most months the thicket areas are shown to hold half or more of the population of feeding animals. This is consistent with anecdotal information suggesting that the sika deer, rarely seen here in the daytime, are hidden away in the thickets. Amongst the other habitats the fields always contain the largest part of the feeding population (varying between 18% in May 1981 and 40% in August 1981) and with very few exceptions the order of priority after this is heath, marsh and finally rides.

During the winter the feeding use of the marsh and rides is very similar and very low indeed (down to 2% of the population in each area in January 1981), but towards the end of the summer the feeding use of the saltmarsh increases to 9% (August). This may be an artificial result caused by access to the area being governed by the tides, or it may be because of a seasonal requirement for salt deposited on the vegetation by those tides. Feeding use of rides does not rise above 3.8% (June 1981) in the entire study time.

Feeding in the oakwoods, as was shown earlier, is confined to the autumn and winter months when the feeding population (4.6% in February) exceeds that found in the saltmarsh and on the rides.

b. Ruminating

On no occasion did the ruminating population contribute more than 8% to the total and the majority was always found in the fields. Obviously the survey has proved inadequate in assessing the activity in overgrown areas undoubtedly exploited in this fashion, but which are inaccessible to car or observer.

ii. Day and night separated

As in the New Forest, splitting the data into day and night sections alters the overall picture very little although at Purbeck relatively few daytime observations are available.

a. Feeding

Data presented in figure 3:12 shows that feeding in the thickets dominates daytime results in the winter months, and it is not until the shorter nights are encountered (from May onwards) that a significant population of sika deer is found feeding in the fields and in the other open areas in daylight.

At this time dawn is at about 04.00 GMT so these areas are secure from human disturbance for at least two hours after daybreak; time employed by the deer for feeding. A similar situation arises an hour or so before dusk in that deer begin to appear from the thickets from about 19.00 GMT (sundown being at around 20.30 GMT). It could be suggested that these trends show an avoidance of humans; the alternative suggestion, the avoidance of insects, is not entirely plausible as animals are bothered by them until long after dark at this time of year.

E. Behavioural preferences

The choice of habitat made by the deer for a particular activity can be displayed using a preference rating. This is calculated from:

$$\frac{\text{n p u a animals in habitat H doing X}}{\text{n p u a of all animals in all habitats doing X}}$$

(See Chapter 2 for the original derivation).

This is not the same measure as is given by the "behaviour occupance" values above. A habitat such as oakwood, for example, may contain most of the feeding animals merely by virtue of its size and yet the n.p.u.a. may be equal to, or even less than, the total n.p.u.a. which would indicate that deer there are not expressing an active preference for the area.

If one assumes that a random distribution of deer occurs if no choice is expressed, a ratio in excess of one must indicate preference. The advantage of this measure is that it is comparable both within and between months, although it is as susceptible to small sample bias as are all the other measures.

i. New Forest

a. Feeding preferences

The feeding preferences for the New Forest sika deer are given in figure 3:13 and show that although containing a relatively small part of the population, the smaller areas; fields, felled areas and rides, are highly preferred feeding grounds. There is a decline in the preference expressed for all these habitats over the winter, concordant with their diminishing food resources.

This trend is also displayed by the prethicket which has a very high index in the spring and summer. Oakwoods, with their high levels of occupance, are also preferred feeding areas at all times except during the summer of 1981.

b. Ruminating preferences

When the preference ratings are calculated for New Forest sika deer ruminating (figure 3:14) oakwoods are again shown as preferred areas, but all the year round. Open areas, like fields and felled areas, are also shown as being selected for lying up during the summer months. This is because once the deer are satiated (having entered the area to feed) they remain to ruminate; there being nothing to cause them to move to a more sheltered location. That these animals are not found ruminating in these areas in the winter supports this interpretation, for then shelter (not provided in these open spaces) is required in order to reduce heat loss, so oakwoods or polestage areas (showing high preference ratings at this time) are selected.

ii. Purbeck

a. Feeding

Calculation of monthly feeding preferences for deer at Purbeck produces a result very closely allied to the behavioural occupance results presented above. This could be expected as these animals (unlike those in the New Forest) undertake a daily migration between resting and feeding grounds so must exhibit a degree of choice as to their final destination. The figures are given in figure 3:15 and show a low preference expressed for thicket. This is the result of the small number of deer found there and the contradiction this produces is the epitome of the small sample bias inherent in sampling dense habitats with an observational technique.

The preference expressed by feeding animals for the saltmarsh is low at the end of the winter but climbs gradually during the summer; peaking at the onset of autumn. There is a very low feeding preference expressed for the heaths.

The preference shown for fields, higher than the other areas, (except marsh at the end of summer) peaks in the spring and declines gradually during the summer. Preference for the oakwoods declines in the latter part of the winter,but the return of the deer to this area is indicated by a very high index in September 1981.

Rides, probably utilised more as a transit route than as a food source, (animals recorded as "feeding" may be merely nibbling whilst crossing) show a higher rating in the summer concordant with the higher quality feed available there at that time, perhaps inducing the deer to linger. Unfortunately any further pattern is unclear because of the small number of observations.

b. Ruminating preferences

Too few ruminating observations were collected to validate ratings for this activity by deer at Purbeck. However, more animals are found ruminating in the fields in the summer than in the winter and a system analogous to that in the New Forest, that the deer feeding there in the summer do not need to move away to ruminate, undoubtedly operates.

2. Activity rhythms

A. New Forest

Graphs are plotted showing the percentage of all the animals found each hour, irrespective of habitat, that were feeding, walking or lying up (see figure 3:16).

All these graphs show that the majority of observations is of animals feeding and a few seem to show a cycle of feeding activity. In January 1981, for example, there are three separate feeding peaks: at 16.00, 24.00 and 08.00 hours. A similar pattern is shown in April 1981 with peaks at 03.00, 11.00 and 17.00, and again in November 1980 with peaks at 16.00, 24.00 and 10.00. These graphs suggest a cycle of feeding activity with an eight hour periodicity.

Some months show no such pattern; for example, September 1981, and yet others have two main peaks. May 1980 has feeding activity peaks at 04.00 and 18.00, December 1980 has peaks at 08.00 and 16.00, March 1981 at 06.00 and 18.00 and June 1981 at 06.00 and 18.00. (All the times given are in GMT).

b. Purbeck

The percentage of all the deer found each hour partaking of each activity is plotted from records collected at Purbeck and are given in figure 3:17.

Deer are rarely observed here between dawn and dusk (contrasting sharply with the New Forest) so could be thought of as being nocturnal. However, the fact that they are not observed does not mean that they are inactive, so the validity of this statement is questionable.

As in the New Forest the Purbeck results show that most of the observations collected were of animals feeding.

Some months, for example, April, May, June, July and September, show a two-peaked feeding pattern created by deer lying up in the open (and therefore visible to the observer) ruminating after four or five hours spent feeding. Without data relating to the other hours of the day, though, one cannot speculate on the existence and period of a cycle.

DISCUSSION

I. Choice of habitat?

Some of the more meaningful results indicate that although all the habitats are used for feeding at one time or other, in the winter open areas are used much less to feed and to ruminate than they are in the summer. During the summer these areas are not necessarily selected for the latter activity (although the possibility of animals "sunning" themselves cannot be discounted), the deer happen to be there when feeding ended and being subject to no stress, chose to remain.

In the winter some feeding does take place in all the habitats in the New Forest, mostly in the oakwoods, but the range of habitats used by the sika deer in which to ruminate is much reduced and all offer a considerable degree of shelter. The modifying effect of the prevailing weather conditions on habitat occupation was described in Chapter 2, and it is clear that in the autumn and winter the sika select drier, more sheltered habitats in which to lie up.

Heatloss from the animals is much reduced by a complete canopy overhead, and windspeed at ground level is reduced by tall vegetation (Grace and Easterbee 1979, Staines 1976). The loss of heat by conduction to the ground is further reduced by a thick layer of needles or leaves as are found in polestage or oakwood habitats (Gatenby 1977). These areas, therefore, are the most sheltered and their selection by the deer reflects this.

A cycle of habitat use is described in Chapter 2 with deer moving between oakwoods and prethicket areas; the details of which change from one season to another. The deer are, one assumes, seeking a food supply which can be exploited with the minimum of effort, and as such, the continuous herb and grass layer in the prethicket (and the fields and rides) seems an obvious choice; the added advantage is that the prethicket is sufficiently dense to reduce disturbance. Autumn and winter exploitation of oakwoods occurs when the acorn crop is harvested at which time some fallen leaves are also consumed and some grazing occurs on the thin grass in the clearings. In this case the animals are able to utilise shelter and food resource simultaneously. Staines (1976) has suggested that red deer seem to tolerate worse conditions when feeding than when at rest, a conclusion borne out by this report, but an ability not required in many instances by sika deer in the New Forest. In the winter, prethicket areas, despite their shelter, are less ideal food sources as the grass has been grazed down very low by the ponies and the forage taken there is mainly pine needles. These are also collected from any area of timber cutting or felling and constitute a substantial portion of the late winter diet.

At Purbeck there is little ground vegetation inside the compartments apart from that on the rides, so dense is the canopy and so low the light levels. The deer are forced to feed in the fields at night to avoid human disturbance. As these areas of feed are relatively unchanging from one season to another, so is the pattern of habitat occupation and utilisation unchanging too. The extensive tracts of heath-land contain sub-optimal forage and this is not a preferred feeding area; the considerable proportion of Calluna in the diet of these animals could have been consumed in the plantations. That sika deer are found in the heaths to the south and east of the Purbeck main block, apparently returning late to the thickets, points to use of superior feeding grounds in areas not reached by the survey.

The seasonal use of oakwood follows the availability of acorns and fallen leaves and as these areas are not as dense as the thickets, it could be argued that they are not exploited for shelter as extensively as in the New Forest because the thickets here are more effective.

That deer are found feeding in the Purbeck saltmarshes (a highly preferred habitat) must be because they are pursuing the high levels of salt deposited on the plants by the tides. The area is very wet and muddy (colonised by hordes of insects in the summer) but also contains the lush vegetation of several halophyte species of grass and herb. The increase in use of this area towards the end of the summer may be an artificial result caused by the tides covering different amounts of marsh on each survey occasion. It was hoped that the length of each period of observation was sufficient to include a time when the marsh was not flooded but even at this level of analysis the differing periods encountered here have obviously effected the records.

It could also be that the animals' need for salt varies with season and that this requirement increases towards the end of the summer when they are depositing fat reserves in preparation for the rut and the winter. This need would be satisfied by feeding on these halophyte plants, themselves washed with salt water twice a day.

2. Utilisation: habitats chosen for specific activities?

The data presented in Table 3:8 (the activity of the theoretical populations) shows that in the New Forest a higher percentage of deer are observed lying up and ruminating in the winter months than in the spring or summer. It might be expected that during the spring and summer when forage production is high, food intake would be rapid (assuming a non-selective feeding strategy: see Chapter 4) and that therefore the time invested in feeding would be reduced with an increase in the time available for ruminating. During the winter the converse would be expected; poor quality, unevenly distributed food supplies would require a greater investment in feeding time. (This increased investment of time could be reduced by adopting a totally non-selective, opportunistic feeding strategy as has been proposed for the sika der in the New Forest - see Chapter 4). However, one finds that in the winter there are more deer lying up than in the spring (although one cannot say whether this is the result of greater numbers lying up for short periods, fewer animals lying up for longer, or merely because they are easier to find when the concealing undergrowth has fallen back).

In the winter when food supplies are poor, a full rumen is achieved less frequently so rumination occurs less frequently. However, when it does, it could be suggested that the quality of the materials consumed is such that extensive periods of ruminating are required to achieve an adequate breakdown of the ingesta (Hungate 1966).

It is also possible that longer periods of lying up are utilised as a means of conserving heat (regardless, or combined with ruminating requirements); it would be less stressful under certain conditions to remain in shelter (even if not feeding), than to expend energy searching for food that is so poor as not to repay the effort invested. This is analogous to the situation reported by Hammerstrom and Blake (1939) and Verme (1965) who state that white-tailed deer (Odocoileus virginianus) may stay in areas of good shelter at the expense of better quality feed during bad weather. Staines (1970) also reports that although red deer tolerated worse conditions when feedng than when resting, their gross winter distribution was largely associated with the availability of good shelter from wind and not by the quality and quantity of the food.

This theory is supported, in different ways, by the results collected from both forests. Fewer deer are found lying up at Purbeck in the winter than in the summer, suggesting initially that they feed for longer. Whilst this is possible, the diet here changes very little from one season to another and the availability of the feed changes little too although there are substantial fluctuations in forage quality. What seems more likely is that the high level of animals feeding in the fields at Purbeck in the winter is maintained by deer returning to the sheltered areas to ruminate, (and then becoming inaccessible to the observer) and being frequently replaced by others going out to feed. In the summer the need to shelter is reduced, although the need to ruminate will arise at least as often, so the deer ruminate in the open; and it is in these months that a feeding rhythm is displayed. This rhythm probably persists relatively unchanged throughout the year (feeding style, diet and food availability being unchanging); in the winter it is not as obvious because it is carried on in a variety of habitats some of which are inadequately surveyed.

In the winter in the New Forest the sika deer feed in oakwoods and polestage areas, sheltered areas (Grace and Easterbee 1979), so do not necessarily need to seek further security to ruminate. That they are found ruminating throughout the 24 hours is probably partly due to the need to conserve heat coupled to the need for extended periods of rumination on poor quality foods. That they are able to invest this extra time may be the result of a change of feeding strategy from grazer in the summer; a feeding style inappropriate in the winter because of intensive competition from ponies, to browser and opportunist in the winter; when pine needles (a forage not exploited by the ponies) are utilised by the deer.

So, the diet of these deer changes from one season to another, not only in composition but also markedly in quality and patterns of habitat use change too.

During the summer the deer are found feeding in a wide variety of habitats and as they do not necessarily need to shelter, they are also found lying up and ruminating in a wide variety of habitats. That fewer are found overall may be because they devote less time to this process (higher quality feeds requiring less breakdown before digestion) or it may be that better concealment is afforded by, and is sought in, the dense undergrowth in an effort to avoid insects, the hot sun and disturbance from tourists.

3. Feeding rhythms?

There is little evidence to suggest cycles of feeding and ruminating in the sika deer, but they are very unclear because inadequate numbers of deer engaged in activities other than feeding were recorded.

It is often stated in general works that the main peaks of activity for deer are around dawn and dusk (eg Prior 1968 on roe deer, Lochman 1965 on red and roe deer) and although no data are offered to support this, more sightings were collected each month at these hours than at any other; the implications of this will be reviewed later. This in itself suggests a cycle of activity which may be due to a periodic need to feed, or to the avoidance of disturbance during the daytime and climatic extremes at night. One suspects, however, that the data upon which these more general statements depend does not contain a full appraisal of the 24 hours.

A period of rumination is required after feeding to continue the mechanical breakdown of material ingested, (speeding biological breakdown) and thus making room in the rumen for subsequent feeding occasions. Thus a cycle must be established but it may vary in period between seasons depending upon the quality of the feed, its abundance and upon weather and behavioural constraints.

The data given above do not support this idea as months with the longer feeding period (of about 12 hours) are distributed throughout the year (December, March, May and June) as evenly as those with the three peaked, 8 hour cycle (January, April and November) but, as was suggested, this is probably because too few of the other animals were found and the record is incomplete.

Lochman (1965) working in Europe, reports seven feeding peaks for red deer and eleven for roe. Jackson (1974) working on fallow deer in the New Forest, suggests that if undisturbed these will feed not only at dawn and dusk, but also in late morning, afternoon and night.

Feeding rhythms of this type seem to be so well established that if upset the food types selected change (Bubenik and Cashnocha 1963). Bubenik and Cashnocha (loc. cit.) showed an increase in red deer browsing in central Europe when their feeding periodicities were upset although stress has also been suggested as an explanation for bark stripping by red deer (Chard 1966, Van de Veen 1973). As if to reinforce this idea, Reimers (1972) reports improved rates of weight gain in reindeer which are left to graze rather than being intensively herded.

4. Representative data?

The data presented above only deal with part of the daily routine of the deer; particularly at Purbeck, for the "true" situation in the more overgrown areas cannot be described adequately with data collected in this way: some alternative technique, perhaps involving radio transmitters, is required.

The majority of records is of animals feeding. This may be because the majority really was feeding, or it may be because the deer were engaged in other activities (perhaps lying down) and were concealed, so were not recorded. As a result the feeding occupance figures and total occupance figures given in Chapter 2 are very similar.

It is also possible that within a habitat, even one as apparently uniform as an extensive stand of conifer, certain areas are not used for lying up as much as others. Maybe the edges of the compartments (surveyed here to a depth of about 50m) are avoided for this activity because they are more disturbed, or more exposed, than the compartment centres. The superior light levels found here may also encourage the use of the edge area for feeding by supporting a richer growth of herbs and grasses than the compartment interior can. It was for these reasons that the dung accumulation plots used to derive an indirect measure of relative levels of habitat occupation (see Chapter 2) were not established within 50m of the compartment edges. The boundaries of the compartments are also those areas in which the deer wait before emerging to feed, and to which they retreat when disturbed; this could create inflated results. The areas of each habitat sampled are, by absolute necessity, slightly more open to allow better visibility and thus may be less representative of the habitat as a whole. Unfortunately one cannot compensate for biases of this nature in this behavioural data.

Animals standing up and moving about are easer to locate in the overgrown thicket at Purbeck, or in the prethicket in the New Forest, and it is likely that this is the cause of the high number of feeding observations recorded there.

When lying down in some areas the sika deer are almost invisible, particularly in the daytime when their pelage merges most effectively with the colour of the leaf litter and tree trunks, and one has not the nighttime advantage of the reflection of a spotlamp in the eyes to reveal concealed animals; sometimes over considerable distances. Unfortunately the bias produced by this does not influence data from each habitat to the same extent; all the deer lying in open fields will be recorded whereas the number missed in the thickets will depend not only on the time of day, but also on the state of the vegetation and hence, on the time of year.

The analysis has attempted to compensate for the difference each vegetation type makes to the survey by converting the results into a number per unit area surveyed, but it is particularly difficult to modify accurately the areas used in order to compensate for regions under deep bracken, or in long grass, where walking or feeding animals may be seen but recumbent ones cannot.

One therefore has to interpret the results bearing in mind that in the more densely overgrown habitats, particularly during the summer, the numbers of animals recorded are likely to be minimal and that the numbers missed will depend very much on what they were doing. These biases might be of less importance if one was comparing prethicket at Purbeck with prethicket in the New Forest. Unfortunately there is no such correspondence between the denser habitats; those that are represented in both forests (rides, oakwoods and fields) are, as more open areas, less susceptible to this error.

It is obvious that animals have to be seen to be recorded, but it does not follow that if no deer are found, there are no deer present.

5. Total occupation values biased?

The information presented in this chapter casts some doubt on the validity of the total occupance values given for each habitat each month in Chapter 2, (results section I.b.i. and 2.b.i.).

If, in a particular month, the majority of sightings is collected at a time when all the deer are feeding, for example, and if, in that particular month, only one or two habitats are selected for feeding(but others may be used for other activities at other times) then the contribution that this survey occasion makes to the total occupance figure for that particular habitat type is excessive. This effect will be particularly significant if a high proportion of the observations is collected over a relatively short part of the day; for example, at dawn or dusk, or during a month where the range of habitats used on this particular occasion is low.

During the winter the sika deer are found regularly throughout the 24 hours and although there is a slight increase in the number of records collected at dawn and dusk, it is probably not sufficient to bias the final result in the way suggested. In the summer, however, there is a very pronounced dawn and dusk peak in data collection, but at this time the variety of habitats supplying the data is much wider so the contribution from each, even if biased, will only modify the relative standing of the habitats a little.

It is unlikely therefore that the results are any more biased by this effect than by the influences discussed earlier. It does emphasise though, that considerable care must be exercised in choosing a representative way of measuring details like habitat occupation particularly if one is unable to be committed to a regime covering the full 24 hours.

CHAPTER FOUR

Diet

DIET

INTRODUCTION

Fundamental to understanding the ecology of an animal is knowledge of its feeding habits.

Methods available for the determination of diet in any large herbivore are; direct observation (Dzieciolowski 1970, Van de Veen 1979), ruminal analysis (eg. Staines 1976) and faecal analysis (eg. Anthony and Smith 1974) as well as combinations of these (Anthony and Smith 1974). Each of these has a variety of methodological problems that limit their application and the validity of their results.

Diet determination by direct observation is impractical in this study as in both areas the animal's head is concealed by vegetation so one cannot identify food particles selected. Heavy grazing in the New Forest study area by the ponies and by other deer, makes identification of fresh feeding very difficult and the separation of deer-grazing damage from that caused by the ponies is almost impossible. Thus, feeding site evaluation is also impractical and although a few observations of undisturbed feeding animals were made from high seats, these results were so limited and collecting them was so labour-intensive, that all direct methods of diet determination had to be abandoned.

Thus indirect methods were employed. These exploited a ready supply of rumina available during the annual winter cull. Diet throughout the year was also determined from the analysis of freshly collected faeces.

METHODS:

1. Collection of material

a. Rumina

Rumen contents were obtained from animals shot during the normal annual culling season (November to February) both at Wareham and in the New Forest. To improve the size of the sample from the coniferous areas, thereby allowing further comparisons with the Wareham data, samples were also collected from five forests in Scotland.

A 250ml specimen of well-mixed rumen content and a small number of pellets from the rectum or the colon was removed from each animal as soon after shooting as was feasible; both were fixed in 10% formalin, labelled and stored.

Samples were collected during four winters in the New Forest and three at Wareham. Scottish material was obtained from two winters thus:-

Number of rumina collected and analysed

	Date	New Forest	Wareham	Scotland
Winter	78'79	22	13	-
	79'80	29	35	93
	80'81	26	14	97
	81'82	35	-	-
		112	62	190
			373	

b. Faeces

Rumina were only available for a few months of the year so to yield an impression of diet over the entire year faeces were collected every month from the dung accumulation plots (see Chapter 2). As pellets were removed from these quadrats at regular intervals, their period of deposition was known, so identification of the component epidermal fragments would show diet for that period. The advantage of using dung obtained in this way is that the samples are representative of the Frame herd as a whole; they could have been produced by any member and are collected throughout the herd's range.

Faeces from these accumulation plots were collected and analysed every month for two years in the New Forest; one year at Wareham.

2. ANALYSIS

a. Rumina

Each rumen sample was washed in a 2mm sieve until emerging water was clear and the particles remaining appeared quite separate and distinct. This removes the very tiny particles which comprise a minute fraction of the total volume but are a significant nuisance value (eg: Sparks & Malachek 1968, Dzicieolowski 1970, Jackson 1974, Staines 1976 & 1981, Kessler et al. 1981).

A 10ml subsample of the particles remaining (measured by displacement) was spread under water in a shallow plastic tray marked with 10 lines 1.5cms apart. Any particle touching or lying across a line was identified using a x5 lens and was recorded as a "line hit".

The particles were allocated to one of the following categories:

1 Acorns

2 Deciduous leaves. This includes all particles which, by virtue of their venation, were recognisable as leaves. Separation of individual species, or even tree leaves from forbs, was not possible.

3 Grasses. Identification of grass in rumen samples is possible for some species but it was felt that fewer errors would result from less detail in a larger sample. Grass species were to be identified in faeces later.

4 Calluna/Erica. This is an easily identified fraction thought to be predominatly Calluna but probably also containing small amounts of Erica.

5 Coniferous needles. The main species grown in the New Forest study area and at Wareham, are Scots Pine (P. sylvestris) and Corsican Pine (P. nigra). Separation of these from needle characteristics alone is not possible. Spruce needles were found occasionally but in very small amounts, so are included here.

6 Fungi

7 Lichen

8 Ulex. This is probably the most inaccurate category as well chewed, young gorse is easily confused with chewed grass and even, occasionally, with the fibrous material derived from pine needles. Confirmation of gorse presence was only possible when spines were found.

9 Bark and wood. This category includes all woody material, particularly coniferous bark, and may also contain larger fragments of pine twigs and *Calluna* stems. Because of its low digestibility this is the longest surviving fraction in the rumen and as a result the amount found is an over representation of the true contribution to the diet. Its exclusion from diet description is advocated by some authors (eg. Jackson 1974) but it is included here for completeness' sake.

10 Moss

11 Ivy

12 Holly

Occasionally small caterpillars were found, thought to be larvae of the winter moth (*Operophtera brumata*) which were probably picked up accidentally.

Once identified and recorded, the particles were removed and stored; one container per record category. The procedure was then repeated with a second 10ml subsample from the same rumen. Initially three sub-samples were treated in this way, but calculation of a running mean showed no appreciable change in result after the second sample, so analysis of the third was discontinued.

To convert the "hit score" for particles recorded to the volume of subsample that they represented, a series of identical trials were conducted using the pure feed categories previously removed and stored. 10mls of each of these were sorted and scored independently in the lined tray, in exactly the same way as the "mixed samples"; all the particles on or touching the lines were recorded as "line hits". Thus for each food type the number of "line hits" one might expect from 10 mls of pure sample was obtained.

A conversion figure can be derived from this so that the number of "line hits" on each food type in a mixed sample can be converted to its volume and thence to the percentage in the rumen (method after Staines 1976). Using this conversion, diet as described from analysis of rumen contents is expressed by percentage composition by volume.

b. Faecal material

Pellets were crushed with a pestle and mortar using 2% NaOH as a lubricant and they were left soaking in this for about 12 hours. The solid matter settled out and the supernant was replaced with 10% NaOH in which the particles were boiled for 5 minutes (method modified from Loudon

1979). This treatment ensured separation of all the particles and also removed gut mucus, bacteria and mesophyll thus clearing the epidermal cells enhancing inspection of their cuticular characteristics.

After cooling, the sludge was washed several times and on each occasion the lightest and therefore the last fraction to settle out, was discarded. The eventual result was a preparation that precipitated out in about 3 minutes leaving clear water above. The material was then centrifuged to compact it (method derived by Mann and Putman). A small portion of this solid matter was spread in water on a plastic tray engraved with a 1.0cm grid. To break down the surface tension and to aid the evenness of the spread, 2 drops of teepol were added. The grid was examined under a microscope using 100x magnification and the first 100 particles touching, or lying across the lines, were identified by comparison with a set of reference slides and were recorded (method after Chamrad and Box 1964).

The lines were examined systematically to avoid bias. The technique was repeated with a second and initially a third portion of the material, but as was found with the rumina, no improvement in the result was obtained from the extra determination, so to reduce the time involved and therefore to tackle a larger sample, two replicates only were used. Thus the composition of each pellet group was described as the percentage of 200 identified particles.

As frequently as possible particles were recorded to species level after comparison with the reference slides. Unfortunately, the level of identification differs substantially with plant type. Several of the grass species are very distinctive (eg *Agrostis setacea*, *A. tenuis*, *Molinia*), but specification of forbs, or tree leaves, or even discrimination between them was thought unreliable so they were scored to category only. Both *Ulex* and *Calluna*, amongst the browse materials, could be readily identified and are recorded at species level. The proportion of particles which could not be assigned to one category or another was low (ca. 10%).

Many particles, despite the destructive nature of the preparation technique, remain opaque and are unidentifiable by transmitted light. However, even with particles as small as these, use of incident light and lower magnification does result in identification of some particles of acorns and leaves.

Five separate faecal groups were analysed for each month whenever possible except at Wareham where occasionally only 4 had been found in accumulation plots.

Faecal material obtained from shot animals was analysed in exactly the same way. These analyses were carried out over three winters at Wareham and in the New Forest, but no faeces were collected in Scotland.

3. Preparation of reference slides

Identification of the plant fragments in both rumina and faeces requires cross-referencing with the characteristics of specimens already identified; clearly the preparation of these is very important.

Specimens of leaves, twigs and stems were collected during the growing season and like the faecal and ruminal material, were stored in 10% formalin. Each specimen was then ground up, using water as a lubricant and some of the epidermal cells separated to be mounted on slides in glycerine. In an attempt to mimic the effect of the ruminant digestive tract, fresh specimens were treated with fungal pepsin and cellulase after mechanical breakdown (method from Jones and Hayward 1975). Regrettably there was no improvement in the clarity of display of the cuticular characteristics.

In the majority of trees and forbs separation of the epidermal cells was not possible and identification from venation was thought to be unreliable. Application of liquid cellulose acetate and removal of an impression of the adaxial and abaxial surfaces also failed to show sufficiently distinctive features, so most of these are recorded as members of a broad category; "leaves".

The materials that did respond well to separation were mounted and photographed for ease of reference.

It is inevitable that the reference collection is not complete and that some material would be found that was distinctive and yet could not be identified. In all some fifty species were mounted and photographed - selected partly by their abundance in the study areas, partly from results of analysed rumina and it was felt that this included the major components of the vegetation; any species left out could only occupy a minor role in the diet concordant with its availability.

4. Nutrient analysis of forage

a. Collection of specimens

In order to obtain information on the nutrient status of the forage species available to the animals and to interpret the observed diet, samples of twenty plant species were collected from both Wareham and Frame Heath Inclosure each month. Initially these plants were selected for being the most common in the areas and several dwarf shrubs (*Calluna*, *Myrica*), grasses (*A. tenuis*, *A. setacea*, *Molinia*), evergreen trees (holly, pine) and deciduous trees (birch, beech, oak) were included. The choice of plants was validated by details from completed rumen analyses.

Clipping of the samples was standardised so that results from each forest could be compared and no attempt was made to mimic the highly selective way in which deer feed (Swift 1948, Van de Veen 1979, Staines et al. 1981).

Grass was cut to within 1 cm of the root-petiole junction, and trees and shrubs had the present season's growth removed; the old scar marking the end of the previous season was easily found.

Vegetation was sampled at the end of the second week in each calendar month from June to December 1981. As far as possible, specimens were taken from the same tree or patch of grass on each occasion. Ekins (pers. comm.) has shown that significant differences in the nutrient status of a species are found when samples are taken from areas with different soil type, drainage or previous management.

The clipped samples were sorted to exclude major fragments of dead leaves, twigs, alien species and obvious particles of soil. They were then oven-dried and milled in a hammer mill to be stored as a dry powder.

Unfortunately, sampling was begun too late to include part of the winter and the spring. However, vegetational analyses of this sort were also carried out during a parallel study within the New Forest and more or less at the same time (Putman et. al. 1981). Results yielded from this work are very similar to those obtained here, for those months that overlap, so data from Putman et. al. are used to supply values for the missing months. These are given in parentheses in figure 4:31.

Because of a discontinuity between these figures and own, resulting from a slightly different clipping regime and the use of different collection sites, the data set as a whole should not be used in other applications.

b. Forage quality; Digestibility

Dry matter digestibility (D.M.D.) was determined in vitro using the method of Jones and Hayward (1975). In this technique digestibility is determined by incubating 200mg of the dry milled sample in 0.2% pepsin (dissolved in 0.10N HCL) for 24 hours followed by a further 48 hours in 125mg of fungal cellulase dissolved in 20mls of phosphate citrate buffer at pH 4.6. The entire incubation is carried out at 40°C. (20mls of phosphate citrate buffer is made from 10.65mls of 0.10m citric acid mixed with 9.35mls of 0.20m Na_2HPO_4). the resulting weight loss - determined after filtering - is calculated as a percentage of the starting weight.

Jones and Hayward (loc. cit.) have tested this technique against in vivo determination of digestibility and they show a very close agreement between "true" in vivo digestibility and digestibility determined by this fungal enzyme method. They offer a regression equation to correct in vitro DMD to in vivo DMD (derived for sheep) of:

$$y = 0.54x + 35$$

(goodness of fit 0.90)

Unfortunately this correlation only works for in vitro DMD values between 39% and 78% and much of the New Forest forage is of poorer quality than this. So, a direct ratio was calculated between mean in vivo and mean in vitro digestibility and by expressing this as a fraction, a conversion was produced for dry matter digestibility below 39%:

$$y = 1.143x$$

(Putman, unpubl.)

The monthly in vitro DMD values obtained from the enzymic technique were converted to in vivo DMD values using this equation. (In vitro DMD figures are given in table 5:22 for the New Forest, 5:26 for Wareham).

c. Nutrient content

To measure the levels of nitrogen, potassium, magnesium, phosphorus and calcium in the forage a small amount of each specimen was dissolved in an acid digest reagent (Allen 1974).

The reagent contains 350mls of 100vols Hydrogen peroxide to which 0.42g of selenium and 14gms of lithium sulphate are added. The final component is 420mls of concentrated sulphuric acid added very slowly with frequent cooling. 4.4mls of this reagent were used to dissolve 100mg of each specimen of powder - dissolution was achieved after several hours refluxing. When cool it was diluted, filtered and made up to a standard 50mls in which form it was stored.

After neutralising the remaining acid by adding 2mls of 2% lanthanum chloride to 8mls of diluted reagent an atomic absorption spectrophotometer was used to determine the calcium and magnesium contents in parts per million. Potassium levels were assessed in a flame spectrometer and the nitrogen and phosphorus status was determined colourimetrically in an autoanalyser. The latter results, after reference to calibration curves plotted for each element, were also given in parts per million.

To convert the results from ppm to mg gm^{-1}, each was substituted into

$$\frac{\text{result (ppm)}}{\text{wt of original sample (gms)} \times 20} = \text{mg gm}^{-1}$$

Calcium and magnesium results were further modified by 5/4 to compensate for the dilution caused by adding the $LaCL_3$. Results used later in this chapter are given, in mg gm^{-1}, in figure 4:31 for the New Forest forages and in 4:32 for Wareham feeds.

RESULTS

1. Winter diet from rumina

a. New Forest

Rumen samples were available from November to January every winter between 1978 - 1979 and 1981 - 1982. Analysis of these offers an indication of the winter diet of sika deer during these years. Mean percentage composition of the rumen, by volume per recognised food category, is given for the New Forest in figure 4:1. This has been plotted with standard errors and results from all the months within each culling season have been amalgamated to represent the mean winter diet of the deer.

It is immediately apparent that differences exist between the years with each diet different from that of the previous winter (differences significant in all cases $p<0.01$).

The acorn crop in 1978 - 1979 was very successful and this is reflected in the high intake. In subsequent years there were fewer available and the proportion of needles and bark in the diet increases. In all years except 1981 - 1982 extensive forestry operations were carried out in and around the study area and needles and bark from brash and felled timber were readily available. In the winter of 1981 there was no such activity and yet the proportion of needles and bark in the diet remains at about 20%, sugggesting that, despite forestry, the majority of this component comes from the 120 Ha of plantations in the area; most of which is in the prethicket stage.

The histograms also suggest an inverse relationship between the intake of acorns and Calluna. In winters of high acorn production (eg. 1978 - 1979) low levels of Calluna are taken, whereas in 1981 - 1982 a considerable proportion of the diet is this (17%), more so though not significantly, than of grasses (16%).

In order to submit more detail and to indicate monthly shifts in intake, each winter diet is broken down to the constituent months (Figures 4:2 - 4:5).

Acorns are consumed in November and December (coinciding with the maximum availability) and when the crop fails, Calluna intake increases in these months. If there are acorns available, Calluna is not taken in a significant proportion until January. On the whole the intake of grasses declines over the winter.

The intake of leaves follows a similar trend. That these are taken at all during the late winter, when they are off the trees and decaying is a surprising result but is reinforced by frequent field observations of sika feeding on old, fallen leaves.

The intake of bark and needles increases towards the end of winter and it is this detail which doubtless gave rise to the assertion that the New Forest sika are browsers (Horwood 1966 and 1971, Horwood and Masters 1970).

b. Wareham

Rumen analysis results from Wareham are presented as percentage content by volume, for three winters and are plotted in figure 4:6.

Inspection reveals annual differences but these are due to the variety of months included; comparison of diet beteen years when calculated from the same months cull shows no significant differences ($p=0.05$).

Winter diet at Wareham consists mainly of grass and Calluna (constituting some 60% of the total between them) with smaller proportions of leaves, gorse and needles. Acorns are taken when available although the area of deciduous woods yielding a supply of these is very small.

When the results are reduced to their constituent months (plotted on figures 4:7 to 4:9) grass intake is shown to decline through the winter. Calluna intake fluctuates and intake of Ulex increases gradually towards the end of the winter.

c. Scotland

To provide a further source of comparison, rumen samples were collected over two culling seasons from five commercial coniferous forests in Scotland where sika deer are becoming increasingly abundant.

The forests that provided samples were:

Shin, near Lairg in North Scotland
Farigaig, on the east side of Loch Ness,
10 miles south east of Inverness
Knapdale, near Lochgilphead at the north end of
the Kintyre Peninsula
Achaglachgach, near Tarbert, midway along the
Kintyre Peninsula
South Kintyre, near Campbelltown, on the southern
end of the Kintyre Peninsula.

The samples were collected, stored and analysed in exactly the same way as those in England and the results, plotted as percentage composition of rumen contents by volume, are presented in figure 4:10.

The results from each forest were not found to be significantly different ($p=0.05$) so the information was amalgamated to a "winter diet for Scottish sika deer" in each of the two years. There is also no significant difference between the two years ($p=0.05$) and the overall impression is that the animals are predominantly grazers.

The diet here is similar to that at Wareham except that these deer take less Calluna. The vegetation in the forests in Scotland and at Wareham is similar; there is a super-abundance of Calluna, Ulex, Molinia and other acid-soil plants, so whilst the diet is clearly governed by availability (small pockets of scrub birch, willow and oak are available but not used much) of interest to the foresters must be the small amount of needles taken and to moorland managers, of the minor consumption of Calluna.

2. Annual diet from faeces

a. New Forest

The diet of the sika deer in the New Forest has been determined each month by microscopic examination of cuticular fragments in faeces collected from dung accumulation plots (Chapter 2 and section 2b in this chapter). The results are given as percentage composition by particle count in figure 4:11 and are plotted for each month in figure 4:12.

Hanson and Graybill (1956) and Anthony and Smith (1974) suggest that to describe diet effectively from faecal analysis at least 15 samples are needed. To check the validity of the smaller samples employed here the results obtained per month from culled animal faeces (increasing the sample to 10 or more on occasion) were compared to those yielded from the faecal transect plots. No significant differences were revealed (p=0.05) and it is suggested that for an animal with a "simple" diet - containing few component species - the profile can be described quite adequately with fewer than 15 specimens: in this case 5.

If the animals were found to have a very varied diet, or the results were to be presented in much more detail than they are here, then a larger sample would be required. When the results are represented bulked up to season (figure 4:13) - at which point the sample size also conforms to Hanson and Graybill's stipulation - extraneous fluctuations obvious in the monthly presentation are removed.

The most immediately striking detail from the monthly figures is the seasonality of intake, not only of acorns (expected because of their limited availability) but also of pine needles; both these are taken predominantly in the winter months. Intake of Ulex (not recognised in the New Forest rumen samples), Calluna, grass (as the "complete" category) and leaves show less of a seasonal pattern although some fluctuations do occur. When intake of grass is broken down to its three main species the relatively constant total is shown to have a fluctuating composition. Molinia, a deciduous grass, is consumed in substantial quantities in the summer months but in the winter intake falls to nil. Agrostis tenuis and Agrostis setacea are eaten in substantial amounts all the year round, but with a larger A. tenuis intake in summer and A. setacea intake in spring. The consumption of deciduous leaves increases in the autumn, coinciding with the leaf fall which brings these items to within the reach of the animals; leaf intake is low during the spring and summer. Calluna consumption is fairly consistent, occupying between 20% and 30% of the diet for most of the year. This increases during the summer as the animals select young shoots before flowering occurs; reported to make these shoots less palatable (Van de Veen 1979).

Comparing the diet in consecutive months shows that there is a gradual change in diet with comparisons necessary over a span of two or three months before a significant difference is obtained (p=0.05). (These results have been plotted on the diet result sheet 4:11a; months compared are bracketed and the significance level is quoted. Every month was compared to its neighbour, if differences were still not significant after a span of six months further analysis was halted).

These statistics indicate that in the spring or autumn food habits change more rapidly than they do in winter or summer. This result supports the idea that these animals are opportunistic in feeding style; being neither predominantly grazers nor predominantly browsers, but that they exploit transient food supplies as they become available, exhibiting a varied diet during the seasons of rapidly changing vegetation. During periods of stable vegetation, as in the summer or winter, diet composition remains constant.

This pattern is summarised in terms of "seasonal diet" in figure 4:13, and the seasons are defined as:

Winter: December, January, February
Spring: March, April, May
Summer: June, July, August
Autumn: September, October, November

Immediately apparent are differences between adjacent seasons (portrayed in figure 4:14) and the considerable similarity between the same season in successive years.

In the autumn the deer have a varied diet with leaves, Calluna and grass comprising roughly 25% of the intake each. The remainder is shared between needles, Ulex, Ilex and acorns (if available).

Winter shows an increase in needle intake and a decline in the leaf consumption. Spring (in both years) and summer show that the deer are feeding on grass (ca. 30% in spring, 40% in summer) and Calluna (30% in spring, 35% in summer) with intake of needles and Ulex declining. The remaining 15% of the intake is contributed by "leaves" which includes forbs at this time of year.

b. Wareham

Details of monthly diet at Wareham have been obtained from collections of faeces over one year only and the results, as percentage composition by particle count, are given in table 4:15 and are plotted by month in figure 4:16.

Occasionally a month is described from four pellet groups, but the majority of results are determined from five. Again, comparison between the results and those obtained from larger samples from culled animals failed to display any significant differences (p=0.05) so the sample size is adequate here too.

The diet has an unchanging composition with a slight seasonality in the consumption of pine needles - a minor feedstuff here. Intake of leaves is very low; the main diet components are grasses and *Calluna*.

Inspection suggests that statistical comparison between monthly diet will not yield any significant differences and this was confirmed by a chi-squared comparison of seasonal diets (p= 0.05). These seasonal diets are plotted in figure 4:17.

Thus, at Wareham seasonal diet contains between 40% and 50% *Calluna*, 30% and 40% grasses and the other components combine to contribute the remaining 20%.

c. Ingestion of grasses

Whilst identification of tree leaves and forbs to species was not practicable, separation of the broad "grass" category was possible because the three main components, Molinia, Agrostis setacea, and Agrostis tenuis were sufficiently distinctive to be reliably recorded during analysis of the faeces.

Data submitted on these individual species in any one month are not very useful so they have been bulked up to season in an attempt to reduce the standard deviations and the fluctuations in the results.

Plotted in histogram form, the figures show the proportion of the grass category that was occupied by each species each season. Figure 4:18 shows the New Forest results.

In the New Forest the most obvious feature is the seasonal intake of Molinia, coinciding with its growing season.

The presence of Molinia in faeces in winter may be due to misidentification of other particles, or to accidental consumption - at this time of year Molinia is not only dead, but is decaying.

The intake of A. setacea, an apparently unpalatable grass, is fairly constant and on the basis of these results would seem to be the staple grass. However, it is the most distinctive of the grasses and the ease of recognition may have led to bias in the data as particles of doubtful origin may have been unconsciously allocated to this category (after Hanson 1970).

Consumption of A. tenuis also follows a seasonal pattern, but less obviously than the Molinia. There is no explanation for the very high intake of A. tenuis in the autumn of 1980.

Data from Wareham follows the same pattern and are plotted in figure 4:19. Molinia is taken during the growing season although it contributes little to the total grass consumption. A. setacea is again shown as being the staple feed; contributing 45% to the grass intake, or 20% to the total diet. A. tenuis, another minor food item, is relatively constant in intake.

There is a large proportion of unrecognised grasses both at Wareham and in the New Forest. This may be due at Wareham to the tendency of the deer to feed in fields or cultivated species which by their very nature are highly digestible and therefore are unrecognisable as anything other than "graminid" in the faecal samples.

d. Modification of faecal analysis results

Diet revealed by faecal analysis differs from that revealed by ruminal analysis in both absolute and relative terms and this is the result of differential digestibility of items in the feed. This causes over or under-representation of the item in the faeces and to a lesser extent, in the rumen.

Faeces are the only material from which diet may be reconstructed for eight months of the year, so a realistic method is needed to compensate for this bias.

Two techniques have been attempted:

1) Correction of faecal data using a regression relationship between rectal and ruminal analyses of material from the same shot animal.
2) Correction of faecal data by applying an experimentally determined forage digestibility figure.

i. Rectal: ruminal correlation:

One possible method of correcting the "raw" results of "percentage species composition of faecal fragments" would be calibration between the observed faecal output and known dietary input. Since this is impossible the closest alternative is to calibrate using faecal and ruminal material collected from the same animal.

Although the faecal sample does not correspond to the same meal, or set of meals, as is represented in the rumen, it may still represent the fate of the rumen contents if one assumes that dietary intake is reasonably constant over a time scale of several days. The ecological chapters above have shown that the habitat usage patterns of the New

Forest deer operate over a finer scale than Wareham and Purbeck animals so this assumption may be valid for the Hampshire animals.

A series of regressions was derived for each forage species relating percentage fragment count in the faeces to percentage composition by volume in the rumen of the same animal. To increase the sample size the deer culled from all winters were used in this calculation although the Wareham and the New Forest data were held separately.

The New Forest results are given in figure 4:20 and the Wareham ones in figure 4:21 and it is clear that few of the correlations obtained are significant (p=0.05). This may be due to the crudeness of the categories used in the regression calculations in that by being so broad, more subtle relationships are concealed. On the other hand, where correlations are possible for an individual species, these still fail to produce a significant result. It is possible that this method would work were the techniques used on the materials less dissimilar. Had a microhistological technique been used on the rumen material, vagaries caused by the differences between "percent by volume" and "percent by particle count" would have been avoided. Greater accuracy would also have been possible as more species - particularly the grasses - could have been identified in the rumen and some of the broad categories could have been refined. Errors of identification might have been virtually eliminated as the same characteristics of each species would be used in each case so the same mistakes would occur. This regression technique could only be applied to the seasons in which rumina are available for the digestibility of forage changes markedly throughout the year, and this would certainly affect the results. The regressions also fail to take account of digestion of the species as modified by the presence of other material in the rumen. Whilst this may not be a major influence, calculation of an effective relationship does depend upon finding representatives of each feed type in both rumen and faeces; the reduced sample size resulting from failure to do this and the modifying effect of other rumen constituents, coupled to individual animal efficiencies and the uniqueness of each rumen content, may combine to produce the inconsistencies reported here. Thus, the technique has failed due to a number of reasons not the least being the crudeness of the food categories used. It also appears as if the assumption that the New Forest food intake (or Wareham, for that matter) is constant, is not valid in which case the method must fail.

In other studies (eg. Easterbee 1979) using microhistological rumen analysis and microfaecal analysis, reasonable agreement between the composition of the rumen and the rectum has been found. Had this technique been successful here, the faecal results from transect collections (for winter diet only) could have been modified to represent the theoretical rumen content they came from. This, although not representing actual ingesta, is more closely allied to it than to faecal composition.

ii. Correction via differential digestibility

An alternative approach to correction of "raw" faecal fragment numbers to compensate for the differential digestion of each species is by using an experimentally derived digestibility.

To this end the dry matter digestibility (DMD) of each food species was determined by finding the percentage weight loss of material following incubation in acid pepsin and fungal cellulose (after Jones and Hayward 1975, see Methods 4b and figure 4:22 and 4:26.) Their own regression, calculated to relate in vivo and in vitro digestibility was used to convert the results to in vivo dry matter digestibility for DMD values greater than 39% a derived equation (Putman unpubl.) was used to convert in vitro DMD values below this.

Faecal fragment numbers as presented above in the description of monthly diet may be multiplied by:

$$\frac{1}{1 - \text{digestibility (in vivo)}}$$

to convert them to figures that represent dietary intake.

Such an adjustment makes a number of assumptions. Digestibilities are calculated as a percentage loss of weight, not as fragment loss, so there is no reason to suppose that persistence of faecal fragments bears any relation to dry matter digestibility by weight. It is more likely to be related to cell wall digestibility (a measure of the ease with which the material disintegrates). Assuming that persistence of faecal fragments (primarily epidermal cell wall and cuticle) is related to cell wall digestibility (C.W.D.) the number of fragments of a particular forage species in the faeces may be multiplied by:

$$\frac{1}{1 - \mathrm{CWD}}$$

to represent the number of intake fragments. If faecal fragment size is relatively constant (which the sedimentation technique is designed to ensure) the percentage species composition of the converted fragment numbers will reflect actual relative proportions of material ingested.

Cell wall digestibility may be independently determined (eg. Allen 1972). However, results published by Koller et al. (1978) in a comparison of digestion capacities of cattle and ponies present figures for in vivo CWD and total dry matter digestibility for a range of forages in both cattle and ponies. If these are analysed further it is clear that a close relationship exists between percentage cell wall digestibility (CWD) and percentage dry matter digestibility (DMD) (Putman et al. 1981).

Regressions calculated for cattle by Putman et al. are thus:

for 24 hours throughput time

$CWD = 0.8616\ DMD - 8.719$

$(r=0.980$, goodness of fit $0.96)$

for 48 hours throughout time

$CWD - 0.8526\ DMD - 3.304$

$(r=0.970$, goodness of fit $0.942)$

Although neither cattle nor ponies are closely related to deer, once the relationship is derived for one species of ruminant, it can be assumed to apply to most other species in a very closely related form (Putman unpubl.). In any case, here one is dealing with the relative proportions of feedstuff and is using arbitrary units, so the absolute values are not important.

Thus, the mean of the above regressions (deer have a gut-passage of time of around 36 hours - Zyznar and Urness 1969) expresses the form of the relationship between the *in vivo* DMD derived earlier and the CWD value required.

The resulting formula:

$$CWD = 0.8572\ DMD - 6.0136$$

$(r=0.975$ goodness of fit $0.95)$;

was used to calculate the cell wall digestibility values given in figure 4:23 for New Forest forages and in figure 4:27 for Wareham forages.

iii. Corrected diet

The results obtained from "raw" faecal analysis (given in figure 4:11 for New Forest and figure 4:15 for Wareham) are changed very little by the digestion correction. The revised figures are given in table 4:24 for monthly New Forest diet and 4:28 for Wareham. (Accumulated seasonal data is tabulated for the New Forest in 4:25 and in 4:29 for Wareham).

On the whole the proportion of grasses is increased and the proportion of Calluna in the diet is decreased.

This is a worthwhile technique that, with forages having higher digestibility than those encountered here, would result in substantial re-emphasis of the final result. In this case nearly all the feedstuffs have low CWD values and those that are highest are found in the diet in such small amounts that even doubling their presence hardly affects the final result. That these highly digestible plants do not occupy a more significant part of the diet is probably because they are less obtainable than others in the field, or possibly is because they break up so easily that they were inadvertently discarded during the preparation of the material.

e. Sexual differences in diet

Data would have been analysed to investigate the sexual differences in diet composition, but as this can only be done with rumina (faecal material cannot be sexed accurately) the resulting sample sizes are extremely small and only represent winter diet. Further, as individual variation is so great (hence the large standard errors in the monthly diet) and as the diet categories employed here are so crude, it is likely that any differences would be concealed.

Dziecieolowski (1970) has reported no significant dietary differences between red deer hinds and stags, whereas Staines et al. (1981) produce the opposite result and suggest that stags and hinds opt for different feeding strategies in the winter; hinds selecting for high quality and stags (by virtue of their larger capacity) surviving on a greater intake of poorer quality material.

f. Diet related to food availability

To see whether diet is governed by food availability, a correlation was carried out between the proportion of each item in the diet each season and the area of habitat likely to contain that feedstuff. Clearly this will only yield a meaningful result if an effective definition of "availability" is employed. For example, except during the autumn deciduous leaves are only available to the deer when growing below four feet above the ground so the availability of these items is in fact represented by a small fraction of the total area of oak woodland. From field observations and from the Braun-Blanquet assessments of the dung quadrats, (used to give ground cover figures) it was possible to represent each food category as an area of land carrying that material. The same technique was applied at Wareham and the seasonal diet was correlated with these results using the Spearman rank correlation coefficient (see table 4:30).

Several seasons correlated well for New Forest data indicating that the deer do indeed feed on material as it is available and thus are yet again shown to be opportunists. The failure of correlation in the summer of 1980 is because of the selection of grasses and not needles. In the autumn and winter of the same year the acorn crop failed, but not totally, so the availability figure devised here is entirely speculative and the likely source of disagreement. Excluding the acorns from the analysis allows a significant correlation between winter diet and availability ($p<0.05$). Correlation between autumn diet and availability still fails but this may be due to a disproportionate consumption of Calluna as a result of the deficit of acorns.

At Wareham only one significant correlation was found (Spring 1981, $p<0.01$). The diet here contains fewer categories so the correlation is less reliable, but the results do emphasise that the deer select grass and Calluna and ignore pine needles; despite their considerable availability.

Although the deer are feeding opportunistically, at least to some extent, there is little doubt that they also show some selectivity.

To investigate reasons for this the diet in each month was examined in relation to the nutrient status of the available forages.

3. Nutrient results

Nutrient values of the forage species analysed are presented in table 4:31 for the New Forest and in table 4:32 for Wareham. As was noted earlier, deficiencies in own data are restored by results from Putman et al. (1981) and these are shown in parentheses.

Overall the nutrient trends in the species follow the same pattern at Wareham as in the New Forest although many of the Dorset figures, particularly the nitrogen values, are lower and the calcium values are higher.

The nutrient levels in complete categories ("leaves" and "grass") were calculated from the means of the constituent species.

a. Intra-monthly diet: selection?

In order to determine whether the selection of items in the diet occurs in order to maximise the intake of a particular nutrient, or whether it is to exploit the most digestible forage, the composition of the diet each month was corelated with the nutrient status of each food item; each nutrient being treated separately.

Relationships were calculated for all months between June and December in both 1980 and 1981. Own data only was used as results from Putman et al. (loc. cit.) contained too few individual species. Ordinal statistics were employed (Spearman Rank correlation) so the same nutrient values can be used in both years as the trends, if not the absolute values, will be unchanged.

Only five significant relationships were revealed; three with calcium (July 1980 $p<0.01$, November 1980 and September 1981 $p<0.05$) and two with digestibility (December 1980 $p<0.01$, and June 1981 $p<0.05$).

Wareham data does not yield effective results by this method as there are too few categories in the monthly diet.

b. Inter-monthly diet: selection?

The alternative correlation seeks to explain the changes in diet between months by relating the monthly nutrient status of each forage with its consumption.

Many significant correlations were found in the New Forest results and these are given from January to December 1980 in table 4:33 and from January to September 1981 in table 4:34).

Because of the incompleteness of own nutrient analysis here, the figures from Putman et al. were used for these calculations except where indicated in which case the seven months of own data were applied.

The results suggest that in the New Forest changes in diet throughout the year are associated with changes in the levels of some chemical elements in the feeds. Curiously, nitrogen levels fail to correlate at all, whereas potassium (present in the plants in minute amounts) correlates the most consistently. Digestibility, arguably related to palatability, correlates inconsistently but these figures are calculated on the basis of only seven months of results and might be improved with the addition of the remaining data.

At Wareham these calculations were carried out using the seven months of nutrient data available from there and only three signficant relationships were recorded (between leaves and nitrogen, leaves and phosphorus, and pine needles and phosphorus - all at significance level of $p<0.05$.)

Increasing the sample size to the full twelve months by using Putman's results, even though these are derived from a different area (using ordinal statistics enables the correlation of trends and leaves the final result unaffected by the absolute values) did not increase the number of significant correlations, nor did it increase the significance of those achieved; instead it produced two positive relationships (between grass and phosphorus, and between leaves and phosphorus), and also a negative correlation (between needles and potassium - all significance values are $p<0.05$).

These results indicate that not only do the Wareham deer not feed as dictated by availability, they are not selective either - or if they are, then these analyses have failed to detect it.

c. Specific correlation: "grasses"

Two broad amalgamated categories have been used in the diet descriptions and in the calculations above; "leaves" and "grass".

It has not been possible to separate the leaf category into its component species, but three of the grass species (*Molinia*, *A. tenuis* and *A. setacea*) were sufficiently distinctive to be identified and as major contributors to the grass category, have been correlated independently with their own nutrient details. The results are given in table 4:35 where the main correlations for the New Forest data are for Molinia. Intake of all three species was successfully correlated to digestibility in 1980.

There were no significant relationships between grass intake and any nutrient details at Wareham.

DISCUSSION

I. New Forest and Wareham diets compared

Substantial differences are apparent between the diets of the deer in these two areas. At Wareham the trend revealed by the rumen analysis is perpetuated by the faecal analyses indicating that diet varies very little. The main constituents are Calluna and grasses, although the precise balance of grass species varies according to the time of year. Together Calluna and grasses account for at least 60% of the intake in any season and the remainder contains small amounts of tree leaves, pine needles and bark, and gorse. Thus the Dorset animals may be classified as "grazers"; a conclusion entirely in agreement with Horwood and Masters 1971) who stated this after macroscopic inspection of some 200 rumina collected over several culling seasons.

When describing the sika in the New Forest, Horwood and Masters (loc. cit.) stated "...in spite of the fact that sedges and grasses are undoubtedly available, and apparently in sufficient quantity, the sika (in the New Forest) appear to be browsers and furthermore, they browse to a large extent on conifers, at least during February when six stomachs were examined..."

This conclusion is not entirely supported by the larger sample given in this present study. That the Hampshire animals do fed on coniferous browse is certain, and yet not only have seasonal differences been described for the diet of the deer, but differences are also found between successive winters. In some years the intake of needles is falling by February (1980-1981), in others it is still high (1979-1980) and to utilise data from this one period to label these deer seems most unwise.

In marked contrast to the similarity of the three winter diets in Dorset, it is apparent that in the New Forest winter diet is more flexible which suggests that the population employs an opportunistic feeding strategy. At the end of the autumn the animals exploit transiently abundant feed (acorns, beechmast, fallen leaves) and when these supplies are depleted, for whatever reason, they switch to a browsing strategy and feed more from dwarf shrubs (eg. Calluna, Ulex, Ilex) and trees; maintaining a steady ,if reduced, intake of grass. Areas of felling operations are heavily exploited (as was shown in the habitat occupation section in Chapter 2) and here feeding site inspection reveals extensive feeding from brash and bark stripping from cut branches.

As winter progresses intake of leaves and grass declines and intake of Calluna and coniferous browse rises. This is directly in contrast to Wareham where only a slight decrease in grass intake occurs and coniferous browse consumption remains low, as does the consumption of leaves.

With the advent of spring and the "new bite", the New Forest deer stop taking coniferous browse and concentrate more on the grasses; a tendancy that becomes more exaggerated during the summer. Intake of Calluna remains fairly steady, as does that of leaves, but now pine needles are not taken at all. In the late summer there is a slight decrease in Calluna consumption (coinciding with flowering - thought to make it less palatable, Van de Veen 1979).

The similarity between the winter diet of the deer shot in Dorset and those shot in Scotland is more striking than between Dorset and Hampshire. Vegetationally the Scots and Dorset forests are very similar; large expanses of coniferous woodland in various stages of commercial management surrounded by acid moorland. The Scots animals are clearly mainly grass feeders with their Calluna consumption less than that of the Wareham deer. They also feed as extensively on deciduous leaves at this time of year, but of major interest to commercial forests must be the low proportion of bark, and the even lower proportion of needles, in the diet.

The diets reported for the sika deer in this study correspond to those reported in the literature. Writing on sika deer on Askold Island Prisyazhnyuk and Prisyazhynuk (1974) report that the bulk of the food is grassy vegetation with a few fallen leaves; 97 plant species taken. Furubayashi and Marauyama (1977) working on sika in the Tanzawa Mountains, Fudakake, Japan, report 106 plant species taken of which 72 were trees and shrubs and 34 forbs and grasses. They reported that plants and plant parts eaten vary widely with season and species and they suggest that diet is more influenced by sika density and plant succession than by food availability.

Robinson (1973) writing about sika in the Lake District, suggests that they feed almost exclusively on grass; a conclusion supported by Takatsuki (1980) working on Kinkazan Island, Japan. He used feeding site examination and faecal analysis to produce this result and he also reports that the composition of the diet varies greatly between habitats. Despite this, the main forages were always grasses such as *Zaysia japonica*, *Miscanthus sinensis*, and *Pleioblastus chino*, a dwarf bamboo which, by virtue of being an evergreen, is taken all the year round. Takatsuki (loc. cit.) also reports a slight separation in food habits between the sexes with stags taking P. chino and hinds M. sinensis.

2. Discussion of methodology

The most commonly used indirect procedure for studying the food habits of ungulates has been rumen analysis. This is quantified either by volumetric (eg: Dirschl 1962, Martinka 1968) or point-analysis methods (Chamrad and Box 1964 et. seq.). However, Jackson (1974) found that when large amounts of fruits and nuts are present their quantitative importance is underestimated by the point-analysis technique and he overcame the problem by removing the bulkier items and assessing their volume by displacement; thus utilising both methods. These techniques have been compared on the basis of accuracy and time by Robel and Watt (1970). They decided that the point-analysis technique saved time only if the investigator was thoroughly familiar with the items in the stomach sample. Heterogeneity of food item size in the rumen caused inaccuracies in the results produced by the point analysis method, but these disappeared when data from several different samples were pooled and the means compared. To wash, sort and determine the volume of each food species in the rumen takes in excess of 4.7 hours (Robel and Watt, loc. cit.); this time investment was drastically reduced when the point-analysis method was used on the same material. The inaccuracy due to different particle sizes was removed by Staines (1976) who proposed that each food fraction identified in the point-analysis be calibrated in terms of number of "line hits" per unit volume, thus exploiting the advantages of both methods.

Unfortunately, Zyznar and Urness (1969) amongst others, feel that details revealed by these earlier methods are misleading as associated with the technique is the problem of differential digestibility - soft foods may be digested more rapidly than woody ones. This was recognised as long ago as 1943 by Norris working with sheep. Not only did he recognise that feed digestibility differed from species to species, he also recorded digestion differences amongst the animals and suggested that within 4 hours about 30% of the feed intake was digested in the rumen. The rumen content is also a composite of several days feeding, (Staines 1976) so the results from these analyses may be biased in favour of coarser material and because of this one may not consider even rumen content to be "ingesta".

Thus, quantitative comparisons between different foods are only approximate indications of their relative importance in the diet (Dzieciolowski 1970). As Jensen (1968) points out though, when comparing diets of large mammals it is generally of little consequence whether a food forms precisely 30%, 35% or 40% of the intake, the crucial point is that it forms about 1/3 of the diet and is therefore a major food. Frequently the method of rumen analysis is impractical anyway due to the difficulty of acquiring sufficient material from rare or timid species, and due to legal constraints rumen contents are only available in quantity over a limited period of the year in this country. Analysis of the material is a relatively simple affair in that it depends upon the recognition of macroscopic characteristics; the separation of pine needles, bark, Calluna, grasses and other broad categories is easily achieved.

Presentation of the results from this technique is awkward because of the bias caused by the inevitable difference in plants susceptibility to mechanical breakdown, but the volumetric correction as outlined above has proved adequate (Staines 1976).

Preparation of material for the analysis is also simple and an analysis by Dirschl (1962) found that there was little difference in the botanical composition of rumen material remaining in sieves of three different mesh sizes (ranging from 2.8mm to 5.66mm) after washing. Bergerud and Lloyd (1964), using smaller mesh sizes (0.4mm to 2.0mm) came to the opposite conclusion and described this to the differential digestion of forage items.

The sample size available in this study is large and this will help to reduce fluctuations in the results. Further, the 2mm sieve retains the largest particles which, one hopes, include the most recent additions to the rumen content. Those items introduced earlier may be more broken down (with the possible exception of the woody items) and may have been washed away. It is hoped that this reduces the error created by the different shooting times of the animals. As the beasts used in this study are culled for commercial and not for scientific purposes, they are shot at various times of the day - after a night feeding in the fields or after a day lying up ruminating - and the physical state of the rumen content reflects this. In the former case rumen material may be dry, almost friable and is much more finely divided and moister in the latter instance.

The relative proportions of species in the faeces can only give an approximate indication of dietary composition. Differential digestibility of foodstuffs causes the absolute proportions of residue in the faeces to vary considerably from the proportions in which they were actually consumed.

The validity of these results is also affected by the different particle sizes in the dung as most results are presented as percentage by particle count (Stewart 1967, Westoby et al. 1976). Some plant species fragment more readily than others and some may contain different proportions of readily identifiable material; it was distortion of results caused by effects like these, combined with the considerable problems encountered whilst identifying the particles that prompted Zyznar and Urness (1969) to question the value of the technique. However, Smith and Shandruk (1979), Vavra et al. (1978) and Kessler et al. (1981) agree that microfaecal analysis is a useful technique that yields qualitative information describing herbivore diets. Faeces are frequently the only material available and as such cannot be discarded (Anthony and Smith 1974).

Rumen material taken from culled animals only represents a small proportion of the population; more representative of the population as a whole is information derived from analysis of faecal material.

Faeces are readily available and may be collected with the minimum of disturbance to either the animals or the habitat, at any time of year, so diet outside the culling season may be investigated (Stewart 1965, Stewart and Stewart 1970, Adams 1957, Hercus 1960 etc.). Since it is thought that every plant species has unique cuticle characteristics and since most plant cuticles survive the ruminant digestive process, forage plants should be recognisable after microscopic examination of faecal samples.

In this report an attempt was made to correct the relative numbers of particles found in the faeces in order to compensate for the differential digestibility of the forages. The sedimentation technique developed here for preparing the material for analysis is designed to at least reduce the range of particles analysed and so to increase confidence in the result; given as "percentage by particle count". This method could, however, have resulted in the total exclusion of a species that regularly fragmented insufficiently, or so much, as to fall either side of the fraction that was used. It is thought unlikely that the finest particles discarded during the washing would contribute significantly to the overall result as one requires a finite size of particle, with a representative selection of cells, from which to make an identification.

Preparation of the material also presents problems for, unlike the rumen material, transmitted light will be used in microscopic analysis as fragmentation has resulted in the loss of major macroscopic features from most of the species. Preparation techniques are many and all have the aim of removing the gut mucus, bacteria, of separating the particles and of clearing the cells to display their cuticular features. Some methods are destructive, for example Martin (1955) and Stewart (1967) used nitric acid to mascerate faecal samples whilst Dunnet et al. (1973) used a mixture of nitric and chromic acids. Milder methods include soaking in methanol (Robertson 1967) and bacterial techniques (Skoss 1955) but all have been shown to produce usable material with the accuracy of the final result thought to be more dependent on the skill of the technician than the ferocity of the preparation technique. The more destructive methods, though, undoubtedly do remove some of the softer particles (Anthony and Smith 1974).

The method used in this study is destructive and was employed after soaking in acid, washing in water and soaking in alkali had been tried; all with varying degrees of success. As in the rumina, a large number of samples was to be analysed and a rapid, easily reproducible preparation technique was required.

Whichever preparation technique is used and however the results are presented, the diet suggested by this method will differ from that derived form analysis of rumen contents, whether from a group of animals, or from the same animal and this is the result of differential digestibility. Neither result can be considered as "true" diet as ingested, (only reliably determined by oesophageal fistulation - Vavra et al. 1978) although obviously rumen content is more closely related to this than is faecal composition.

To overcome this discrepancy many workers have attempted to apply a "correction factor" to faecal analysis results in an effort to relate the faecal contents to material ingested (eg: Dearden et al. 1975). For example, fragments of leaf cuticle are identified in the faeces and the areas of each plant species can be determined. It is sometimes assumed not only that all plant species eaten can be detected, but that the areas of cuticle of each plant species in the faeces are proportional to those ingested. The latter assumption is only justified if leaf cuticle is unaffected or if all species are equally affected by digestion, but this has not been shown. Slater and Jones (1971) have found that clover may be undetectable in sheep faeces and Stewart (1967) suggests that some species of grass leave "fewer epidermal fragments" in the faeces than do others. As long ago as 1943, Morris showed that sheep had individual efficiencies at digesting grassy material and since then many comparative studies have looked at faecal and ruminal material taken from the same animals, (Anthony and Smith 1974, Dearden et al. 1975, Kessler et al.1981).

Here faecal and ruminal analyses have been used to complement each other and as one of the aims of the study is to compare diets of the deer in two different forests (in areas of markedly different vegetation) the biases in the methods are perhaps less significant as they apply to both sets of data. The biases discussed above must be borne in mind, however, when comparing these results to those from other workers.

3. Validity of the described diets

In this report an attempt has been made to describe the diet of the sika using tried and tested techniques involving assessment of faecal and ruminal material. The results described above, outlining in a fairly crude fashion the pattern of food intake, are prone to many biases, outlined in the methodological discussion earlier. The inclusion of woody material in the ruminal results is defended on the grounds that it does form an important component of the animals' diet and must be selected as it cannot be obtained in these quantities by accident. Because of the rumen's ability to retain the less digestible material and therefore to bias the analysis of the contents in favour of it, previous workers (eg: Jensen 1968) advocate segregation of the particles and their exclusion from the results; an attitude adopted by Jackson (1974). Van de Veen (1979) has shown that red deer seem to have a basic requirement for less digestible foods and as such they must be included. Woodier items were not recognised in the faecal analyses and although a fair proportion of faecal material is opaque after preparation and therefore is unidentifiable (and possibly is woody) it is clear that a high proportion of this tougher material is eventually digested.

Further bias is inherent in ruminal analysis in that other items, less obviously indigestible, may also be held back by the rumen and as such the contents include particles representing items from many days feeding. Staines (1976) has shown that Calluna and grass may be found in the rumen 8 and 7 days respectively after the last time they were included in a feed. Employing a large (2mm) sieve is thought to alleviate this problem slightly for items with longer retention times in the rumen may have been broken down more than more recently investigated ones so are removed,or are reduced in quantity, by being washed away.

The major part of this diet determination rests upon successful analysis of faecal material. The main criticism of this method is that it fails to acknowledge that some items in the faeces are over or under-represented as they are highly or poorly-digestible to the animal. In order to compensate for this two techniques were tried.

Regretfully the simplest and the most logical, that of rectal:ruminal content correlation, failed to yield a satifactory result. This was due to a variety of reasons of which the main one was that the categories were too crude; had a greater depth of resolution been employed the result might have been more successful. Although this method would automatically compensate for differences in susceptibility to breakdown (both mechanical and chemical) and once derived the regression could be used for correcting transect faeces to their probable rumen origin, it in fact takes no account, nor can it, of the modifying effect of other items present in the rumen. That there is considerable variation between rumen contents of animals shot in the same area, at the same time on the same day, would be expected; an adequate sample size will reduce the variation from this, but some items may be selected purely for their beneficial effect upon the digestive process (Juon 1963). It has been suggested, for example, that bark may be taken in fair quantity during the spring as some compounds in it inhibit cellulolysis and therefore slow down what might be an excessively rapid throughput of young grass (Van de Veen 1973). Prins and Galeen (1968) tentatively suggest that substances present in the bark of species subject to severe attack have an antimicrobial effect and hence slow digestion in the rumen. Winter consumption of this, they suggest, would prolong ruminal fill and promote a feeling of satiation.

As mentioned earlier, (eg: Van de Veen 1979) deer seem to have a basic requirement for fibre and may select less digestible items in order to maintain this requirement (Prior 1968, Bubenik 1959). As long ago as 1943, Norris showed different individual efficiencies of sheep at digesting grass; with this in mind it is likely that fibre requirements will vary from animal to animal too.

The final assumption upon which the method relies is that dietary intake is of relatively constant composition. The New Forest animals have been shown (see Chapter 2) to occupy a fine-grained environment and to feed regularly throughout the 24 hours. At Wareham the structure of the habitat is very different and although few observations were made of deer feeding during the daylight hours it does appear as if they feed mainly at night, at which time they are out in heathland, bog and field areas, returning to the plantations during the day. Thus, at Wareham food may arrive in the rumen in discrete "batches", grasses from fields at night followed and preceded by a mixture of items gleaned on the journey to and from the fields; this is in contrast to the New Forest where food intake, although containing more species, may well be of more constant composition.

This being true, when added to the methodological and technical problems outlined earlier invalidates this ideal technique here. That the correlations failed to work out consistently for any category or individual species indicated that the method itself may be at fault. Digestibility of food items changes throughout the year (as do animal nutritional requirements - due to stresses imposed by pregnancy, lactation, moulting or antler growth), so a year-round supply of rumina is required as these regressions must be calculated at least every season, if not every month.

Thus, a series of published formulae were used to derive the CWD of the forage. This was then used to modify the faecal analysis results to represent the actual ingesta. It was argued (Putman et al. 1981) that correction of faecal fragment numbers was more logically achieved using cellwall digestibility (a function of the breakdown of the material) than by using dry matter digestibility; itself determined as a weight loss.

The cell wall digestibility was calculated for a gut passage time of 36 hours (Zyznar and Urness 1969) and was applied to the faecal fragment results. In this instance the majority of the digestibilities are so low due to the poor quality of New Forest and Wareham vegetation (only Hedera helix and some early spring tree leaves reaching 50%) that the corrections made little difference to the overall result. That the most highly digested particles are least represented in the faeces is obvious; correction of these figures by this method could produce a large overall change in the declared diet profile. In this study the overall effect has been slight but, in some categories or species, the proportional effect of these alterations has been considerable.

4. Sexual differences?

The details given here do not lend themselves to investigation of sexual differences in diet as only rumina can be used; faeces cannot be sexed reliably. In the south of England a small proportion of the total cull is of males and within that most are calves and yearlings, who by travelling with their dams might be expected to have a similar pattern of food intake. In Scotland the comparison is also impossible for here the majority of the cull is of mature stags and the number of hinds shot is small.

It has been suggested that the stags occupy different areas to the hinds for most of the year (see Chapter 2) but that during the rut the use of habitat by the two sexes in the New Forest is the same. As it could be suggested that use of exclusive areas may be partly due to specific feed requirements and as rumina are only available for the time when the sexes are sympatric, none of the analyses would be likely to yield any differences even if the sample sizes were large enough.

Staines et al. (1981) have shown significant differences in the nitrogen levels in the rumen contents of culled red deer hinds and stags and have proposed that the sexes adopt different feeding strategies. The stags, by virtue of their large capacity, can ingest greater quantities of poor quality forage and the hinds are able to select for quality; better quality feed being required at this time of year due to the stresses imposed by pregnancy. This will be reviewed in Chapter 6 and 7 when the segregation of the sexes is discussed.

5. Sika diet related to feed availability?

In an attempt to discover whether the deer surveyed here are truly opportunistic or selective, a series of correlations was carried out between seasonal diet and the areas likely to yield the diet components. Significant positive correlations were obtained for all but two of the monthly New Forest comparisons but for only one of the four Wareham comparisons.

The success of these correlations does indeed suggest that the New Forest deer feed on matter as it is available; the failures of correlation can be attributed to early selection of pine needles and _Calluna_ when tree leaves were still abundant and when the acorn crop was very poor.

This opportunistic pattern of feeding is evolutionarily sound in the varied habitat of the New Forest where local failure of a resource is of little consequence as there are others that can be substituted. The seasonal diets were compared pairwise across the years and were found to be very similar ($p<0.01$) thus indicating that although the animals are opportunists, they are repeatedly so. They are clearly influenced by seasonal change in availability which would be expected, apart from total crop failure, to yield to same pattern of food intake each year.

At Wareham the same availability calculations were performed and the pine needles and Calluna were revealed as super-abundant, yet grass and Calluna are the major components of the diet. Here the animals are selecting feed and this selection continues irrespective of season - the use of transient supplies was not detected. For animals in such a large homogeneous area to be dependent upon occasional abundance of a resource would be non-adaptive, so the feeding strategy here is also evolutionarily sound.

It is perhaps curious that this selection was not correlated to details of forage chemistry, but as no attempt was made to mimic the selective feeding styles of the deer it is possible that the samples were different from those that might be chosen by the animals. It is also possible that the deer at Wareham select their feed using criteria not included in this study, for example, palatability.

6. Diet related to forage chemistry?

It has been documented from many years ago (Swift 1948) to the present day (Van de Veen 1979, Staines 1981) that deer are capable of selecting the most nutritious forages. The feeding style of the roe deer, that of taking the nutrient-rich shoot endings, for example, is often reported (Hosey 1974, Henry 1978, Loudon 1979). To be successful the animal must exploit signs, or an innate ability, not available to the human observer; indeed a worker selecting forage fails to maximise intake as successfully as a tame deer (Van de Veen 1979). Thus, it is likely that the samples clipped and analysed here actually bear less resemblance to the plant parts that would be taken by a deer than one might hope.

The clipping technique that was adopted was designed to be reproducible and the introduction of subjective selection by the author was avoided. It is also likely that the nutrient values determined are minima.

In the statistical analysis performed an ordinal method was employed so the actual values obtained from these nutrient assessments became less important. Further, as the growing season progresses the proportion of leaf to twig, or of stem to leaf, alters so that each month's data represents a slightly different combination of tissues. The observer has absolute control over the proportions that can be presented for analysis, but the situation encountered in the field was that followed; clipping being at the scar marking the start of the new season's growth. The material was taken within a height range accessible to the deer and an attempt was made to reduce extraneous variation by sampling from a limited number of trees and shrubs and from the same grass swards although all are subject to local influences like flooding, rainsplash and drought.

The failure of the intra-monthly correlations was the result of food choice being governed by availability and not by quality.

Although seasonal variations in the selection of a particular species are usually taken to be a reflection of changes in the nutritive status of the vegetation (and such selection has been described for deer (Klein 1970) and for cattle and sheep (Bedell 1971) food choice by some species eg. roe deer, do not always reflect these differences (Loudon 1979).

The significant correlations yielded by the inter-monthly comparisons between forage chemistry and diet for the sika deer indicate, at least superficially, that these do select feed on the basis of nutrient status and that changes in intake each month are influenced by changes in nutrient content.

However, nutrient patterns follow seasonal trends in growth; for example, nitrogen levels increase during the summer, peak, and then gradually decline so correlations would be expected between this feature and a seasonally available feed. This is shown very clearly in the correlations in 1980 between _Molinia_ consumption and quality. _Molinia_ is a deciduous grass with a brief growing season followed by a period of relative stasis and then decay. Intake patterns follow this trend very closely, as do nutrient levels; all except calcium which rises throughout the year and is indicative of older or woodier materials; calcium failed to correlate with intake.

Thus , one cannot state that diet patterns are exclusively due to selection on the basis of nutrient qualities in the New Forest, even though some do correlate very well. Diet has also been shown to correlate to availability; seasonal growth and availability are, to an extent, synonymous.

On the strength of this argument one would expect no correlations between diet and nutrient trends at Wareham, as diet is unchanged from one season to another, although nutrient levels change as before. This is what was found.

The failure of correlation of the grass intake conforms to the pattern above except for Molinia whose particular correlation coefficients, despite their lack of significance, were higher than for the other species.

Further cause of failure of either correlation is that the deer may on occasion select feed on characteristics other than optimal quality. "Palatability" varies between plants; gorse and holly, for instance, are protected by long thorns and despite their considerable nutrient contents, are taken very litle. When intake of these does rise it is in autumn and winter when they are sub-optimal, but may be superior to other forage.

7. Competition

The fact that in the New Forest sika deer exploit the relatively small proportion of their habitat yielding coniferous browse to excess of 25% of intake when Wareham animals, in the midst of extensive plantations, fail to take more than 10% - and that rarely - is probably due to competition.

Comparing New Forest sika diet with fallow deer in the New Forest (Jackson 1974 and 1977) reveals many similarities. Following the analysis of 325 rumina from animals killed in the New Forest over three years (some shot in the usual culling programme, others were road casualties) Jackson described three main phases within the pattern of annual diet:

1. March to September: grass dominates the intake, but broadleaved herbs and trees are included.
2. September to Christmas: acorns and beechmast (obviously this study did not include a year of mast failure.)
3. Winter: includes brambles (*Rubus*), bilberry (*Vaccinium*), grasses, *Calluna*, *Ilex*, *Hedera* and coniferous browse.

This pattern is very similar to that of the sika although Jackson also reports that *Molinia* and *A. setacea* are not often taken by fallow deer. The population of fallow deer in Frame Heath Inclosure is not in itself enough to cause competition for these feeds but the situation is aggravated by the presence of the New Forest pony. In theory the ponies are excluded from the inclosures and were this the case in practice, there would be no competitive effects to discuss. To illustrate the impact of these animals, ten years ago it was necessary to cut the grass on the rides inside the inclosures as it constituted a fire hazard; nowadays intensive grazing by ponies and deer makes this unnecessary (F. Courtier, pers. comm.).

Putman et al. (1981) have described the diet of the New Forest pony and many similarities are revealed between this diet and that of the sika (or the fallow) deer. During the summer the ponies feed to a large extent on grass (over 80% of the total intake) of which around 20% is Molinia. The consumption of Molinia follows the same seasonal pattern as in the sika, and declines during September and October.

However total grass intake remains high as ponies then consume A. setacea, another grass utilised by the sika deer. During the winter the ponies feed increasingly on gorse and tree leaves (mostly holly),(resources little utilised by the sika) and they also increase their consumption of Calluna. The structure of the horse intestine is such that it relies on a high throughput of material to obtain basic requirements and it seems likely that as the quality of the feeds decline, so intake would increase. With its opposed incisor teeth the pony can graze much closer to the ground than can the deer so can compete successfully with them, continuing to obtain forage from grassy areas that can no longer support deer. The ponies do not eat pine needles (Ekins pers. comm.) and here is the remaining resource for the sika. In the summer the grasses, herbs and shrubs can produce sufficient new growth to supply all the animals but when offtake exceeds productivity in the winter, the deer are forced to utilise a different forage. At Wareham there are a few roe deer and even if these were mainly grazing animals (which according to Hosey (1974) they are not) the feed supplies are more than adequate for present population levels. Work on Japanese sika in Japan (Takatsuki 1980) states that these deer are grazers and so they appear to be in Scotland although here the competitive effect of the red and roe deer is unknown. Hofmann (1982) suggests that the sika rumen is typical in many ways of the bulk and roughage eaters (grass eaters) as examined and classified in Hofmann and Stewart (1972). He produces a revised feeding-type classification for European game ruminants using three main categories, "concentrate selectors", "intermediate types" and "grass feeders"; derived from the morphology of the rumen. Sika lie just inside the "intermediate" category (and just outside the "grass feeders" section) and within this are classified between red and fallow deer.

There is a lot of evidence, therefore, which leads one to suggest that the New Forest situation forces the sika to feed more extensively on coniferous browse and less on grass and leaves, than might be predicted. These deer are, however, particularly efficient at breaking down fibrous food (even if poor quality) and in building up energy reserves (fat deposits) (Hofmann 1982) so seem adapted to either the New Forest or the Wareham situation.

CHAPTER FIVE

Population structure
and
social organisation

Population structure and social organisation

INTRODUCTION

Information on the age and sex-structure of a population is traditionally derived from the analysis of culled material (eg. Mitchell 1973, Staines 1978) but there are potential errors in such an approach, the result of the nature of the sample (Roseberry and Klimstra 1974) and whether it is deliberately or unconsciously biased.

In this study material from culled animals complements data obtained by direct observation as the rigorous survey technique, employed to investigate patterns of habitat occupation, can be adapted to yield data on the social organisation and on the age and sex structure of the populations.

These details, coupled with those of the animal's ecology described earlier, may be used to formulate an effective management policy for the sika deer. In order to stabilise the numbers of any animal population at a level below its natural maximum by cropping (thus protecting the environment and allowing exploitation of the population) the number of females, the age-specific fertility and the survival of these females must be known with reasonable certainty. Where such data are not available, cropping fluctuates between being too severe or ineffectual (Lowe 1969).

METHODS

1. Direct observations

Records were obtained from the driven transects carried out as described in Chapter 2. As far as was possible the age class and sex of every individual found at the sample sites along the route was noted. The size of each group of animals was also recorded, with the habitat in which it was located.

The "group" is defined here as "an assembly of animals, probably in visual contact, interacting latently or overtly." Within each group the age and sex of each individual was noted although the ease with which this was accomplished varies with the size of the group and the denseness of the vegetation holding it.

This analysis uses animals classified into one of the following categories:

i. Mature hind

ii. Yearling female

iii. Calf; of indeterminate age

iv. Yearling male

v. Stag

Records were discarded if vegetation or poor visibility inhibited the accurate assignation of animals to these classes. If the presence of large numbers of deer hindered the accurate counting of group sizes, the lowest of two estimates was noted.

Stags were usually recorded with the number of tines on their antlers (towards future identification of individuals). Age classes, as above, rather than more specific ages, were used in all cases because ageing deer on the hoof is extremely unreliable even when characteristics like antlers are available (Chaplin and White 1969). These details can be used to define the population structure by analysing the most successful transect driven each week (in terms of the number of observations collected), and from which the total number of deer assigned to each age and sex class is determined. A monthly mean is then produced using one circuit from each survey occasion. One cannot use all the circuits performed each month for this determination (unlike habitat occupance which is measured in terms of "animal presences") because deer are certain to be recorded on several occasions although in the case of the stags, some of which are identifiable by their antler characteristics, this error may be reduced.

Data collected on group composition (social organisation) were collected in the field and may be used in two ways. Firstly the mean group size, and, as far as possible, its composition in terms of deer of each age and sex class, is calculated each month with respect to the habitat in which the groups were found. A second analysis looks at seasonal trends in mean group size, irrespective of habitat. In these instances repeated recordings of an individual are unimportant, so data from all the circuits may be used.

2. Post mortem methods

a. Information from the carcass

A rough estimate of the age of each animal shot was determined from an external examination of the fresh carcass and classification of the individual into the age classes used for the observational data was easily achieved. Stags were again noted by the number of tines on their antlers although these had frequently been shot because of the poor quality of the antlers, or because of injury; for example, a fractured pedicle.

i. Reproductive tracts

Details of the reproductive condition of each female shot were also collected, whether pregnant, pregnant and lactating, lactating only or yeld, and if possible the sex of the foetus was noted.

ii. Jaws

A more precise estimate of the age of the animal can be made by examining tooth wear, eruption pattern or by sectioning a tooth and counting the layers in the cementum. Both lower jaws were collected from as many animals as possible for this purpose; were boiled clean and stored.

b. Laboratory analyses

A common technique for ageing animals is by tooth wear and eruption. This technique is thought to be somewhat unreliable, particularly if used for comparisons between populations as different levels of silica on, or in the feed, and individual susceptibility to wear may influence the results (Mitchell 1967, Lockard 1972, Aitken 1975). However once a population has been "calibrated" by reference to known-aged material, comparison by wear characteristics can yield perfectly acceptable results with the miminum of time invested (Aitken 1975).

i. Sectioning teeth

The counting of dental cementum layers and relating these to age was first described in studies of marine animals (Scheffer 1950, Laws 1953). Since then the technique has been refined, principally by Mitchell (1963 and 1967) and Lowe (1967) in red deer. It is used, for example, in ageing fallow deer (Chaplin and White 1969), white-tailed deer (Lockard 1972) and roe deer (Aitken 1975).

No known-aged material is available for sika deer from the New Forest, nor from Wareham, so some teeth had to be sectioned to display the layers in the dental cement.

Following Mitchell's guidelines (1967) the first molar in each mandible was extracted and sectioned at right angles to the line of the jaw in such a way as to cut the cementum pad located between the roots. These cut surfaces were then polished with a fine carborundum stone; distinct layers of opaque and transparent material were visible when viewed with incident light and under low magnification. These layers are caused by rich and poor deposits of cementocytes corresponding to summer and winter growth periods respectively. These layers were counted and the age of the jaw determined.

The first molar was selected (although rings or layers can be found in the cementum on all the teeth - Mitchell 1967) because it is present throughout the life of the animal and there is no dispute over its time of eruption. The other molars are thought to emerge at about 12 months and 20 months after birth, although doubtless there is some individual variation.

To age jaws from juvenile animals guidelines on the tooth eruption sequence of the red deer were followed (Mitchell and Youngson 1969), as indeed they were in a similar analysis of culled sika material by Horwood (1971).

RESULTS

1. Population size from field data

A variety of direct census methods are available for assessing the population of animals in an area. In open country animals may be counted along set transects either from the ground (eg. Hirst 1969) or from the air (eg. Graves 1972, Floyd et al. 1978), and direct counts can be made in the field (eg. Lowe 1969, Stewart 1976) or from photgraphs. In denser vegetation a drive-census technique may be employed, or indirect methods such as faecal accumulation may be used (Bailey and Putman 1981).

a. New Forest

The Forestry Commission estimates the sika deer population in Frame Heath Inclosure each year using the drive-census technique. However, many deer remain hidden and others double back through the line of beaters, so unless a very large number of beaters is employed a low estimate of the total population will be obtained.

Earlier, data yielded by the driven transects were used to calculate a theoretical population for each habitat over a variety of time-scales (see Chapter 2) each of which was expressed as the "occupance" of the area at that time. Here, using a timescale of one calendar month, the observed number of deer per unit area in each habitat has been calculated and when multiplied by the area of the habitat available to the animals, gives the theoretical number of deer held there. Summing the values thus obtained for each habitat produces a population estimate for the month and these are plotted on figure 5:1.

All the reservations voiced about the representative nature of the survey used to derive these data; effects caused by disturbance and the validity of the calculation (discussed in Chapter 2) apply, but even if the total population figures are not acceptible, relative changes in the values may be useful and these criticisms will be less relevant as they apply to all months.

The total population of the sika deer in this part of the New Forest, calculated from the mean of the ten months outside the rut is 173 (±12.5) and for the months of the rut is 214 (±12). These values are more meaningful and can be compared with those from other studies if expressed as a density; 226 per 1,000ha outside the rut and 290 per 1,000ha during the rut. These are very much higher than those reported for red deer in Scotland, for example a density of 139 red deer per 1,000ha was reported on the Island of Rhum (Inner Hebrides) and 131 red deer per 1,000ha in Glen Feshie, Central Highlands of Scotland (Mitchell and Lincoln 1973).

The New Forest values proposed above have been separated because of the tendency of the stags to move in and out of the study area; as has already been discussed. The values produced are, however, in fair agreement with those from the Forestry Commission census (J. Ealing, pers. comm.).

Two major peaks in population are shown in figure 5:1, one coinciding with the rut (October and November 1980) and the second with the latter part of the summer; the calving season. The trough between these marks the departure of most of the males from the study area and also coincides with deaths caused by culling.

There are inevitable fluctuations in data between months and as the population structure will be described on a seasonal basis, the population size is also presented seasonally in figure 5:2. The arrival of the males, the increase in sightings associated with the death of the vegetation (causing improved visibility) and the rut is reflected in the high population of the autumn of 1980. The subsequent departure of the stags with some of the yearlings, coupled with winter mortality (natural and man-induced), is reflected in the decline in the population from 230 to the spring level of 160.

b. Purbeck

Identical treatment of information collected at Purbeck fails to yield a clear pattern of population size, possibly because too few months were sampled and there were too many influences on the data.

The mean annual population size for the period of the study (January to October) is 340 (±70) which represents an animal density of 194 sika deer per 1000Ha. This is lower than in the New Forest, but still considerably higher than red deer densities in Scotland (eg. Mitchell and Lincoln 1973).

The monthly populations are plotted in figure 5:3 and values fluctuate wildly; these variations are reduced by calculating seasonal figures although the huge standard errors plotted cast considerable doubt on their value. (figure 5:4).

There is an increase indicated in the spring population which may be due to calving, or to a better sample produced by more clement weather and superior food supplies attracting more animals to the survey areas. The apparent decline in the summer (contrary to that expected from calving) may be caused by adequate feed now being generally available, reducing the necessity to feed in the fields and this, when coupled to the denseness of some of the vegetation, produces a poor sample. An increase in the autumn figure is indicated, but is derived from only one month's survey, so although of doubtful value, it does support the expected increase resulting from the return of the stags (Horwood and Masters 1970).

2. Population structure from field data

a. New Forest

As was outlined in the methods section, the number of animals in each age and sex class was determined from the most successful transect in each survey occasion. A monthly mean was derived from this and these field results (expressed bulked to seasonal values to reduce the scale of the inevitable fluctuations) are given in figure 5:5 both as original figures and each as a percentage of the total.

Theoretically the population structure will not change much from one month to another (outside the rut and the main calving season). However, because of the different sample size encountered each month, significant fluctuations do occur and this is why the data are presented seasonally.

The major component of the population, between 50% in autumn 1981 and 84% in the spring of 1981, is of mature females, although these values may be slightly over-estimated due to misidentification of older female yearlings. The seasonal appearance of the stags is clearly shown (contributing 12% and 14% to the autumn population in 1980 and 1981 respectively, but only 1% during the summer of 1980). Because of this migration and because of the spread of delivery times of the calves, the optimum period from which to describe the structure of the entire population is during the rut in either 1980 or 1981. At this time between 56% and 67% of the population is of mature hinds and between 11.9% and 14.1% is mature stags. Juveniles; calves and yearlings,contribute between 10.1% and 22%, and 10.7% and 8% respectively. These latter figures include both male and female yearlings; combined because yearling males are only identifiable as such for part of the year so are inevitably confused with females at other times.

The population structures presented here from spring, summer and winter are all biased not only by the absence of the stags and by problems with identifying yearlings, but also by problems associated with finding small calves in tall undergrowth.

The apparent changes in population structure can be used to identify mortality, survivorship, fecundity and the sex ratios of breeding-aged animals. To achieve this the population structure is expressed more meaningfully as a series of seasonal ratios; of hinds to calves, of hinds to stags etc. These have been derived from the same field data as the percentages and are given in figure 5:6.

The ratio of hinds to calves in 1980 is given as 6.7 to 1, and in 1981 as 2.5 to 1. These values are taken from the autumn when most, if not all, of the calves have been born and visibility is at a maximum; suggesting a fecundity of between 15% and 40%. The former figure is obviously very low but the latter corresponds exactly with that offered by Mitchell (1973) for red deer hinds in the Scottish hill-land environment, not what might be expected from the richer, less rigorous woodland habitat in the South of England.

A sharp drop in the ratio of hinds to calves in the population occurs between the winter of 1980 - 1981 and the spring; from 1:6.5 to 1:13.2. This may be due to winter mortality although no carcasses were ever found to support this. Forestry Commission culling is carried out in this area between November and February but the number of calves taken is too low to create an effect as marked as this, particularly as a similar number of yearlings, hinds and stags are also shot creating no net effect on the population structure as a whole. Assuming therefore that as many hinds as calves are killed (Forestry Commission policy being to kill the calf if the hind is taken) the drop in the hind to calf ratio over the winter suggests 50% mortality.

This value can be checked. If there was no calf mortality and assuming that approximately the same number of calves is born each year, the ratio of calves to yearlings (of either sex) would be around one to one. In fact the ratio is remarkably stable at around 1.3 to 1 and even allowing for some yearlings to be wrongly placed as hinds, this still suggests a 30% calf mortality.

The sex ratio, that of hinds to stags, shows a seasonal fluctuation because of the stags' seasonal migration. When the males are in the study area for the autumn rut the ratio rises to 6 or 4 to one (1980 and 1981 respectively). This is far removed from the expected birth ratio of one to one, even allowing for the hind value to be inflated by misallocated yearlings.

The sex of each foetus obtained during the cull was recorded if possible, but the sample was too small (n=17) to show a significant departure from parity as reported by Horwood and Masters (1970).

b. Purbeck

Direct observation data of the type collected in the New Forest is available from the Purbeck transects but unfortunately a much smaller number of records are available.

The greater distances involved and the poor visibility frequently endured as the result of mist, rain or thick vegetation reduced the proportion of observations that can be reliably assigned to sex and age classes; varying between only 6% (n=249) in the spring and 34% (n=318) in the autumn.

The same age and sex classification; hinds, calves, yearlings and stags, was used here as in the New Forest. The monthly values presented are again derived from the most productive transect driven on each survey occasion and have been amalgamated to yield a seasonal value in an attempt to increase sample sizes and to reduce the fluctuations in the results.

Expressed as a percentage of the total observations in the sample allocated to each age and sex class, the seasonal population structure is given in figure 5:7.

The largest part of the population is shown to be mature females, contributing between 47% of the autumnal observations and 83% of the spring ones. Stags were only found occasionally (rarely in the spring or summer) contributing 16% of the records during the autumn. The proportion of calves in the population drops in the spring from its winter value of 26%, possibly because of mortality, and then gradually increases during the summer and autumn as new calves join the population. The number of yearlings recorded (a very small number of observations) remains relatively stable at between 4.5% and 7.5%.

When expressed as a series of seasonal ratios (figure 5:8) the breeding success of the hinds (deduced from the hind to calf ratio) is shown to be high, between 63% and 42%, although the latter figure, obtained during the winter, may be depressed by mortality. The promotion of calves to yearlings is suggested by changes recorded in the calf to yearling ratios although these too may be influenced by winter deaths.

The ratio of hinds to yearlings is remarkably constant; between 8.5 and 7.5 to one, and suggests that calf mortality is about 30%. (If there were no calf deaths one might expect the hind to calf ratio in the autumn of one year to approach the hind to yearling ratio in the next.)

The hind to stag ratio fluctuates considerably and the migratory tendency described for males in the New Forest, and suggested by Horwood and Masters (1970) for males in the Poole Basin, is shown by the seasonal changes in the ratio. During the spring and summer the stags are found rarely, but in the autumn rutting season the ratio of hinds to stags reaches three to one. This figure is inaccurate as the data used to calculate it is biased. All the stags located at this time of year are recognisable as such because their body size and shape is very distinctive even if their antlers cannot be seen. However, only a small proportion of the female deer found on each circuit were allocated to a particular age or sex category as they are not as readily distinguished from yearlings or even calves. It was stated earlier that 66% of the observations collected in the autumn were unidentified; taking the extreme view and assuming that all these were hinds produces a hind to stag ratio of about 16 to 1. Obviously this is not correct either, but doubtless the "true" value lies somewhere between these extremes.

3. Population age structure; from culled material

Greater detail as to the age structure of the population can be determined by examining jaws from animals shot during the annual culling season.

As these deer are killed for commercial and not for scientific purposes, the cull could be considered non-random, particularly as a specific quota of males and females is set. Ageing deer accurately, post-mortem, is difficult enough, ageing mature individuals on the hoof is virtually impossible even for experienced stalkers. Within the mature male and mature female sectors of the cull therefore, the age structure may well be random, despite apparent selection by the stalker, although the sample is derived from a small number of specimens. Further, it is not possible at this time of year (November to February) to distinguish pregnant hinds from yeld hinds so the reproductive status of the females may also be randomly sampled. Calves and yearlings are distinguishable from features like body size and the shape of the face.

a. New Forest

The cull in some years was small (see Chapter 2) and some jaws were lost during collection and cleaning, so the data from the four winters sampled in the New Forest have been amalgamated. It is unlikely that the age structure of such a population will alter significantly over such a short period. The age structure of the total cull from 1978 to 1982 is plotted in figure 5:9.

The largest part of the sample consists of juvenile animals, calves and yearlings, which are selected for. The rest of the sample, assumed to be as nearly random as possible with respect to age, shows a gradual decline in the number of animals aged 2 years to those aged 8. No deer were found aged more than 9 years. The decline in the age profile suggests an age-related mortality of 25% between the ages of 2 and 4 and 50% between 4 and 6, although these values are derived from very small samples indeed.

The total number of male sika deer shot in the New Forest is very low (18 in four winters contributing 24% to the total cull for that period) and of those that were aged, only three were mature. These were included in the overall age profile described above as by themselves they reveal nothing (although they may have been selected on their antler charactersitics); their inclusion would not markedly influence the result, but their exclusion would diminish an already small sample.

b. Purbeck and Wareham Forests

No culled animal material was available from the forest areas at Purbeck, but three winters-worth of samples were collected from the coniferous forest at Wareham. Whilst it is not valid to compare these directly with equivalent details collected in the field at Purbeck, they may be used to describe the situation in a different population to that in the New Forest; one, moreover, in a vegetationally different environment.

The age structure of the Wareham cull (plotted in figure 5:9) shows, as in the New Forest, that calves and yearlings comprise a major part of the total harvest. After this the age structure shows little, if any, decrease in numbers of animals aged between 3 and 9 years.

Male sika are shot at Wareham (some under licence, from which jaws were not available) and are included in the age profile for the same reasons as in the New Forest. Of the 20 stags killed during the three years (contributing 35% to the total cull) jaws from five were not collected and twelve were juveniles.

4. Population growth: post mortem material

Some indication of the reproductive performance of the population was given by data collected in the field and expressed earlier as the ratio of hinds to calves at different times of the year. These suggested a fecundity of between 15% and 40% for 1980 and 1981 respectively.

Supplementary information is available from the deer shot during the annual cull. The reproductive condition of each hind killed was assessed when in carcass and the results, as the percentage of the mature female cull that was pregnant, lactating, pregnant and lactating or yeld, are plotted in figure 5:10. A mature female is taken as being over the age of two; the four years of data yielded three yearling pregnancies.

a. New Forest

Of the total hind cull of 38 individuals 84.2% were pregnant. The percentage of milk hinds who were also pregnant was 44.7% indicating that they were breeding two years in a row. The proportion of yeld hinds (females apparently infertile) was 10.5% and the proportion of hinds in milk from the previous calf but not yet fertilised from the recent rut was 5.3%.

i. Reproduction with respect to age

Despite the small size of the samples, the reproductive status of the females was compared to their ages as deduced from tooth sectioning. Animals of all ages (except calves) were found to be pregnant and/or lactating and it appears as if none of the Frame sika deer has passed the age at which they cease to breed.

b. Purbeck and Wareham

No deductions were made from the population ratios as to the fecundity of the population because of the small, biased nature of the sample. The reproductive condition of all the hinds killed at Wareham during the annual cull was assessed and the percentage of the total that was pregnant, pregnant and lactating, lactating only, or yeld are plotted on figure 5:10.

No yeld hinds were killed and there was one yearling pregnancy. Of the mature females there was 92.3% fecundity (sample size is 31) and of these 35.5% were lactating so had reared a calf in the previous year. The proportion of the cull in calf and lactating (breeding two years in a row) is 35.5% and of the total cull only 9.7% were not pregnant but these were lactating so had bred the previous year.

i. Reproduction with respect to age

A better sample of age-related reproductive condition is available from Wareham than from the New Forest for fewer jaws were lost from the culled material collected, although the sample size (n=28) is still very small. The results are given in figure 5:11 and show that the majority of pregnant hinds (whether lactating or not) are aged between 3 and 5 years although animals of all ages were found to be in calf.

5. Social organisation

Social organisation can be defined as "the manner in which the members of a group are positioned in space and time, relative to each other".(Morrison and Menzel 1972 - quoted in Hirth 1977).

Doubtless this is influenced by many factors, not the least of which may be the habitat type in which the animals are observed. The "group" was very loosely defined earlier as "an assembly of animals, probably in visual contact, interacting latently or overtly with each other". This is a very vague definition but one that can be made to work in practice although it does not allow for distinction between social groups and feeding aggregations; assemblies that are formed for different reasons and are, under this definition, inseparable. Larger feeding aggregations are formed in areas with extensive feed resources (eg. fields) and groups within this may be recognisable if they are functioning as an entity - if the distances between the members are substantially less than between themselves and the members of another group. Occasionally the deer are evenly distributed (whether they arrived together or not) so are taken to constitute a single group. The implications of this will be reviewed later.

In this section it is proposed to investigate seasonal changes in group size (irrespective of habitat) and then to investigate the relationship between group size and habitat. It is possible that if a relationship is found between group size and habitat, then the seasonal changes in habitat occupation discussed in Chapter 2 may be the source of the seasonal changes in group size themselves.

a. New Forest

i. Monthly group sizes

The mean group size from all the sightings per month was calculated and plotted in figure 5:12. The size of the standard errors shows that the results are not too wildly varied so it is not necessary to present the figures on a seasonal basis. To do so would detract from data collected in the autumn when changes in group sizes associated with the rut may arise rapidly.

It is clear from the graph that there is a distinct change in the mean group size from one month to another and also that the same pattern of changes is not shown by both years of data.

During the summer of 1980 the mean group size decreases to 1.7 and then increases gradually until, at the time of the rut, it achieves a value of nearly 2.2. Immediately after the rut there seems to be little change (which one might not expect if anticipating the break up of the harem, for example) and then there is a rapid increase to the annual mean maximum of 2.7. A gradual break-up of the group through the spring is then indicated leading to the middle of the summer when many of the hinds are solitary and awaiting the birth of their calves. It has been reported that after the rut the stags form into male parties and the hinds into female parties (Horwood and Masters 1970) and this "sociability" is clearly shown by the peak in mean group size in February and March 1981.

After calving the hinds are frequently found accompanied by their new calves and perhaps also by a yearling; this is demonstrated by an increase in mean group size from 1.5 in June to 2.1 in July. The rut commences in the late autumn and in anticipation of this, the mean group size increases from October.

ii. Monthly group composition

To look at the composition of the groups found on the driven circuits the ratios of the animal age and sex classes in the groups were calculated for each month; irrespective of habitat.

In every month the ratio of hinds to calves in the groups was between 1:1 and 2:1 whilst that of hinds to yearlings (showing less of a parental tie, perhaps) could always be found between 2:1 and 1:2. This means that in any group of sika deer found in the New Forest, at any time, in any habitat, one would expect to see a calf for every hind (or two) and a yearling for every hind (or two). Occasionally an extra yearling is associated with the group.

Of groups containing mature and immature stags outside the rut the ratio of mature to immature males was 1:1 or very exceptionally 2:1 or even 3:1. These last two are rarer occurences found during the post-rut period when male and female parties develop. During the rutting season the stag to juvenile stag ratio was still mainly 1:1 although occasionally two, or even three, yearling males would be seen with a master stag.

The ratio of stag to hinds fluctuates considerably. It has been shown that the sexes live separate lives for much of the year; on the few occasions when males and females are found together, outside the rut, the ratio within the groups fluctuates between 3:1 and 1:2. However, during the rut (October to December) the number of hinds associated with each mature stag increases most dramatically and although many of the records are still 1:1; ratios of 1:2

and 1:3 are more common than at any other time of the year. The highest ratio recorded was that of one stag to fourteen hinds, but this is exceptional.

b. Purbeck

1. Monthly group size

The mean group size found each month was calculated from driven transect data, exactly as in the New Forest, and the results are plotted on figure 5:13.

The graph shows a gradual increase at the end of the winter with the mean group size reaching 4.45 in April, this is followed by a slight then a rapid decrease to 2.65 in June. This corresponds to the calving season and may be caused by hinds becoming more solitary as calving time approaches. After this the mean group size increases rapidly to peak at 5.4 in October. The figure given for November (3.9) is derived from an incomplete survey and is probably very unrealistic.

ii. Group composition

As was stated earlier, survey conditions at Purbeck were not conducive to accurate identification of individuals as to age or sex class. Therefore no data on group composition can be presented.

c. Group size related to composition

The relationship between group size and composition has been looked at using New Forest data alone, for only here could animals be assigned to age and sex reliably and in sufficient quantity, to yield a valid analysis.

A large part of each month's records contain sightings of solitary female deer and the number of stags recorded varies considerably between 1.1% of the groups found during the summer and 31% in the late autumn.

To investigate the effect that the stags have on the size of a group, mean monthly group size of small deer (hinds, yearlings and calves) was calculated irrespective of habitat. This is superimposed upon a graph showing the mean monthly group size of all male groups and the mean monthly group size of mixed-sex assemblies (including at least one mature stag) (figure 5:14). Immature males are classified with small deer groups for several reasons. They are not easily recognisable as males during the early part of their second year, they change allegiance from hind groups to all-male groups just after the rut (Horwood and Masters 1981) and at this age they are subordinate to both hinds and stags.

Apart from two months - March and April 1981 - all-male groups are significantly smaller than small deer groups ($p<0.05$) and on every occasion mixed-sex groups are larger than either single-sexed group.

During the year the mean size of the female group changes very little indeed, being around 1.75, suggesting that as many hinds are found alone, these are hind and calf, or hind, calf and yearling assemblies. The male groups are also relatively unchanging in composition; the absence of many of the standard errors on this graph is because in these months only single males were detected. Both the male groups and the female groups increase in size in early spring in 1981. Horwood and Masters (1970) report that after the rut the sexes separate and form larger unisex assemblies; this trend is clearly shown here where the mean group size for females rises from an average of 1.75 to 2.75 in February; for males the mean group size rises from the more usual value of 1 to 3.25 in April 1981.

The graph indicating the size of the mixed-sex groups is erratic and the large standard errors indicate that on many occasions it is based on a few observations. Nonetheless, the presence of males in the group obviously does cause the formation of larger assemblies and this tendency does not, in this case, seem to be restricted to the mating season (October, November and December) although these particular values are slightly larger than most others.

The composition of these mixed groups appears to be quite flexible, although one frequently finds one or more lesser stags (usually with fewer tines on his antlers, of apparently lower body weight and probably younger than the "master" animal) acting as "satellite stags". These are tolerated by the dominant male, but are always displaced by him. Associated with this grouping is a collection of hinds, calves and yearlings of both sexes. It is unusual to find more than one dominant male associated with such an assembly.

Any more detailed analysis of the composition of mixed groups is complicated by their extremely variable structure and by the widely differing sample sizes, although it could be suggested that the small-deer component of these is derived from collections of the hind and calf, or hind, calf and yearling units mentioned earlier.

Single animals have been recorded as "groups of one" because they constitute social units and are important components of social organisation (Walther 1972, Hirth 1977). Here in the New Forest solitary hinds always contribute more than 37% of the group sightings even during the rut; this proportion increases to over 60% during the height of the summer and the calving season. Calves were rarely recorded alone although the ease with which they are found depends very much upon the size of the animal and the state of the surrounding vegetation. Hinds are reported (H.Cutler pers. comm., Milner–Bennetts 1981) to leave very young calves for substantial periods whilst feeding, only returning occasionally to suckle.

Yearling males (brockets) were excluded from these analyses but they do associate with the hinds and calves at least until the spring of the second year when their pedicles and antlers are beginning to show. In some cases, brockets in hard horn are found with small-deer groups but it is impossible to say whether they are familial attachments or not. During the summer brockets are rarely found, but seem to be solitary, some joining mixed-sex groups during the rut, others remaining independent.

It is certain that the main social unit in this population is that of the hind plus one, or more rarely two followers. In every month the number of groups containing solitary animals or pairs of animals, contributed at least 60% and usually more than 70% of the sightings. It seems likely that the larger aggregations are based upon this fundamental structure although without marking a substantial part of the population, one cannot be certain.

d. Group size related to habitat: Purbeck and New Forest

The figures given earlier (5:12 and 5:13) shows the mean monthly group size for sika deer in the New Forest and at Purbeck and is calculated from all the observations collected each month. Greater detail than this may be obtained by calculating the mean monthly group size per habitat and for the New Forest, these values are plotted in figure 5:15, for Purbeck in figure 5:16.

Protective cover has been recognised as having a major influence on the social organisation of wild ungulates (Dasmann and Taber 1956, Estes 1967, Jarman 1974). Those species that characteristically occupy woodland habitats with dense cover tend to occur singly or in small groups. Plains or open-land ungulates, associated with little cover, typically occur in large groups or herds. Several hypotheses have been advanced to explain this and one of the most popular is that this is an adaptation against predators. Those animals in thick cover rely upon their small body size to remain undetected whereas those in the open, themselves too large to stay hidden, obtain greater security from being in larger groups and in the event of an attack, the individual chance of being killed is reduced.

As it is possible that predator defence strategies are modified under the cover of darkness, the mean monthly group size in each habitat was compared between day and night in each forest. Only a few significant differences in the New Forest were found in 1980 ($p=0.05$); in fields in May and on rides in June. In each case the larger groups were found in daytime. In 1981 a few more significant differences were found and these also tend towards larger groups in daytime. Significantly bigger assemblies of deer are found in the oakwoods between January and April and again in September and October. (This trend was shown the year before but failed to achieve statistical significance). One also finds bigger groups in the felled areas in the daytime during the spring months.

Comparisons between these day and night records at Purbeck were limited by the scarcity of daytime data in some months and on only one occasion (September 1981 in the heaths) was a significant difference found between mean group size at night and in daytime (p=0.05); the larger assemblies again being found in the daylight.

Despite these few differences the majority of the data suggests that night or day has no real effect upon the mean group size found in a vegetation type so these periods were amalgamated to produce the values plotted for the New Forest in figure 5:15 and in figure 5:16 for Purbeck.

Oakwoods constitute the major habitat in the New Forest study area and therefore contribute the greater part of the results. It is perhaps no surprise that the overall monthly mean group size graph (figure 5:12) and the mean monthly group size graph for oakwoods (figure 5:15a) are very similar. Less expected, particularly in view of the much smaller sample sizes, is the close resemblance to the overall result borne by the graphs from the other habitats. They all show a peak in group size at the end of the winter or in early spring and after a significant trough, a second peak at the end of the summer; the absolute values differ, though, from one habitat to another.

The similarity between these graphs suggests that the seasonal change in social organisation is independent of habitat and probably has an innate behavioural basis.

At Purbeck a slightly different situation is found. Again one habitat, the fields, contribute the most data and this does bear a close resemblance to the overall monthly group size group graph shown earlier (figure 5:13). The other habitats exhibit a wide variety of patterns, probably because of the differing sample sizes and the incomplete nature of the records. Values from transects carried out in November and October are submitted but they are derived, particularly in the latter case, from even fewer circuits than the other months as bad weather frequently made surveying impossible. March results are absent because the area was closed by foot and mouth restrictions.

The range of group sizes encountered in the New Forest oakwoods (figure 5:15a) is from 1.5 (July 1980, June 1981) to 2.6 (April 1981) whereas in the polestage habitat (figure 5:15c) it is between 1.35 (June 1980) and 2.2 (February 1981). In the prethicket in the New Forest (figure 5:15b) the range in mean monthly group size extends between 1.44 (July 1980) and 2.66 (April 1980) although the result in this particular habitat is more varied than in the others, probably because of the smaller number of results collected.

At Purbeck the range of group sizes is large; in fields for example, (figure 5:16a) it varies from a mean of 3.4 in June 1981 to 13.9 in October. In the closed habitat, the thicket (figure 5:16a), the range is much reduced and only extends from 1.38 in September to 2.75 in May 1981.

Despite the variety of trends displayed by these figures it is clear that the mean group size in the open habitats at Purbeck (fields, heaths) is consistently higher than in the closed areas (p=0.05). The rides, classified as neither an "open" nor a "closed" habitat (animals never being far from cover and are frequently overhung by surrounding trees), hold group sizes consistent with this intermediate classification; of mean size between those encountered in closed and open areas.

This overall situation is duplicated in Frame where larger groups are to be found in the fields and felled areas than in the denser habitat; prethicket (p=0.05).

Comparisons between the mean group size found in the habitats represented in each study area (oakwoods, rides, fields) fails to show any significant differences (p=0.05). A further comparison was attempted, between the mean group size found in the thickets at Purbeck (the major "closed" habitat) and the mean group size in the prethicket at Frame; again no significant differences were revealed.

Comparisons between the mean group size found in each habitat within a month, in the New Forest only, suggests another trend; one that was suggested earlier. Groups found in the oakwoods are the largest in any habitat in the winter, but the smallest in the summer; polestage contains the smallest mean group size nearly every month and those groups in the prethicket (with the exception of July 1981) are also small. Despite the low samples, fields always hold the largest mean group size,(except in the winter when very few deer are found there at all).

DISCUSSION

1. The definition of the "group"

The definition of the group that has been applied here is that of "an assembly of deer, probably in visual contact, interacting latently or overtly." Thus, although one may find 40 deer feeding in a field, that they are evenly distributed suggests some form of interaction and so they are considered to constitute a group, despite the fact that this may be composed of several smaller units that arrived, and will probably depart, separately. On the other hand, the same field with an obvious clumping of deer at each end would be said to contain two groups if the distances between individuals within each group were substantially less than those between the groups.

It could be argued that this definition is far too flexible and subjective and that assemblies of deer located in denser habitats will inevitably be recorded as smaller than those in the open areas because the observer cannot see all the individuals, so cannot assess the distances between assemblies. Counter-argument suggests that the deer cannot do this either and if they cannot see each other, they cannot interact, so cannot be considered as a group. Indeed the importance of visibility is clearly revealed by Loudon (1979) who claims that roe buck territory size is inversely related to the denseness of the constituent undergrowth; probably because maintaining large territories in dense habitats is impossible as intruders are not detected.

That some individuals are not located on the survey is certain; that this error will be higher in the closed than in the open habitats is also certain, but this is inevitable. It is also likely that some individuals are easier to find and to record than others depending on the size of the animal, its colour and the activity in progress; one can only hope that this error influences a low proportion of all the observations taken over the month.

This point was investigated by Downing et al. (1977) who checked the accuracy of sex and age ratio counts of white-tailed deer (Odocoileus virginianus) at different times of the year. They concluded, after five years of data collection, that at no time during summer or autumn were the sex and age classes equally observable and this was attributed to differences in feeding and bedding time and not, surprisingly, to group size or the use of cover. This explanation is probably less valid in a study of this kind where surveys were carried out over the entire 24 hours, but as the most successful transect on each occasion provided data on the age and sex structure of the sika population, the bias may apply.

The inclusion of the solitary animal as a "group of one" is defended on the grounds that this does indeed fulfil the definition of the group; that the solitary animal constitutes a social and behavioural entity capable of interacting with any other individual or group. Further, knowing that a finite population of animals occupies a particular area of woodland, maintaining a solitary existence may be a deliberate policy and as such, the individual cannot be ignored.

2. Recognition of sex and age classes

The ratios given to describe the structure of the populations in this report depend upon accurate assignation of individuals to age and to sex class. These classes have been made as broad as possible to reduce proportional errors, but some mistakes are inevitable.

Calves are easily recognised as their juvenile dentition (iiicpppm) occupies a much shorter jaw line than does the adult pattern (IIIC PPPMMM) (Mitchell 1967). At this early age, however, calves are easily recognised by virtue of their body size, but by the time that they are nine months old they will have achieved between 60% and 75% of the adult weight and when the second and third molars are functional (at about 12 and 20 months respectively) the similarity of body size and the increased jaw length (with the loss of the characteristic "baby" face) makes recognition of the animal as an adult or as a yearling, much more difficult. If found alone, an 18 month-old female may well be labelled as an adult, whereas if with an adult, she would be designated a yearling. A similar problem has been noted in red deer when not only are yearlings and adult females confused, but also immature males and hinds (Lowe 1969). This error cannot occur with the male sika for by this age they are developing pedicles and antlers and are observed over much shorter distances than those used by Lowe; aiding identification enormously.

Recognition of mature males is a simple business as their body size, shape and colour (particularly in the winter) are all different form those of the females. However, they cannot be aged reliably from their antlers which is why the category has been left as "adult male". Horwood and Masters (1970) suggest that the male carries six tines between its second and fifth year and may well produce eight points in the fifth year although this latter point is by no means certain. There is a lot of variation around this and they report the shooting of a juvenile male with six points (its first head is usually assumed to carry a pair of unbranched spikes). Chaplin and White (1969) tried, unsuccessfully, to relate the age of wild and of park fallow deer to antler characteristics and although the cull samples were too small to test these findings here, ageing from antlers is viewed with some scepticism. Indeed, Lockard (1972) suggests that antler characteristics are as much indicators of the animal's inheritance and nutritional state as they are of age; for these reasons the age classes were restricted to juvenile and mature males.

Calves cannot be sexed because the males do not start to develop their pedicles until they are about seven months old and these cannot be seen clearly until the animal is nearly a year old. The first antlers develop after 14 months or so but as there is so much individual variation, male and female yearlings are grouped together in the population as a whole.

3. Seasonal population changes: are they real?

Some of the data presented above suggests that the size and the structure of the populations alters dramatically from one season to another. Some of these changes would be expected (the influx of males for the rut and their departure afterwards, for example) and all the changes can be attributed to one of three effects: immigration ,emigration and sample bias.

The main source of immigration is from the annual migration of the males. Mature stags are rarely found in the study area between February and September during which period they are thought to move out of the Frame area into the Beaulieu Estates to the east, or to an area known as Brockenhurst Manor to the west. A few remain in the west end of New Copse Inclosure but as the vegetation here is extremely dense, they are rarely seen. The stags return to Frame and remain there between September and the end of January for the rutting season, causing the observed ratio of hinds to stags to drop from 79 to one to 4 to one.

This latter ratio is the sex ratio observed for adult animals in this population but it is not the breeding ratio. In an earlier section on group composition it was shown that the ratio of stags to hinds in each group varies between one to one and one to 14, but that the majority of the groups contain a composition of around one to three.

This detail, coupled to that above, leads one to suggest that the breeding ratio encountered here in the New Forest is probably around twelve mature hinds per master stag.

The second source of immigration derives from the birth of calves to between 40% and 80% of the females in the population. These do not run with the hind immediately; the mother leaves the young one whilst she feeds and returns periodically to suckle it. After a few weeks the calf does accompany the mother, but as this time of year coincides with the densest vegetation the calves are invisible in tall grass or bracken, as, on occasion, is the mother. Thus, the contribution of the calves to the population occurs gradually and this is why the hind to calf ratio alters slowly during spring and summer, only stabilising in the autumn and winter when the animals are larger (but still recognisable) and are less hidden by herbage.

Emigration is the second cause of changing population composition. Stags have already been reported as leaving the area from February onwards, and many of the brockets accompany them. These animals are seldom found during the summer and the ratios of hinds to stags, hinds to yearlings, and calves to yearlings, reflects this.

Mortality must occur in any population and it was hoped that some impression of the scale of calf mortality, in particular, could be gleaned from the population structure ratios. A large drop in the ratio of hinds to calves coinciding with the end of the winter and the onset of spring may be due to mortality (and suggests a value of around 50%) but it is also probably partly due to the mistaken identification of older calves for yearlings.

This value is very high when compared to data collected on red deer on the Island of Rhum (in the Inner Hebrides). Here 18% of new calves died before the end of September and a further 11% died during winter and early spring (Guinness et al. 1978), but even that only produces 27% overall mortality.

A second estimate of this value is deduced from the calf to yearling ratio in the winter; a time when all the calves have been born and the male yearlings are still in the area. Stable at 1.3 to one, this ratio suggests 30% mortality but as calculated from data throughout the winter - up to the end of January - it takes no account of late deaths. The spring figures are not applicable as by then the brockets have left the area with the mature males.

One could suggest a check on this value for (considering the relatively mild conditions endured in southern England) these values seem to be very high. Assuming that the actual breeding population of hinds alters relatively little between one year and the next (with a lifespan of at least 12 years, achieving sexual maturity at the age of 18 months and with several unnatural deaths in this particular population each year, this seems reasonable) one might expect the hind to calf ratio of one year to resemble the hind to yearling ratio of the next, if mortality was negligible. The autumn or winter figures must be used for this again as the presence of all the calves and brockets is required, together with the easier recognition of the female yearlings. This check does not support the previous estimate of between 30% and 50% for the ratios are given as 6.7 to one and 6.9 to one in the autumn of 1980 and 1981 respectively. This suggests a mortality of around 3% so perhaps none of these methods yields a satisfactory result as sample bias and identification errors are too great.

That mortality occurs in other age classes in the population is obvious but the real extent is impossible to determine as slight differences in population structure will be recorded each month, or each season, but whether the result of different sized samples, different "observability" of individuals (Downing et al. 1977) or of true changes in structure, one cannot tell. A tentative estimate was made from the culled animal age structure with 50% mortality proposed between the ages of two and four and 25% between four and six. This again seems very high.

Culling takes betwen 22 (1978 - 1979) and 35 (1980 - 1981) animals from the New Forest population but as these animals are randomly distributed throughout the herd (apart from the calves and yearlings) this is unlikely to affect the population ratios very much and therefore would not influence the calculations of mortality.

No jaws were obtained during the cull from animals more than about 9 years old although it is certain that some sika live at least 14 years. A hind, collared by Horwood and Masters in 1969 when already an adult, was seen in the company of a calf on several occasions at Purbeck, so is at least 14 years old and if with her own calf, is still reproducing. It is possible that the repeated poaching and culling has shortened the age profile of the New Forest population (as animals have different vulnerability to guns - Roseberry and Klimstra 1974) but this does not seem very plausible, particularly as the same age profile was found at Wareham. The alternative explanation is that the samples were too small and the age estimates from the sectioned teeth are too inaccurate (accuracy being hindered by the small sample size reducing the level of expertise achieved from inadequate practice - Rice 1980) to describe the age profiles adequately.

4. The representative nature of the selective cull

In two of the three forests surveyed, the New Forest and Wareham, the Forestry Commission carries out the annual cull with the keepers instructed to achieve a predetermined quota of male and female deer. To this end and in an attempt to maintain the population, the keepers "select" individuals; old, weak or "poor" specimens using external characteristics like size, shape and antler features as the basis for this decision.

This would lead one to expect the cull to be unrepresentative of the population as a whole as considerable control can obviously be exerted over its precise composition. It is also policy to shoot a calf if its mother is shot. However, Roseberry and Klimstra (1974) showed during the massacre of 11,000 deer that an apparently random cull was not as representative of the population as they had expected and that some animals, by virtue of their age and sex, were more vulnerable to the harvest than were others. So even if the New Forest cull was thought to be representative of the population, it probably is not; as it is selected, it seems as if it could be even less representative than ever. Within the sample are data that cannot be discarded and the cull as a source of such material (representative or not) cannot be ignored.

Chaplin and White (1969) showed that ageing male fallow deer from antler characteristics is unreliable when they failed to correlate these with age deduced from tooth eruption and wear in both wild and park deer. Horwood and Masters (1970) report an occasion when a six-point sika stag, assumed to be an adult, was shown after shooting, to have juvenile dentition. It is possible, therefore, that the adult male cull is not as selective as is thought.

It is not possible to age females in carcass. The culling details collected from the keepers (for interest's sake only) included their estimate of the age of the animal and a brief comparison between this estimate and that obtained from sectioned teeth or eruption sequence showed that the keepers consistently over-aged the animals by up to 5 years. Even allowing for an error in the sectioned age of ±2 years, this still suggests that the adult female cull may contain a random age distribution.

At this time of year it is not possible to distinguish those females in calf from those that are not, as the foetus is, at most, 15cms in length from nose to tail and causes no noticeable change to the adult shape. Thus the reproductive performance of the hinds can be assumed to be revealed from a random sample provided that those, by being pregnant, are not more susceptible to the guns.

5. Discrepancy between fecundities

A large discrepancy is revealed between the fecundity of the female deer as derived from the observed data (about 40%) and from post-mortem data (over 80% in the New Forest and 90% at Wareham) although these values are comparable to those given for red deer on Rhum. Here the fecundity is given as being between 72% and 92% (Guinness et al. 1978) although in Scotland as a whole this may be as low as 40% (Mitchell 1973).

This difference in the estimates of New Forest sika fecundity may be due to the bias discussed earlier in that calves may not be as effectively sampled as hinds, or it may even be that some hinds, with their calves, move out of the study area during the autumn seeking superior forage and are not included in the census. Further, the 80% or 90% figure refers to fecundity up to the end of January and thus takes no account of spontaneous abortions, of still-birth, of neo-natal mortality nor of predation by foxes and dogs. Indeed Staines (1978), studying a declining population of red deer in Glen Dye in north-east Scotland, reports that between 29% and 44% of foetuses and calves are lost between mid-pregnancy and 2 months post-partum.

The ratios given earlier suggest that over the winter of 1980 - 1981 there was a mortality of 30% amongst the sika calves. Even if one decides that this value is 100% too high because of sample bias, it is still possible to lose a large number of calves immediately after birth. The area is well-populated with foxes so one need not expect to find any carcasses. Indeed only two corpses were found during the 2½ years of fieldwork, both mature females, and in each case these were removed in a week so a calf carcass would not remain for very long.

6. Population growth rates

There is much information published on age-related fecundity in the red deer (eg. Lowe 1969, Mitchell 1973, Mitchell and Lincoln 1973, Staines 1978, Guinness et al. 1978) showing that fertility and reproductive success is related to the age of the hind, its reproductive status, its condition and perhaps to the quality of the home range and the density of the population. The proportion of red deer pregnancies is usually higher amongst hinds that had not reared a calf the previous year; those hinds recorded as "yeld" were invariably in better body condition than those with calves and are more successful with the new calf (Mitchell et al. 1976).

In the study presented here, insufficient data were obtained to undertake elaborate analyses of age-related fecundity but although the sample age profile was brief, there was no apparent decline in fecundity amongst the older hinds.

Mitchell (1973) regards the mature "yeld" red deer hind as being symptomatic of nutritional distress and suggests that whereas hinds clearly are capable of calving every year in some environments, a large proportion of Scottish hinds fail to do so; often taking a year to recover from producing and rearing a calf. He gives a pregnancy rate from seven areas in Scotland of 71% for milk hinds (prime animals aged between 5 and 10) and 30% for old animals (between 11 - 16).

These definitions suggest that the New Forest and Wareham sika deer are all prime. Here the percentage pregnancy rates amongst milk hinds are 44.7% and 35.5% respectively. These values are comparable to figures given by Mitchell (loc. cit.) and further, only 10.5% of the New Forest cull and none of the Wareham cull was infertile.

Figures published earlier by Horwood (1971) suggest an 88.2% fecundity for sika deer in the Poole Basin (n=51). He also reports 40% calf pregnancy (n=5) and 75% yearling pregnancy (n=20) from culled animal material collected between 1965 and 1969, although whether from Purbeck or Wareham is not clear. These figures indicate a very high population growth rate with these deer attaining an early puberty. Regretfully no details of hinds in milk are offered.

It is generally accepted that between 25% and 40% of the Scottish red deer population is yeld (Mitchell 1969, Lowe 1971). Details from the New Forest and Wareham suggest a high population growth rate in these sika herds. The animals are living in a relatively equable environment and yet at very high densities; New Forest 226 - 290 deer per 1,000 ha and Purbeck at 194 deer per 1,000 ha. These are much higher than figures reported for various red deer populations in Scotland; 28, 80, 131, 132, 139 and 153 animals per 1000 ha (Mitchell 1973).

Perhaps the presence of yeld hinds in the New Forest, despite the apparent richness of the environment, is indicative of nutritional distress as suggested by Mitchell (1973) and this may be partly due to the competition from the New Forest ponies. This competition was proposed earlier as the cause of the high coniferous needle intake; a situation exascerbated by the high deer density. At Wareham the animals do not ingest needles; they feed throughout the year in cultivated farmlands and are present at a much lower density. Here there are no yeld hinds so perhaps the population is in better condition. Unfortunately the collection of carcass weights was inconsistent and so this detail cannot be checked.

There has been a heavy shooting pressure at Wareham for many years (E. Masters pers. comm.) and coupled to the inevitable poaching this may have reduced the population to below the carrying capacity of the area (as was indicated by the low number of observations collected on the driven transects and the small amount of dung found in the accumulation plots). The population is, therefore, despite the poor quality of the forest vegetation (see diet Chapter 4), able to reproduce at a high rate. In the New Forest the high density of deer coupled to a relatively low shooting pressure (J. Ealing pers. comm.), the low level of poaching and the competition from the New Forest ponies has resulted in the population approaching the carrying capacity for the area and the reproductive rate in the population is dropping.

7. The validity of ageing from jaws

Counting dental cementum layers as as ageing technique was described first in studies with marine mammals (Scheffer 1950, Laws 1952). Studies with known-aged deer have shown that annular structures are directly related to age (Low and Cowan 1963, Thomas and Bandy 1973). Earlier studies concerned growth layers in dentine (eg. Eidmann 1933 in the red deer) but as dentine grows internally, gradually filling the pulp cavity, the rings get progressively smaller and more difficult to count. Cement grows on the root surface, apparently at a constant rate throughout the life of the animal, so the annual increments are relatively constant and much easier to count.

Mitchell (1963) showed how growth layers in the dental cement of the red deer could be exposed by sectioning the cement pad found under the crown of molar teeth and the technique has been refined and applied in many studies since then (eg. Mitchell 1967 - red deer, Lowe 1967 - red deer, Lockard 1972 - white-tailed deer, Aitken 1975 - roe deer). The method has been criticised by Rice (1980) on the grounds that false layers in the cementum were found in 50% of a sample of sectioned teeth and that considerable practice is required before these are recognised.

The technique depends upon the identification of layers of white cement (deposited in the summer and autumn and caused by prolific cementocytes) and transparent layers (deposited in the winter and spring and caused by a defecit of cementocytes) and appears simple enough. Unfortunately, there is considerable skill involved in preparing the material and in counting the lines for many are not continuous and Mitchell (1967) amongst others, reports the presence of an extra translucent layer in the cement pad of males which is deposited around the time of the rut.

Rice (1980) using thin, decalcified sections cut from incisors, identified three cement layer types which could cause error in these counts and which he labelled false, split and compound annuli. Further, he describes how these irregularities are not consistent between paired incisors and reports irregular structures in more than 45% of the teeth sectioned. The inaccuracy caused by this in ageing samples is given as about 8%, a value which decreases over time as experience and expertise improve.

Aitken (1975), working with roe deer, aged a large sample using wear characteristics compared with jaws of known age and he then sectioned the teeth to determine the level of agreement. Exact correspondence was achieved in

63.5% of the cases and to within one year, in 90.5%. The discrepancy was attributed to varying amounts of tooth wear as a result of the individual susceptibility of animals within a certain age class. For the purposes of population description this level of accuracy is perfectly acceptable.

Despite the apparent shortcomings of the technique, in that layers may be irregular, or may not exist at all (if there is no seasonal variation in weather conditions to cause a period of stress for the deer no layers form - Lockard 1972, Aitken 1975), and the problems of making an adequate preparation, the method is still the best for many species of deer. It does rely upon comparison of material of known age for confirmation of the results and as yet there is no such information available for sika deer,

Briel (1978) has commented that the cementum technique is effective for the sika deer of Sauerland, but he offers no calibration and works from a very small sample. Toothwear assessment is a much more rapid method but lacks precision and as animals of the same age often show wide variations in the extent of tooth wear, it is likely to lead to inaccuracy.

Thus, Mitchell's (1967) guidelines for ageing red deer from eruption sequence and his exposition on tooth -sectioning was used to provide an objective estimate of the ages of the animals shot in the study areas.

8. Group size affected by composition?

A definite relationship has been demonstrated indicating that groups containing mature male sika deer are larger than groups containing males only, or small-deer.

Horwood and Masters (1970) suggest that at the end of the rut, the males "...or some of them, reappear in the fields where mixed groups of stags and hinds can be seen feeding together..." implying that until then they had not been seen feeding together. In this forest they maintain that the stags hold a territory and cover receptive hinds as they cross these areas and therefore do not collect a harem. In the New Forest, no evidence of territorial defense was found (see Chapter 6) and observations from here suggest that the stags associate very closely with the females (along the lines of the harem), although the possibility of both systems occurring together simultaneously cannot be discounted.

However, larger groups are associated with mature males irrespective of the time of year; whether these are chance accumulations around a particular feeding area, or are based on associations formed during the rut is impossible to state. These mixed-sex groups are rarely found between February and September suggesting that, as in the red deer (Clutton-Brock et al. 1979) the sexes segregate for much of the year. This as also reported by Horwood and Masters (1970).

Without marking a large part of the population it is not even possible to state whether the individuals are faithful to one particular male during or outside the rut, although on the limited amount of data offered in Chapter 6, it appears as if the males are not.

Horwood and Masters (1970) in work with marked hinds at Purbeck showed that although the hind has a small home range and may be seen feeding in the same fields or group of fields on a number of occasions, her companions differ. This led to the suggestion that they are no more than the members of a very loosely-knit community which may feed in the same fields at night, but lie up independently during the day. This idea prompted Putman (1981) to review the social organisation of all deer species and this will be discussed later.

9. Group size related to habitat type?

An inverse relationship is proposed between group size and cover density in both the study areas and as this has been often found in other studies of ungulates (eg. Estes 1967, Jarman 1974); a variety of hypotheses have been proposed to explain it. The strongest and the most widely accepted argument is that this represents an adaptation amongst ungulates for predator avoidance (eg. Dasmann and Taber 1956, Eisenberg 1966, McCullough 1969, Hamilton 1971, Jungius 1971, Estes 1974, Jarman 1974, Hirth 1977).

The predator avoidance hypothesis holds that an animal as large as an ungulate is more likely to avoid detection in dense cover in a small group when it is effectively concealed. In the open the reverse is true and as most ungulates are too large to escape detection when feeding in exposed sites, they form bigger assemblies so as to maximise their detection of predators and to reduce the chance of being taken by creating confusion when attacked, or by repelling attack by counter-attack.

Observations on the sika conform to this basic pattern and although there are now no natural predators in the United Kingdom from which a defense is necessary, there are in Japan. In evolutionary terms the sika have been in Britain for a very brief period and have probably not yet adapted to the new situation.

A second hypothesis, equally plausible (neither hypothesis need necessarily be exclusive) is based upon feeding strategy and the avoidance of intra-specific competition.

Feeding in large groups on a diffuse food supply is not possible if intra-specific competition is to be avoided, so in areas where feed is unevenly distributed (as in this case the oakwoods), small assemblies of deer are favoured. If grazing in a field, where forage is more plentiful, a larger group is possible as competition from individuals is less likely.

The distribution of food resources within the habitats will alter with the time of year and so group sizes may vary on this basis too. For example, a plentiful resource in the oakwoods is afforded by the acorn crop (supplemented by falling leaves) which allows larger groups to form in the autumn than might be expected. During the summer though, the height of the canopy and the poor light levels create a diffuse food supply that is only effectively exploited by smaller groups of animals.

Prethicket areas are the densest areas encountered in the New Forest study zone and these are found to hold consistently small groups. These benefit both from a rich and relatively continuous supply of forage, but because of the denseness of the vegetation the animals are unable to interact over substantial distances and so remain in small groups. A similar feature has been reported by Loudon (1979) who claims that the size of roe buck territories depends, in the main, upon the visibility through the undergrowth.

Rides cannot be classed as either an "open" or as a "closed" habitat as animals feeding there are not far from the shelter of the plantations. They may also be overhung by trees. These regions hold groups of feeding deer intermediate in size between those typical of fields and of prethicket areas. The proximity of cover may allow smaller groups to feed than would be expected from consideration of predator defense in an open area, but the relatively prolific food supply permits larger groups than might be found in the closed areas.

Predator defense was mentioned earlier and the effect of day and night upon group sizes dismissed as few of the data achieved statistical significance. However, those that did achieve a significant difference and many that did not, pointed towards larger assemblies of deer found during daylight hours than at night. It oculd be argued that this is a sample bias occasioned by poor night-time visibility, but animals concealed during the daytime (and which may well be missed) are betrayed by the reflection of the spotlamp in their eyes at night; it is possible that on some occasions the night-time sample is the more complete. Perhaps there is a difference between day and night predator avoidance strategies although the same food resource constraints must apply irrespective of the time of day. No studies have been found in the literature to support this but larger groups were found in all the habitats in the New Forest in the daytime, except the fields. Under the cover of darkness feeding aggregations form in field areas and that these are larger than in the daytime may be due to the superior food supply, predator defense considerations and the avoidance of daytime human intervention.

At night in the closed habitats deer are frequently found lying up and ruminating (see Chapter 3) in small groups. Certainly no feeding strategy affects these animals, nor is there likely to be any intra-specific competition for a particular patch on which to lie when 700 Ha are available, but perhaps by spreading themselves out more thinly the animals reduce the chances of being found by a potential predator, as, by being caught when recumbent, they may be more vulnerable.

In summary, a definite pattern relating group size to habitat type is common among ungulates and a very similar trend has been found in the sika deer in both these study sites. The relationship can be explained both as a means of avoiding predation, as a means of optimising feeding efficiency and of reducing intra-specific competition.

Similar findings are reported by Ito (1968) with sika deer in Japan, Walther (1972) with gazelles, Jungius (1977) with reedbuck and Hirth (1977) with white-tailed deer.

10. Population structures compared

Only a very limited comparison between the population structure in the New Forest with that in the Poole Basin is possible because of the unique problems encountered whilst working at Purbeck. It was most unfortunate that so few of the observations could be classified accurately.

There are many similarities between these two populations despite the vegetational differences and the differences in the estimated population densities in the areas; 194 deer per 1,000 Ha at Purbeck and 240 per 1,000 Ha at the New Forest study site.

In both areas hinds regularly contribute the largest proportion of the data and allowing for the small sample collected at Purbeck, even the actual percentages are similar: 75%, 84%, 63% and 56% in the New Forest, 63%, 83%, 71% and 47% at Purbeck in winter 1980, spring, summer and autumn 1981 respectively.

More convincing perhaps are the proportions of stags found: 4%, 3.6%, 3.2% and 14% in the New Forest, 4%, 0, 2.4% and 10% at Purbeck in the winter 1980, spring, summer and autumn 1981 respectively. The numbers of other sightings at Purbeck were very low so a comparison is not worthwhile.

These percentages have been translated into a sex ratio and in each case the hind to stag ratio is around 4 to 1. It was proposed earlier that the breeding group contains several other males and that the true breeding ratio is nearer 12 or 14 to one, but this applies equally in each area.

The winter calf mortality suggested by these figures is similar too, being around 40%, a value that seems to be extremely high when over 80% of all the hinds shot were in calf. No post-mortem specimens were collected at Purbeck, so speculation on the precise fecundity or population growth there is fruitless.

The detailed age structure, determined by sectioning teeth from shot specimens was very similar in Wareham and the New Forest; no animal being found over the age of nine years and disregarding the heavy predominance of calves and yearlings (selected by the gunman), the same gradual (although probably insignificant) decline in the numbers of older animals was noted.

Overall the data shows two populations of animals with a very similar age and sex-structure surviving, although not exactly thriving, in very different habitats.

CHAPTER SIX

Social behaviour

SOCIAL BEHAVIOUR

INTRODUCTION

Data on the social organisation, the social structure and the ecology of the sika deer which were presented and discussed above were collected in a rigorous fashion from a restricted survey.

Data on social behaviour, by its very nature, cannot be collected in this way; it has to be recorded spontaneously and as a result most of the data presented in this chapter are anecdotal.

As in Chapter 5, the majority of these records refer to the New Forest alone.

METHODS

Observations on social interactions were collected during the course of all the other data collection techniques.

RESULTS

1. Female : female interactions

Horwood and Masters (1970) suggest that the annual cycle of the sika hind at Purbeck is a very "humdrum affair". It seems as if they remain in a small part of the forest where they lie up ruminating during the day and feed in a particular area of fields (not necessarily those closest to their home range) at night.

a. Group cohesiveness

In Chapter 5 it was suggested that the large feeding aggregations found in the more open habitats are composed of several groups of animals and that these are constructed from even smaller units (Putman 1981) perhaps, in the case of the sika deer, based on the hind calf.

These feeding aggregations are very flexible in membership (Horwood and Masters 1970) and the component units may arrive and depart independently. Whilst feeding the component units were seen to lose their identity, although hinds and calves tend to stay closely attached, and it is by no means certain that they reform when departing (Putman 1981). If a feeding group of sika is disturbed it scatters with several parties disappearing into cover; individuals not necessarily selecting the nearest available shelter. Certainly hinds and calves remain together and they are often joined by a yearling although one cannot be certain this is the same animal with which they arrived for, unlike the calf, the yearling feeds independently of the hind.

Putman (1981) suggests that in the case of the fallow deer (where the units may contain up to eight individuals) these departing parties are not necessarily of the same composition as when they arrived. Rand (pers. comm.), working on recognisable individuals, suggests, again with fallow, that the yearling seen with a hind may well not be her own progeny.

On some occasions these small-deer parties do maintain their identity. One might see a feeding aggregation on a ride and a second party of small-deer, invariably led by a mature hind, crossing the ground through the middle of the feeding party. Those grazing do not acknowledge the transients (even by raising their heads) although it is certain they do hear them so are not unaware of their presence. The travellers walk in file and rarely halt on their way across, although occasionally one may remain behind to feed.

It is interesting to note that these rides have traditional crossing places where so much animal traffic passes that a path is worn in the grass and the banks around the edges are cut away.

b. Dominance

Direct interactions between individuals were observed too infrequently (and most hinds are indistinguishable, anyway) to allow the construction of a dominance hierarchy. That one exists is suggested by the fact that some feeding hinds may be displaced by others and that in a feeding aggregation the small deer seem to be evenly spaced. It is likely that a dominance hierarchy has been established earlier and is maintained by signs that are, on the whole, too subtle for the observer to detect.

This is in spite of the fact that a high proportion of the hind's life is spent in habitats where small groups are maintained (see Chapter 2 on habitat occupation and Chapter 5 on social organisation) and where the opportunities to establish such a hierarchy must be limited. Ozoga (1972) recorded white-tailed deer feeding at cutting sites and found that not only was a dominance hierarchy rapidly established, but also that the energy spent fighting was minimal. This being the case, a temporary hierarchy might be established in these feeding aggregations of sika deer or, if the same animals feed together on subsequent occasions (as they do at Purbeck - Horwood and Masters 1970) as members of the same "super herd" or clan (Putman 1981), then the hierarchy may be gradually established over a longer period and merely consolidated on these occasions.

The existence of such a hierarchy would prove evolutionarily favourable for it has been suggested in Chapter 4 that some feed resources are limited and intra-specific competition, minimal under such a regime, would be reduced so that more time can be spent feeding.

The reduction of intra-specific competition was suggested as one reason for differences in group sizes in different habitats (see Chapter 5). Larger accumulations of animals form on more continuous food resources (fields, rides) where the evenly distributed, high quality forage, coupled to the regular spacing of individuals will ensure that all feed adequately.

The highly selective way in which deer feed (eg. Staines 1982) was reviewed in Chapter 4 and it may be that an individual higher in the hierarchy will succeed in improving the quality of her intake by displacing subordinates from superior forages. Those animals seen to displace another are always adults and it may be that older individuals, under stress due to lactation or pregnancy, are able to meet these greater needs by being higher up the hierarchy and commanding better quality forage. This is purely speculative and although it is possible to detect differences in the chemical composition of feed between the sexes (Staines et al. 1982) the amount of individual variation already present would probably inhibit comparisons of diet quality between individuals in a hierarchy.

In habitats with a more diffuse food supply, for example oakwoods, the feeding groups are much smaller and frequently are family groups of hind, calf and yearling. In these cases the hind is always dominant although a fair amount of stratification could occur if all three chose to browse.

2. Female : juvenile interactions

a. Female : calf interactions

Most calves are born between the end of May and the end of July but there is considerable leeway in this. Indeed two calves were recorded whilst still in baby coat and very small, in mid-November ; Horwood and Masters (1970) report one which was probably born as late as January, another born as early as 12th April.

This is an identical pattern to that observed for red deer. Hinds are polyoestrus (Guinness et al. 1971) and the majority of hinds from a much-studied population on the Island of Rhum (in the Inner Hebrides) conceive between the second and the third week of October, though some conceptions may occur between late September and early January (Guinness et al. 1978). The females will remain polyoestrus with 18-day cycles occurring from October to March if pregnancy is prevented experimentally (Guinness et al. 1971). Mitchell and Lincoln (1973) using data from Rhum, and from Glen Feshie in the Central Highlands found that conceptions in the wild were spread over about 100 days from late September to late December with most occurring in October.

Around calving time sika hinds are seen to lead a solitary existence, perhaps accompanied by the calf from the previous year, but they are not now associated with the larger assemblies so characteristic of March and April. Until the new calf is about three weeks old it is not seen with the hind, being left alone for much of the day whilst she feeds, returning occasionally to suckle it (Milner-Bennetts 1981).

Later, when stronger, better co-ordinated and substantially larger, the calf does accompany the mother; the family group now constitutes the hind, the new calf and last year's calf (the yearling having departed) and observations on hind to calf relationships can now be collected. The mother suckles the calf often (how frequently is not known) but none of the dozen or so records of this activity lasts for more than 2 minutes. She grooms it frequently and on rare occasions so does the sibling. When lying down to ruminate the hind has the calf closely alongside; the yearling may be a couple of metres away. When feeding in a larger assembly the new calf may be nosed by other hinds although these are always chased away by the mother. It is unclear whether by having a calf the hind now occupies a position higher in the hierarchy than she did before.

As the calf grows it begins to feed, ineffectually at first as as much material falls out of its mouth as is swallowed, but by the end of June or the middle of July they feed extensively and they and hinds are found in larger feeding aggregations than of late and hind:calf interactions become less frequent. The calf feeds further away from the mother, accompanies her constantly, but its attempts at suckling are now repulsed more often than they are accepted. On four occasions a yearling was seen attempting to suckle but it was bitten, kicked and chased away.

When about seven months old the male calves start to develop pedicles. These can be detected on shot animals but they are not obvious in the living deer at this time. The calves feed entirely for themselves now and were never seen suckling. On two occasions hind and calf were shot simultaneously and the contents of their rumina were found to be identical in composition. Lactating hinds shot during the winter have minute quantities of milk in a much-reduced mammary gland and this is not consistent with continued production. The examination of mammary glands from red deer shot throughout the year (Mitchell et al. 1976) shows a gradual decrease in the weight of the organ from shortly after parturition until February or March at which point milk production is barely detectable.

The hind to calf feeding distance has increased still further at this stage and there may be occasionally one or more animals between the hind and calf without apparently causing either animal any distress.

Interactions between individuals of this age were very few as the majority of observations are of animals feeding in preparation for the winter. Occasionally calves, siblings and on two occasions mature hinds were seen grooming each other; paying most attention to the head and neck (areas which the animal cannot reach for itself). Grooming bouts seldom lasted longer than three minutes and the compliment was always returned. On seven occasions homosexual behaviour was seen; yearlings or adults mounting each other but the dominant animal was never above the other for more than five seconds.

b. Female : yearling interactions

When the pedicles are developed and before the mature males move away to shed their antlers, Horwood and Masters (1970) report that the stag calves are "rounded up" by the mature stags and that the female calves remain with the hind until the next calf is due at which point she is "driven off"; a split , they report from observations in the Poole Basin, that appears to be permanent.

No records were collected to support either of these observations. That male parties develop is certain and that some include male calves with well-developed pedicles is also certain, but some brockets (as they now become) are seen associated with the small deer group until well into the summer and although they may be growing their first antlers they remain subordinate to the hinds and are frequently displaced at feeding sites. The female calf (or yearling as she now becomes) seems to remain attached to the mother at least until the next winter, but sometimes until the next summer when she becomes a two-year old. It is not certain though that these hind and yearling pairings are related to each other, indeed Rand (pers. comm.) has stated that in fallow deer, they usually are not.

The family group of hind, calf and yearling is often found bedded down together, a situation that Horwood and Masters (1970) would deny by inference although the nature of the vegetation on their study areas must surely reduce the sightings of those animals lying anywhere but out in the open. When deer in this study were found lying out in the Purbeck fields not only were they too far away to be reliably recognised, but no familial attachments of the type described for the New Forest were observed. It may be that hinds with young calves retire to a more sheltered situation to lie up and by the time that this is no longer necessary the calves are also indistinguishable over the considerable distances involved, so are not recorded.

As was pointed out in Chapter 5, it is likely that some of the older female yearlings are unwittingly included with the adult females but it is hoped that this would only affect a small number of observations and as female:yearling interactions are so rare but so similar to those described above between mature females, the effect of this must be neglible.

3. Male behaviour

a. Male : male interactions outside the rut

Most male sightings were collected during the autumn and winter when the rut is in progress. It is proposed to discuss this period separately.

Outside the rut (from the end of December to the beginning of October) the stags seem to be solitary and secretive. Certainly they rarely associate with other males (see Chapter 5) although they are occasionally found feeding in the company of hinds and calves. Because of this solitary tendency and because of their departure to other grounds for much of the year (areas in which they moult and shed and replace their antlers), very few male to male interactions were collected outside the rut and one can say nothing of importance about them.

Interactions between mature and juvenile males are also few and far between. When feeding the juveniles are always displaced by the stags, or if approached whilst walking they always back away or change direction. Male calves are even more easily displaced and frequently run away from the stags.

b. Male : female interactions; reproductive behaviour

Older males start to fray the velvet from their antlers in August and by the middle of September all are in hard horn. In the New Forest it is about this time that stags are again found in the deer sanctuary area at the centre of Frame Heath Inclosure; none having been recorded there since the end of March. The stags have also moulted and their necks are expanding in preparation for the rutting season.

For the purposes of this discussion the rutting season is taken as being between the beginning of October and the end of December for it is in this period that the majority of stag sightings are collected. The rut is generally accepted to last a few weeks (Horwood and Masters 1970) but it does not seem to be the frenetic affair in the New Forest that is reported for the red deer in Scotland (eg. Clutton-Brock et al. 1979).

Horwood and Masters (loc. cit.) report the rut as taking place between early September and the end of October but it could be argued that the rut in the New Forest is slightly later than this (H. Cutler pers. comm.).

It is certainly possible that differences may be found between forests although as the hormonal cycle is triggered by day length (Goss 1969 a and b) it is unlikely that Frame and Purbeck are sufficiently apart for this to have any effect.

No attempt was made to assess the sexual state of the stags by determining sperm counts as the number of stags killed at this time is too small; the first indication of sexual activity in the males is an increase in the frequency of their calling.

This extraordinary noise, a shrill whistle repeated two or three times, may be heard occasionally throughout the year and cannot be confused with the single alarm shriek of the hinds. It becomes much more frequent during late September and October when it may be heard at any time throughout the 24 hours. Records collected during this study fail to reveal a dawn and dusk peak in the frequency of calling as reported by many other observers but they did not stay in the area for the entire 24 hour period; if anything, calling is more frequent during the night than during the day. As the rut progresses the note changes and becomes more of a groan or gurgle (rather like a protesting hinge) and these sounds may be heard up until the end of January in the New Forest.

Published information on the rutting behaviour of the sika (Horwood and Masters 1970) proposes that the stags mark out and defend territories in the woods; territories which the hinds have to cross in their nightly migration to the fields to feed. These territories are marked by thrashed *Calluna* bushes and frayed perimeter trees and Horwood and Masters report that the stags remain on their territories throughout the main part of the rutting season and do not resume feeding in the fields until the end of October.

At this time of year the master stag tolerates the presence of younger, attendant stags, who may accompany him much in the same way as junior stags accompany the harem master in the red deer (Clutton-Brock and Albon 1978).

Fighting between stags, Horwood and Masters report, is commonplace, both between the mature male and one of his attendants or between neighbouring territory holders.

The stags wallow, are invariably matted with mud and smell very rank although the red deer practice of urinating in the wallow (Staines 1980) was not seen.

i. Identification of stag ranges

The details of the rut in the New Forest are very confused indeed, not the least because of the dense vegetation and the large number of males present. To resolve the question as to whether the males have harems or territories, and to compare with the rutting behaviour reported by Horwood and Masters (1970) a more detailed survey was undertaken during two of the New Forest ruts by identifying, recording and plotting the sightings of individual mature males.

The basic pattern of antlers for the mature sika stag is of eight points, four on each antler which are known as the brow, trez (or trey) rear and top. There are many variations on this basic theme and when coupled to other more permanent physical features like torn ears, blind eyes or distinctive coat markings, these characteristics allow identification of some of the individuals.

During the 1980 rut written descriptions were compiled of the stags and further sightings were identified by reference to this. This technique proved unreliable after two individuals were confused because each had an identical break in an antler; it was not until several records had been collected that a nick in the ear of one was noticed and the mistake rectified. Small details like this are difficult to see, so rapidly must identifications be made, so in the next year a photographic technique was used instead.

Using the equivalent of a 400mm f5.6 lens and Ilford HP5 film uprated to 1600ASA (and occasionally 3200ASA) a head-on photograph was taken of as many mature males encountered on the circuits as was possible.

Pictures from the side or from behind were rarely attempted as superimposing the antlers made identification even more difficult; particularly if a fair degree of enlargement (reducing picture quality) was necessary. Using a data-back on the camera these pictures were numbered and the numbers were entered in the field notes. After development and printing the stags portrayed could be identified at leisure and, it is hoped, with fewer errors. The further advantage of the method was that the car served as an ideal photographic hide and animals could be approached to within 15m although 25m was more usual. On foot the closest one could expect to get, undetected was 50m.

Some night-time photography was also attempted using the roof-mounted spotlamp as the light source. Deer closer to the car than 25m were illuminated by flash.

In both years the sighting records of these stags were plotted on maps and to give credence to the plots it was decided, quite arbitrarily, that at least 5 sighting occasions were needed and that sightings on consecutive transects were to be treated as one occasion.

It might seem as if an inordinate amount of disturbance would be caused by the photography but the stags appeared unconcerned by the flashgun and one assumes they could not see behind the spotlamp, so were no more alarmed than usual. Indeed animals lying up and photographed under these conditions were invariably in the same place on subsequent visits.

During the 1980 rutting season, nineteen mature males were recorded of which ten were only recognised from their written descriptions thrice. Thus for this season only four maps are supplied with the sightings and their dates plotted.

The most complete record available refers to an animal who had lost the left antler immediately above the brow tine and whose right antler carried an unusually long trez and a very long rear tine. This individual was recorded on 17 separate occasions between 31/10/1980 and 29/11/1980. He was seen (see figure 6:1) all over the study area and was frequently accompanied by small deer groups of different sizes (between 2 and 10) and occasionally with other stags (a 7-point, an 8-point and one juvenile male on different occasions).

During the 4 weeks of these records he was very mobile indeed and although it is possible that two stags with similar broken antlers could have been confused (as above) the detail on the one remaining would be sufficient to distinguish him.

A second male, again with a broken antler but this time fractured above the trez and leaving a splintered end, was identified on eleven occasions between 11/10/1980 and 29/11/1980 (see figure 6:2). These sightings are all within ½ a mile of each other and suggest a much more limited range for this individual.

Figures 6:3 and 6:4 also show a diffuse scheme of sightings spread between 10/10/1980 and 21/11/1980, and 10/10/1981 and 29/11/1980 respectively.

The stag in figure 6:3 was sighted first in New Copse Inclosure in October (where all the male summer sightings are collected) but after that leads a solitary existence in Frame being seen with three hinds on only one occasion.

The animal shown in figure 6:4 seems to be as mobile as the others. He was not as solitary though, being seen on various occasions with a 6-point stag, an 8-point stag, two hinds and a calf, seven hinds, two brockets and an 8-point stag, and finally six hinds and a brocket; and all in the space of two weeks.

During the second year in which records of individual stags were collected (1981), 36 different males were photographed of which 17 were only recorded on that one occasion. (Out of the 224 mature male sightings collected in this season, 55% remain unidentified even after being photographed).

Of the remaining 19 animals, only eight were recorded on more than five occasions and of these five have been plotted on maps (figures 6:5 to 6:10 inclusive). Two of the remaining males were only ever found in one small area and although a valuable observation, it has not been plotted. The final stag was first sighted on the 21st August and by discarding records collected before the middle of October has to be excluded from this account of the rut.

The maps produced by plotting these sightings give a different impression of the behaviour of the stag during this rut than was gained from the records last year. Here each figure shows that for a period of between 5 and 7 weeks these animals were very limited in their movements and although records are necessarily unevenly distributed in time (and the deer could have moved away and returned between sightings) this does seem to be a reasonable interpretation and suggests, exactly as did Horwood and Masters (1970) in the Poole Basin, that the males remain in a "territory" for the rut although little evidence for the marking and defense of this territory has been collected.

These stags were frequently found to be alone, occasionally in the company of one other male, but more often with small-deer groups containing between one and twelve individuals.

The more reasonable nature of the results from this part of the study (and their uniformity) underlines the superiority of the photographic technique although it can be expensive.

Although most of the sightings shown here are centred on the deer sanctuary in Frame Heath Inclosure it should be stressed that these are by no means the only "stag areas" in the locality. The denseness of the thickets in New Copse Inclosure hinders sightings of animals and although several distinctive beasts were found there most were recorded only two or three times.

ii. Harem or territory?

It is not clear from the data in this thesis as to whether sika stags mark out and defend a territory as suggested by Horwood and Masters (1970) or whether they collect and defend a harem as in the red deer (Lincoln et al. 1970, Lincoln and Guinness 1973). Certainly stags are found with groups of small deer. When disturbed the male is the last to depart and on a few occasions his actions could be described as "rounding up" the hinds. On the other hand, even during the rut mature males are frequently recorded alone, so either the area contains many unsuccessful males and a very few dominant individuals who collect the harems, or the stags "float" and cover receptive females as they find them.

Those animals that could be identified seem to spend the rutting season in a relatively small area of the woods (an area, moreover, which does not seem to bear any relation to the vegetation types included, nor to the rides and tracks which have been proposed as convenient boundaries to territories in the Poole Basin : Horwood and Masters 1970).

Further, when the outermost sightings plotted for each animal are joined up to give an indication of the range of each individual, a considerable degree of overlap is shown (see figure 5:10) suggesting that these "stag areas" are not exclusive.

Lengthy periods were devoted to watching wallows and several different stags were seen using these so they too do not seem to be exclusive to one animal.

Horwood and Masters (1970) suggest that stags defend their territories having marked out the boundaries with thrashed Calluna bushes and frayed perimeter trees.

This was not found in Frame although many trees are badly scored, showing deep channels that the stags have cut into the bark with their antlers. Various explanations for this activity have been offered including territory marking, (MacNally 1973), rutting stand marking, feeding and frustration at the paucity of females (Carter 1981).

The deer do eat bark at this time of year, in quite considerable quantity (see Chapter 4), but on the few occasions that this scoring behaviour was watched (the stag stands beside the tree and cuts the bark with the antlers by raising them and pushing up and backwards) no bark was consumed; it was left hanging in shreds or lying on the ground. It has been shown that this damage is unrelated to tree species, tree size or location (Carter 1981); in some cases over 90% of the trees in a compartment are damaged in this way and this hardly suggests the marking of a territory boundary. Trees are also scored on several occasions and some of the most severely damaged specimens are the result of damage inflicted over several years.

In 2½ years and four rutting seasons, only three stag fights were recorded (all heard, none seen) although fights must be more common than this suggests, viz. broken antlers.

However, the level of fighting is not consistent with the territorial defense that might be expected if the degree of overlap proposed above is to be avoided.

iii. Calling

It was stated earlier that the rutting season was advertised by the increasing frequency of the stag calls.

The exact function of the call is unclear. It has been suggested that in red deer it is a means for potential protagonists to assess each other and the likely outcome of combat (although it would be surprising if individuals assessed their opponents on the pitch of their roars since the fighting ability varies during the rut and declines with age while the pitch of the roar seems to remain approximately constant after they attain full body size -Clutton-Brock et al. 1979).

Sika stags may call as often as twenty times per hour but never approach the two roars per minute reported for red deer (Clutton-Bock and Albon 1978). The relatively low level of fighting observed may occur because these do not defend their territories; they may meet less often because of the dense undergrowth in some areas and therefore seldom assess each other's fighting ability so call less frequently.

The loud calling of the males in the rut is not the only vocalisation heard at this time of year. On a number of occasions two males were seen together walking along parallel routes with their heads tipped right back and their chins extended; each producing a deep gurgling noise. This behaviour pattern seems almost identical to that reported for red deer (the parallel walk of Clutton-Brock and Albon 1978) and was in this case invariably halted by the withdrawal of one of the males. In the red deer this is suggested as the second process whereby the likely outcome of combat is assessed and the weaker animal given the chance to retreat.

iv. Mating

No copulations were observed during this study although the chases reported by Horwood and Masters (1970) have been seen. It is suggested by Horwood and Masters that when a stag attempts to mate with a hind in oestrus, she is either receptive to his attentions or she bleats and runs away. This bleat is claimed to trigger a chase in which stags from neighbouring areas participate; the strongest male eventually covering the hind. The part of this pattern of behaviour observed in the New Forest on several occasions was a rapid chase led by a hind (bleating plaintively) on one occasion with three mature males and a brocket close behind. The animals were rapidly lost to view so the outcome is unknown.

The sex ratio has been determined at around four hinds to one stag but it was suggested that the breeding ratio is much higher than this; in the region of twelve to one. Horwood and Masters (1970) report that master stags frequently have attendants and they also suggest that these lesser animals may be involved in matings whilst the dominant male is otherwise engaged. This is as reported in the red deer where males between the age of 2 and 5 years seldom hold harems during the peak of the rut but instead associate with the harems of dominant animals and attempt to abduct hinds when the master male is distracted (Gibson 1978). This strategy, referred to as kleptogamy appears to be largely unsuccessful although it may allow the adolescents to learn the behavioural skills required for the successful handling of hinds (Clutton-Brock and Albon 1978).

The same general pattern is found in the New Forest sika for a mixed sex group may contain a master stag, one other mature male (generally with fewer tines on the antlers) and one, exceptionally two, brockets. These other males are tolerated by the master stag, but are always displaced by him. However, these males do not associate with him for long, only following the hinds and feeding with them for a brief period before leaving the group. No two mixed sex groups (formed round an identifiable male) ever held the same satellite males in consecutive records.

In Dorset the stags are reported not to feed during the rut (Horwood and Masters 1970) although most of the data in Horwood's reports (1969 and 1971) is derived from one driven circuit around the fields during the night, invariably before midnight and it is possible, though not very likely, that feeding occurs in the plantations or in the fields, later in the night or in the early morning. During the rut, red deer males in Scotland fed for less than 5% of the total 24 hours (during the rest of the year the norm is 50%). These red stags may lose up to 20% of their total body weight over this period (Mitchell et al. 1976) and it is thought that it is this declining body condition, associated with changes in hormone levels which produces the abrupt end to the Scottish rut (Lincoln 1971).

That stags apparently do not diminish in condition so dramatically in the South of England, although so few are killed that no actual figures can be offered. This coupled to the fact that they are seen feeding as often as not (although the value of the feeding bouts cannot be estimated) may be why the New Forest rut seems to tail off gradually as the different stags, not quite in synchrony, end their activities.

v. Conclusion

It is possible that a combination of the harem and the territory operates here. Horwood and Masters (1971) showed how limited was the home range of a population of marked hinds at Purbeck. Some anecdotal records of hinds in the New Forest (obtained from a female with a tattered ear and a second hind with a very tiny ginger calf) suggest that these females do not venture far either. This being the case, and there being no nightly migration to cause the hinds to cross the stag territories (as at Purbeck - Horwood and Masters loc. cit.) there would be no advantage in the stag holding an exclusive territory as the hinds would be there whether the area was defended or not; the minimal amount of fighting would occur when two males found a receptive female at the same time. Equally, as the rut occurs during the autumn when food resources in the woods are plentiful (acorns, fallen leaves and grass) fair-sized collections of deer may accumulate to exploit these (a feeding strategy not usually possible in these areas because of unacceptible levels of intra-specific competition). To find hinds in season a male would only need to patrol an area holding these food supplies. That each "male area" shown includes a variety of habitats, none exclusively and none excluded, is acceptible under this interpretation for the hinds are feeding in all habitats at this time of year (see Chapter 2). If not tied by the pressures of defending a territory, a stag would be able to invest more time in searching for females and to following those about to come into oestrus, but he would also have time to feed and by maintaining his condition be able to prolong the rut to cover those hinds who come into oestrus late. He would also be better equipped to withstand the winter; not severe here in Southern England, but very severe in the native Japan.

It has been suggested that stags return to the same rutting stand each year (H. Cutler pers. comm.). One particular stag (with a very wide angle separating the antlers) was recorded in three successive years in the same area of woodland but was never found in the period between the ruts.

No rutting stands of the type described by Bromley (1956) were found in the New Forest although Horwood and Masters (1970) suggest that, in Purbeck, "..most, if not all territories have a focal point which can perhaps be described as a rutting stand comparable with Bromley's "platform", where one or two patches in close proximity to one another are cleared of vegetation and flattened.."

That nothing remotely resembling these stands was found in the New Forest is consistent with the idea of the wandering stag pursuing hinds in oestrus attracted to his temporary home range by food resources.

CHAPTER SEVEN

Review and final discussion

REVIEW AND FINAL DISCUSSION

INTRODUCTION

The social organisation, feeding habits, patterns of habitat use and social behaviour of sika deer have been investigated in two areas in southern England which support different vegetation types. One, the New Forest in Hampshire, is predominantly deciduous woodland, the other, Purbeck Forest in the Poole Basin in Dorset, is an extensive area of commercially managed coniferous plantation.

The main aim of this work was to investigate the ecology of this introduced species to supply information upon which an effective management policy might eventually be formulated. The need for information on these deer has become particularly urgent recently as they are spreading rapidly through the north and west of Scotland and also hybridise readily with the native red deer (Harrington 1973, 1974).

In order to establish a framework for fuller discussion of the results reported earlier in this thesis it is convenient to present a summary of the main findings here. Although this will involve some repetition of previous sections, it was felt that it would be helpful to review the main conclusions before discussing them in more detail.

REVIEW

1. Habitat occupation

Details of habitat occupation by sika deer in the New Forest were investigated during 26 months of transect surveys, some carried out on foot, others by car.

A seasonally changing pattern of habitat occupation was revealed with the majority of animals occupying the oakwoods during the entire winter, continuing to use the oakwoods after dark in the summer, but moving around in the daylight to make extensive use of many habitats and, in particular,prethicket.

Minor habitats like fields, rides and felled areas received varying amounts of use, usually being exploited more in the summer than in the winter.

An identical survey was conducted amongst the commercial coniferous plantations in the Poole Basin, although for only eight months, and a seasonally unchanging cycle of night exploitation of cultivated fields and daytime use of the extensive, thicket-stage plantations, was observed.

2. Habitat utilisation

a. Activity related to habitat

Detailed analysis of data collected on the driven transects revealed that most of the observations collected in both study sites were of deer feeding. It also appeared as if the animals in the New Forest spent more time lying up during the winter than during the summer.

These findings may be because animals feeding are more easily found than those, for example, that are lying down and ruminating. It is also possible that this is a valid result in that the areas surveyed were selected mainly for feeding. The regions sampled on either the driven or walked transects are by necessity slightly more open than other parts of the same habitat and by being nearer the edges of the compartments, may be more exposed and more disturbed so less ideal for ruminating. That more deer are found lying up in the winter may also be a valid result, or it may be merely because the vegetation has died back and deer further away from the compartment edges can be seen.

However, seasonal differences in habitat use were found in that animals do not lie up to ruminate in exposed situations (for example, fields, clear-felled areas) in either daylight or at night during the winter but prefer to remain in shelter. In the summer, animals from both study sites were found lying up in all habitats.

b. Activity rhythms

Some of the data collected in the New Forest suggested that the sika deer there showed a feeding rhythm with either an eight or a twelve-hour periodicity. It might be expected that the longer period would correspond to the winter when poor quality and reduced availability of forage would induce longer feeding periods followed by longer periods of rumination (Hungate 1966). In the summer when forage is more plentiful and more digestible, a full rumen would be achieved more rapidly and a shorter period of rumination would be required before feeding could resume. This theory was not supported by the data as the different periodicities were encountered irrespective of season. It is possible that these rhythms are artificial and are partly the result of the excessive contribution of feeding animals to each sample with inadequate numbers of ruminating deer found to provide a meaningful division of the data.

A feeding rhythm was observed during the summer at Purbeck as here deer remained in the fields all night, but lay down to ruminate four or five hours after starting to feed. It is likely that this rhythm persists throughout the year but it was not observed in the winter as then, perhaps by being under stress from the weather, the deer return to shelter in the thickets so are not found.

3. Diet

Investigation of feeding habits from monthly collection of faeces (and winter analysis of rumen contents) showed that the diet of the New Forest sika deer changes from season to season. In the summer the animals could be classified as grazers although a fair proportion of leaves and a small quantity of *Calluna* is also taken. During the autumn the acorn crop (if available) is heavily exploited, the intake of leaves increases whilst grass consumption gradually declines. During the winter, leaves, *Calluna* and pine needles provide the staple intake with a small amount of grass. As spring approaches and the "fresh bite" emerges, grass is once again in the diet as a major component.

No deer were shot at Purbeck to yield samples for this study but the vegetational similarities between this area and Wareham suggested that these animals would feed in a similar fashion.

Faeces could have been collected at Purbeck using dung accumulation plots that would also yield an indirect and cumulative measure of habitat occupation (as they did in the New Forest and at Wareham). These could have been analysed microhistologically to describe the diet of sika deer here. However, no dung accumulation plots were established at Purbeck as the greater diversity of habitat available at Wareham was already being assessed in this way when the Purbeck survey began. To have moved the quadrats from Wareham would have resulted in a small amount of data from both areas and as extensive diet determinations were already being carried out at Wareham using rumen content and faeces, supplementing this with material from Purbeck was thought to be unnecessary.

At Wareham the diet was shown to be seasonally unchanging with a high intake of grass and Calluna throughout the year but very few pine needles. Further comparisons with the diet of sika deer in other coniferous forests (in Scotland) showed that a grazing habit appears to be the norm. Feeding site and faecal examination of sika deer in their native Japan (Takatsuki 1977, 1980a and 1980b) yields the same finding and it would seem as if, by consuming extensive amounts of coniferous browse, the New Forest animals are unusual.

4. Population structure and organisation

a. Structure and growth

As a result of the enormous difficulty encountered in assigning the deer at Purbeck to age and sex classes, the majority of the details on population structure and organisation have been derived from the more extensive records collected in the New Forest.

Observational data were analysed to yield the structure of the New Forest herd where 56% of the population consists of mature females, 14% stags, 22% calves and 8% yearlings. These details were collected during the autumn when most calves had been born and when (as far as one can tell) most of the males are in the study area. (The mature stags are not found for much of the year and are thought to spend the spring and summer replacing their antlers on the Brockenhurst and Beaulieu estates to the west and east of Frame, respectively.)

These population proportions can be manipulated to suggest a sex ratio of four females per stag, and a breeding ratio (bearing in mind the structure of the breeding group - see Chapter 6) of about twelve hinds per stag. Fecundity is also estimated from observational data at about 40% and total calf mortality (derived from changes in seasonal population ratios) seems to be about 30%.

In the Frame Heath Inclosure herd 11% of the mature hind cull was infertile and overall fecundity was 84% (n=38). This is slightly lower than at Wareham where 92% of the culled animals were pregnant (n=31). The New Forest figure differs enormously from that derived from field data probably because the cull data takes no account of late abortions, winter and early spring calf mortality, and still-birth (very few animals were shot after the end of January). It is also possible, although extremely unlikely, that as different aged and sexed animals have different susceptibilities to guns, (as Roseberry and Klimstra (1974) showed for white-tailed deer) hinds in calf are more easily shot than those that are not.

In the New Forest 45% of the mature sika hind cull was breeding two years in a row (being both pregnant and in milk) whereas 36% of the Wareham cull was in the same condition. Here, though, none of the hinds appeared to be infertile.

Similar observational results were collected at Purbeck although a very small proportion of the sightings were assigned to the broad age and sex-classes used. Nonetheless, it was proposed that 47% of the population consists of mature hinds, 30% calves, 16% stags and about 8% yearlings. A fecundity of around 63% is tentatively suggested but speculation on the degree of mortality (estimated at 30%) is not really very valuable because of bias in the data.

These details can be reinforced with results from culled animals, but as none was available from Purbeck, Wareham details have been substituted. One does not suggest by this that the population structure and growth at Wareham and Purbeck are the same; the data are used only in comparison with the New Forest.

b. Social organisation

An annual cycle in group size, irrespective of habitat, was shown for the New Forest sika with a relatively solitary existence proposed for the females between the end of the winter, when large small-deer groups form, (locally, hinds and followers are known as small-deer) and the rut, when the stags seem to create larger assemblies of animals.

The males in the New Forest are also shown to lead a solitary life and the mean monthly group size of all-male assemblies is always less than that of small-deer groups. The latter are undoubtedly based upon the hind and calf, or the hind, calf and yearling. Mixed-sex groups, containing at least one mature male, are always larger than either of these others, irrespective of the time of year.

Feeding aggregations are effectively assemblies of these basic units and as such, the overall composition of the group is not affected by its size. However, the inclusion of the mature male may provide a focus for these assemblies and in the New Forest this occurs irrespective of the habitat, or of the time of year.

The relationships between group size and habitat type was investigated and the inverse relationship between cover density and group size, proposed for other ungulates (eg. Jarman 1974), was displayed by data collected at both study sites. Not only that, but the mean group size found in a habitat type common to both areas, (eg. rides, oakwoods, fields) was the same. This point will be followed up later in the discussion.

5. Social behaviour

Some observations of the behaviour patterns displayed by sika deer were collected as they occurred during the other surveys, and although the number of interactions noted was small, a few points may be raised.

It was proposed that the social unit amongst the New Forest sika deer is the hind and calf and this may be supplemented, occasionally, by a yearling. It is likely, though not certain, that this system operates at Purbeck too, as was discussed by Horwood (1971).

The existence of a dominance hierarchy amongst the hinds was proposed; suggested by the even spacing of feeding individuals, the apparent ease with which some hinds are displaced and the lack of fighting between females that might be associated with the establishment of such a hierarchy.

Stag behaviour in the New Forest was investigated during the rut (too few males being found at other times for many details to be collected) by plotting sightings of individual animals; recognised by their antler characteristics. Stag home ranges in the New Forest were shown to be overlapping and the use of wallows was also found to be catholic. When these details were coupled to the relatively low calling and fighting rates it was proposed that these animals did not defend a territory, nor did they select hinds for a harem; they seem to patrol areas of superior food quality and cover hinds in oestrus when they find them.

This seems to be a very negative strategy and offers no explanation whatever for repeated sightings of distinctive animals in the same location in successive years, nor does it fit in with reports of stags "rutting" in areas recently clear-felled (F. Courtier, pers. comm.). However, as hinds have been shown to have a relatively limited home range (Horwood and Masters 1981) and as the population densities in the New Forest are so high and competition, therefore, is so severe it could be argued that the greater the investment of time in mating, the greater would be the benefit to the individual stag.

In an area of intensive competition for mates, the defence of a territory would normally be the best strategy. However, if the denseness of the undergrowth hinders the formation and maintenance of a large territory, as Loudon (1979) claims in roe deer, and if the hinds remain in a small area in the New Forest (there being no diurnal migration to feeding grounds) so may not travel to a rutting stand, then surely the stag optimises his reproductive ability by remaining mobile?

At Purbeck, very few details of social interactions and behaviour were recorded, mainly because the animals were frequently too far away to allow reliable recognition of hinds, calves and yearlings. In the large feeding aggregations found in the fields, no familial attachments were recognised and no changing patterns of social groups, as is described above for the New Forest sika, were observed.

DISCUSSION

1. Habitat occupation explained

During the summer the majority of the sika deer in the New Forest feed in small groups in prethicket areas (although all habitats are used to a certain extent), exploiting the extensive forage supply, and benefitting from the security of the relatively dense habitat. Diet at this time of year shows a high intake of grass and leaves (forbs and tree leaves being indistinguishable) and these items are readily available in all habitats.

At night, still in small groups (based upon the hind and calf, perhaps accompanied by a yearling) many animals are found lying up in the oakwoods or benefitting from the shelter of the extensive polestage areas. A few deer may be found ruminating in the open.

In the autumn, when acorns and leaves fall, the characteristics of a large part of the New Forest habitat change rapidly. Oakwoods are poorly represented at Wareham and Purbeck and seasonal changes in the vegetation are less marked here.

In Frame, the prethicket still provides a good food supply but is inferior in quality to that offered by the oakwoods which also provide a considerable amount of shelter. Unlike the rest of the year when it could be suggested that the need to reduce intra-specific competition precludes the formation of feeding aggregations in this habitat (the consequence of the widely dispersed forage here) the relative abundance of acorns and leaves allows larger feeding groups to collect. This time also coincides with the rutting season and it has been suggested that the males provide a focus for the accumulation of groups of small-deer (see Chapter 5).

The use of the oakwoods and polestage habitats in the New Forest increases at this time and the exploitation of the other habitats declines not only because of the distribution of food supplies, but probably also because of the need to reduce heat loss; achieved in these more sheltered areas.

At Purbeck, a seasonally unchanging pattern of habitat use is observed with the deer spending the majority of the daylight hours in the thickets and the nights feeding in the open habitats, particularly the fields. Although no determination of diet was undertaken for the Purbeck animals, diet at Wareham (vegetationally very similar) is seasonally unchanging, being mainly of grass and Calluna.

Grace and Easterbee (1979) have shown that heat loss in red deer is reduced by the presence of a canopy overhead. Staines (1970) suggests that the gross winter distribution of red deer in Glen Dye was largely associated with the availability of good shelter from wind and not by the quality and quantity of food, although he also proposes that red deer tolerate more rigorous conditions whilst feeding, than when at rest. Hammerstrom and Blake (1939), discussing white-tailed deer and Robinson (1967) writing about roe deer, suggest that the animals feed upon less palatable species when inadequate shelter influences areas of superior forage.

During the autumn and winter, food supplies in the New Forest are limited and after the acorn crop has been exhausted (or earlier, if it fails) and the fallen leaves are decaying, the diet of the Hampshire sika deer contains a significant quantity of pine needles and Calluna. These are available from a variety of habitats but needles and bark, in particular, may be obtained from areas of forestry operations. The diet contains little grass now; Molinia has died back and the ponies have competed successfully for much of the remainder although even they consume considerable amounts of gorse and holly during the latter part of the winter (Putman et al. 1981).

It could be argued that as food resources are more thinly distributed during the winter in the New Forest, the amount of time invested in feeding would be greater than in the summer. Data are not available to support or to contest this, but the feeding rhythms described earlier do not conform to this suggestion.

That more animals are found lying up and that these seem to be lying up for longer in the winter in the New

Forest may be because they really do so, or it may be an artificial result brought about by the death of the vegetation and the improved visibility in sheltered regions. The range of habitats used for this activity is narrower in the winter and deer ruminating are rarely found in areas other than oakwoods and polestage areas. At Purbeck fewer deer are found ruminating in the fields at night in the winter (where deer are always found feeding) than in the summer. It is likely that, suffering the same stresses as the New Forest animals although benefitting from a more continuous, higher quality (if exposed) food supply, the deer feed in the open and retire to shelter and to ruminate in the thickets. That the fields were not found empty during the night was because not all the animals feed and lie up in synchrony and that those retiring are replaced by others emerging. If the deer are ingesting poor quality feeds in the winter (see Chapter 4), particularly in the New Forest where needles, *Calluna* and bark are major food items at this time of year, they may well require a lengthy period of rumination to achieve adequate breakdown (Hungate 1966). This necessity may also result in an effective heat conservation strategy.

Heat loss is reduced whilst lying up in sheltered areas (Staines 1976, Gatenby 1977, Grace and Easterbee

1979) and it is possible that in some conditions to remain static is more beneficial than expending energy searching for low quality forage that does not repay the investment.

So, in unfavourable conditions one might expect to find a reduction of the numbers of animals in open areas and if lying up, deer are more likely to be in the oakwoods and polestage areas. The prethicket, although holding vegetation tall enough to reduce the windspeed very considerably (Grace and Easterbee 1979) has been grazed down to such an extent by deer and ponies that it is no longer a favoured resting area.

Jackson (1974) worked on the feeding behaviour of fallow deer in the New Forest and considered a statistical analysis of the effect of the weather on the animals' behaviour was inappropriate. The data in the present study was collected in an organised fashion and would seem to be suited to a comparison between the numbers of deer found under one weather condition and the number of deer found under the opposite condition (for example, rain:dry, windy:still). Unfortunately, as much variation was found in the results collected under identical conditions as under opposite, so the evaluation was not possible here either.

A daily weather record was collected by residents of Frame Heath Inclosure and details from this (see Chapter 2) were used to determine how representative of a month were the weather conditions encountered on survey occasions. The extensive survey in the New Forest was found to be representative of the weather conditions as a whole, so it was suggested that the animal activities and the habitat occupation patterns reported were representative of the month as a whole. At Purbeck, because of the smaller number of survey occasions and because of the exaggerated effect of bad weather (particularly influencing visibility) upon the data, the results here are probably not representative of the month as a whole. As the pattern described each month is so similar, however, this may not be as serious a defect here, (where the diversity of habitat is fairly low,) as it would be amongst the more varied habitats in the New Forest. Thus, anecdotal reports on the effect of the different weather conditions on the behaviour of the deer in both study areas were offered; and these conform well to those already published in the literature.

Finding deer in the winter, particularly when lying up, is enhanced by the death of the vegetation and it is hoped that possible bias caused by this is compensated for in the occupance calculations.

It is obvious that those habitats that were sampled the most extensively might be expected to yield the greatest number of sightings. To reduce the bias created by this, each month's data was converted to a number of animals located per unit area surveyed. Even this is not an adequate measure though, for not only does it merely report the observed impact of deer on the vegetation type (and not the status of the population as a whole) it is susceptible to enormous fluctuations; the result of the movement of a few deer from a small area of one habitat to a small area of another. Thus, although each "density" was calculated to take account of the different visibility in each habitat, the value of the result was enhanced by multiplying it by the total area of the vegetation type available and so producing the theoretical population held in the habitat. Some of these values were blatantly absurd, but when expressed as a percentage of the monthly total, the values gave an indication of the status of the entire population and not just of those animals in the sample, so allow valid comparisons to be drawn between habitat types in terms of the level of occupance sustained. If the calculation is carried out with more detailed data, using animals lying up in each habitat each month rather than all the animals in each habitat each month, for example, then valid comparisons can be made between the proportion of the population lying up in each community type, within or between months (see Chapter 2).

In the winter the animals' coat colour is cryptic, weather conditions are more severe and, of course, the nights are longer so search conditions are as difficult as in the summer (if not more so). A small bias in the data may exist and the occupance calculations may not compensate completely for the differences in the areas surveyed, but it is proposed that the finding that more deer lie up in the winter in the New Forest is a genuine result.

It is therefore suggested that in the south of England conditions are rarely severe enough to modify feeding behaviour for long periods, and it seems more likely that the quality and distribution of the food governs the behaviour of the deer as much as do weather constraints and the need for adequate shelter.

2. Food choice?

In order to offer explanations for the food habits of the sika deer, extensive monthly analyses of forage chemistry and quality were undertaken and correlations attempted between these details and the importance of the feed in the diet. The annual diet of both the Wareham and New Forest sika deer was determined by analysis of epidermal fragments remaining in the faeces. Information on food intake during the winter was supplemented by analysis of rumen samples.

In both areas correlation between the annual dietary profile and the nutrient status of the component forages was unconvincing. In many cases it was felt that the correlation obtained was more the result of food being ingested in relation to its availability and that this was, itself, related to its nutrient status; particularly in the case of deciduous plants like Molinia. The failure of many species to correlate successfully was because they were consumed when they were below their own optimum although they may have been superior in quality to others available at that time. For example, holly and gorse are consumed during the winter when their digestibilities are higher (about 50% and 42% D.M.D. respectively) than other feeds but their nutrient levels, (particularly nitrogen) are considerably lower than earlier in the year. At that time other, higher quality forages (not protected by spines) were available and so were selected.

The alternative correlation, calculated between the nutritional quality of a food species and its importance within the diet, within a month, was attempted and this also failed. This was undoubtedly because the availability of some feeds (probably partly due to competition from the ponies and from other deer) was too low to enable them to be taken in relation to their quality.

As both these correlations failed it could be suggested that the deer are opportunistic and in support of this the New Forest diet did correlate very well (see Chapter 4) with the availability of some forage species when expressed in terms of the area of ground likely to produce them. An equivalent correlation was attempted at Wareham but failed because here the deer exploit the superior quality of the cultivated fields and virtually ignore the extensive supply of coniferous needles. Dietary intake fails to correlate to nutrient status as, by feeding in these areas throughout the year the diet is unchanging although the nutrient status of the feeds change with the seasons. Here, therefore, forage selection is probably based as much on distribution and accessibility as on quality.

Hofmann (1982) classified the sika deer as an "opportunistic feeder" on the basis of rumen morphology and the same conclusion was reached independently here from an assessment of diet. In their native land sika are reported to feed on grasses. Takatsuki (1980) used faecal and feeding site examination to investigate diet and suggets not only that the main dietary component is grass, but that dietary composition varies considerably between vegetation types; a result closely allied to that reported here. Robinson (1973) reports the Lake District sika to be grazers, as do Prisyazhnyuk and Prisyazhnyuk (1974) working on Askold Island. Furubayashi and Maruyama (1977) find that sika in the Tanzanawa Mountains in Japan consume 106 species of which 34 are grasses and forbs.

It appears, therefore, that by relying so heavily on coniferous browse (up to 23% in the winter: March 1980), the Hampshire animals are unusual in their feeding habits. This was pointed out by Horwood and Masters (1970) after examining about 200 Dorset rumina and six New Forest rumina; the latter collected in February. Whilst the findings in this study do not support their blanket classification of the New Forest deer as browsers, the suggestion that the Dorset sika are grazers is vindicated.

In the New Forest the ponies are officially excluded from the Inclosures but in practice they are free-ranging and consume so much of the ground vegetation that the practice of cutting the grass on the rides to reduce the fire-risk (common until a few years ago) is no longer necessary. In the summer forage productivity is sufficient to support off-take although some areas of the open forest are very heavily grazed indeed (see Putman et al. 1981). In the winter the ponies, by virtue of their opposed incisor teeth, can graze closer to the ground than the deer and as their intestine relies upon a rapid throughput of large volumes of material, it might be expected that large amounts of graze will be rapidly consumed. It seems as if the deer cannot compete effectively and this may be why they feed on coniferous browse; a resource not exploited by the ponies (Pratt, pers. comm.). This situation is not encountered elsewhere as competition is not as severe and the more usual diet, grass, is maintained.

3. Nocturnal?

Horwood and Masters (1970) propose that sika in southern England are nocturnal. In this report it is suggested that this is not entirely accurate as a considerable level of activity was observed amongst the New Forest deer throughout the day and night, particularly in the winter.

The nocturnal lifestyle of the Purbeck deer was observed for part of the study in that during the winter few animals were found outside the plantations in daylight, but many were found feeding in the fields at night. It seems as if, by selecting the extensive forage available in these cultivated fields, the deer are forced to feed at night to avoid the inevitable human disturbance.

Thus, to benefit from good feed supplies the nocturnal lifestyle is a necessity here during the winter but in the summer, when nights are shorter and long periods of daylight are free of human disturbance, considerable numbers of animals are found feeding in the open in daylight (for up to 2 hours after dawn and also an hour before dusk).

In the New Forest there is no equivalent field system so maybe the higher level of activity recorded is because here the deer have to feed throughout the 24 hours. The investment of time required may be reduced by adopting an opportunistic strategy so exploiting transient feed supplies but the advantage gained by this may be cancelled by competition for similar resources from the ponies.

Counter-argument suggests that in the closed habitats of the Dorset plantations, it is merely the fact that the deer cannot readily be observed except when they emerge into open fields during the night which leads one to propose a nocturnal activity pattern. In the New Forest, where all community-types offer reasonable visibility, activity was observed over the entire 24 hour period. Had the deer at Purbeck been as accessible in all vegetation types, activity over the full 24 hours might have been reported here although, unlike the New Forest, they were not seen on the rides or in small, sheltered clearings during the daytime.

4. Group size in relation to habitat

Earlier, it was stated that the inverse relationship between feeding group size and habitat density common to many species of ungulates (eg. Jarman 1974) has been found amongst the sika deer of both study sites. In the New Forest the annual mean group size found in fields was 3.45 (±1.8) whereas the annual mean group size found in closed habitats, polestage, for example, is 1.74 (±0.289). These values are barely significantly different, but the trend, that of larger groups in more open situations, was found each month in the New Forest data. At Purbeck, where fields are better represented so yield a superior result, the mean group size found during the eight months of survey was 6.49 (±2.97) as compared to the mean group size in the thickets of 1.85 (±0.52). The mean group size found in closed habitats in Purbeck and the New Forest were not significantly different, nor were they in open areas nor on the rides ($p=0.05$). The latter habitat is classified here as neither an "open" nor a "closed" habitat by virtue of its proximity to cover and its (occasionally) overgrown condition.

Two hypotheses (not mutually exclusive) have been proposed to explain this relationship; one is based on predator defense strategies, and the second on feeding strategy (coupled to the avoidance of intra-specific competition).

Work by Jarman (1974) on East African antelope and gazelle suggested a clear correlation between social group size, social organisation and various ecological parameters; notably feeding style and predator defense.

For example, small antelope, feeding selectively on the young shoots of a limited range of tree species, tend to be found in small group sizes and are territorial. As a direct result of their selectivity their food supply is sparse and so a particular area can only support a small number of individuals. At the other extreme are non-selective grazers who feed on a variety of plant species in continuous swards. These are faced with an uninterrupted supply of forage (usually seasonal) and form large, mobile groups to follow the forage. Between these Jarman proposed a five-point classification with intermediate feeding styles and group sizes.

The argument gains extra credence from consideration of the differences within one species of animal found in areas of different vegetation. Jarman himself cites the example of the African buffalo (*Synceros caffer*) which lives both in the savanna and in the forest. In these habitats both quantity and dispersion of food are distinctly different and a regional variation in group size, with larger groups corresponding to the more prolific food supply, is found.

Hirth (1977), working with white-tailed deer (*Odocoileus virginianus*), also reports highly significant differences between group sizes in three habitat types on one of his study sites; the largest groups were found in open areas with little or no cover. Jungius (1971) reports the same observation for reedbuck (*Redunca arundinum*) in South Africa, as does Walther (1972) amongst Grant's gazelles (*Gazella granti*) in the Serengeti. Franklin et al. (1975) report a decline in group size in Roosevelt elk (*Cervus canadensis roosevelti*) as they move from open prairie to forest cutovers. Takeo Ito (1968), working on sika deer on Kinkazan Island (near Japan), showed that the average herd size varies with season, topography and vegetation type, and he reports a mean group size of 5.8 in open fields and 1.7 in forest.

In this report the mean group size of sika deer in the open habitats, whether at Purbeck or in the New Forest, was found to be significantly larger than in the more closed thickets, prethicket or polestage communities ($p=0.05$).

In Britain it is more likely that the formation of large feeding groups in these open areas is to take advantage of the more extensive forage supplies and the reduced level of intra-specific competition, than it is to avoid predators.

In the New Forest feeding group size is shown to be affected both by habitat structure and by the availability of food. During the summer the feeding groups found in the oakwoods are small; usually of hind, calf and yearling. When the acorns and leaves fall in the autumn, group sizes increase as the more prolific food resources encourage larger aggregations to form as competition for resources declines. The prethicket areas are much denser than the oakwoods and although holding a continuous ground cover with a varied floristic composition, the visibility in the habitat is so low that large groups cannot form, being unable to remain in contact.

The sika are a relatively recent introduction to this country and have not yet adapted to the absence of natural predators; they probably never will, as their defence strategies would work equally effectively against humans. In support of the predator avoidance hypothesis the mean group size of sika deer in the New Forest in any habitat was found to be larger in the daytime than at night. It could be suggested that by being more widely distributed at night and if lying up (in dense habitats) by being in small, family groups, the chances of being found by a predator are reduced.

Deer at Purbeck seem to use the fields at night to avoid human disturbance, but even under the cover of darkness, when a predator-avoidance strategy might be less important, large aggregations form. Unfortunately, insufficient data were collected on deer in these areas in daylight to compare the mean group size under these two conditions. Such information as is available is inconclusive although the values tend to point to larger night-time aggregations.

5. Segregation of the sexes

The feeding strategies discussed above do not suggest reasons for the segregation of the New Forest male and female sika deer described in Chapter 2 and which was also discussed for the Poole Basin sika by Horwood and Masters (1970).

In the red deer the stags live separate lives for at least eight months of the year (eg. Lincoln et al. 1970, Clutton-Brock and Albon 1979). Reasons for this are unclear but a popular hypothesis is proposed based upon consideration of the nutrient status and quality of the forages available in each area.

Watson and Staines (1978) working at Braemar, Aberdeenshire, report that the ranges occupied by red deer hind groups over the winter had more base-rich rock and well-drained grassland than those occupied by stags. They suggest that wintering on rich ground probably gives a hind superior nutrition and so may improve the chance of survival of the foetus and later, the calf. That these are not displaced by the dominant stags may be because they have different nutritional requirements to those of the hinds or, having lost condition over the rut, the stags may require more shelter (possibly lacking in the better areas). Alternatively, those stags that allow the hinds access to better forage may be benefitted if the chances of their calves surviving are improved.

It has been shown (Staines et al. 1982) that stags and hinds adopt different feeding strategies with each achieving an adequate nitrogen intake; stags by being able to consume large amounts of poor quality feed and hinds by selecting higher quality material. The stags are thought to eat poorer foods because they are unable to obtain sufficient digestible material from heavily grazed swards. This problem is exacerbated by stags occupying areas with less grassland anyway, for reasons other than food supply; perhaps because of shelter and social requirements.

There is no reasonable parallel to this in the sika deer in the New Forest. Numbers of each sex shot were too low to allow a realistic comparison of diet between them (individual variation is considerable - see Chapter 4) and certainly nutrient content comparisons were impossible. It is unlikely that the males are in as poor condition at the end of the rut, in Hampshire or Dorset as is reported for red deer in Scotland (Mitchell et al. 1976). Males are seen to feed during the rut in the New Forest and do not appear to indulge in such frenetic activity as is reported in the red deer (eg. Clutton-Brock and Albon 1978).

It is possible that the stags have different nutritional requirements to those of the females during the spring and summer (when replacing their antlers) but they also remain with the hinds immediately after the rut and so share their forage at the time of greatest shortage. It could be argued, though, that at this time, although pregnant, the stresses imposed by the foetus on the female may be minimal compared to those imposed externally and that increased competition from the males may not affect the hind's condition, or the ultimate survival of the calf.

When the hind is under most stress, during the early spring, (whilst recovering from the winter and when heavily pregnant) the stags are no longer in the area and competition for the limited forage is reduced.

As the geology is unchanging from one compartment to another (the whole New Forest study area being based on sedimentary deposits) it seems likely that the forage quality varies but little. Ekins (pers. comm.) has found that on the open forest there are distinct differences in the digestibility and the nutrient status of plants from areas with different soil type, drainage, or previous management regimes. This is unlikely to result in the separation of the sexes reported here (bearing in mind the varied composition of the diet at this time of year).

It is suggested therefore, that in the New Forest and perhaps, at Purbeck, the males leave the hind areas during the spring and summer not because of more exacting nutritional requirements but to reduce the level of competition for feed (particularly in the high animal density in the New Forest) and so may benefit by assisting the survival of their calves.

6. Annual cycles in group size: group cohesiveness

Superimposed upon the different feeding group sizes found in each habitat is an annual cycle of social group size.

During the autumn the stags return to the study area in the New Forest to rut. During this time it appears as if larger mixed-sex aggregations are found but whether this is entirely due to mating behaviour, or is the result of a prolific autumn supply of feed, is unclear. The stags remain in the area at the end of the rut and larger groups of animals form as the males associate with the females and their followers. Group sizes gradually diminish after this as a general reduction in the availability and quality of forage intensifies the search for adequate feed. In February, March and April, in Frame, larger aggregations of animals collect with separate male and female parties forming in the latter months. The precise reason for this is unclear as forage is still scarce but when the stags depart with many of the immature males, competition for remaining food and for the new growth is reduced. The hinds are heavily pregnant by the end of May and the larger groups characteristic of early spring disintegrate. The animals feed extensively at this time and seem to lead a fairly solitary existence accompanied by last year's calf and, perhaps, a yearling. This is despite the fact that improved food supplies now encourage the formation of larger feeding groups. Calves are dropped from June onwards and hinds appear with their young when they are two or three weeks old and feed in slightly larger groups again.

Such a clear cycle was not observed at Purbeck where the majority of the records are of aggregations of deer feeding in the fields and within which familial attachments and changing patterns of social groups were not detected.

Horwood and Masters (1981) have shown, from their work on marked sika hinds at Purbeck, that the same animals may be seen feeding together in the same areas on several occasions - a finding that might be expected in the New Forest. They go on to suggest that although this does not imply that these deer are members of a tightly-knit herd, it is possible that they are members of a large community which feeds in the same fields at night but lie up independently (within hind and calf groupings) during the daytime, joining forces on the way to the feeding grounds, or once there.

Putman (1981) took the idea a stage further by suggesting that whilst there may be hinds who associate regularly, there may be equally well be some assemblies that never form. He proposes that those that are seen together regularly are members of a "super herd" or "clan", based on a specific area of woods and within which any group combination may occur. Animals from two separate clans, however, would not be expected to appear in the same group.

It may be argued, as Putman himself points out, that this is the inevitable consequence of a population of animals spread out in a large area of woods with limited, but peripheral feeding areas which, if reached by the shortest route possible, makes the formation of alternative groupings very unlikely.

However, Putman also suggests that as these feeding aggregations are so flexible in nature (within the limits he describes) it is likely that the basic social unit is quite small and that each of the larger aggregations is built up from several of these smaller units.

In this study it has been proposed that the social unit amongst the New Forest sika deer is the hind and calf, perhaps accompanied by a yearling, but without marked individuals no further comment can be made on the "super herd" ideas in this area. During the rut a certain amount of flexibility in group structure was noted in that the groups of animals accompanying individual stags (recognised by their antler characteristics) were never of the same composition on consecutive occasions; the rut may though be a special case.

It also appears as if a dominance hierarchy exists amongst the hinds. This supposition is based upon observations of evenly spaced feeding animals and the apparent ease with which an individual may be displaced from a feeding site.

The existence of a hierarchy does seem rather unlikely if one considers the solitary tendency of the hinds, and the fact that the feeding aggregations within which it was observed are temporary, so may not contain the same individuals on consecutive occasions. This latter point is discussed further by Horwood (1971). Whilst watching white-tailed deer (*Odocoileus virginianus*) feeding at cutting sites, Ozoga (1977) finds the rapid establishment of a hierarchy with the obvious result that a minimum of time is spent fighting and the maximum feeding. If the "super herd" theory is to be accepted it could be extended to suggest that a hierarchy might exist within it. This could be gradually established over a number of meetings and might be maintained by signs too subtle for the casual ecologist to have detected. This hypothesis does rely upon the ability of the hinds to recognise each other and whilst one cannot discount the possibility, it is equally likely that the temporary feeding associations found at Purbeck, and in the New Forest, are governed by a rapidly established hierarchy that disintegrates as the deer depart. The alternative suggestion discounts all these elaborate theories and proposes that each animal maintains its own personal space and that although this might be interpreted as a hierarchy in operation, it in fact merely ensures even distribution of individuals and could be likened to a personal, mobile territory.

7. Population fecundities

It was reported above (Chapter 5) that the fecundity of the New Forest mature hind cull was 84% (n=38) but that the equivalent figure derived from population ratios collected in the field is only about 40%. Of the New Forest hind cull 10% was infertile. At Wareham the fecundity of the mature hind cull was 92% (n=32) and a conservative estimate from field observations collected at Purbeck suggested fecundity here was 63%. Whereas in the New Forest 45% of the hinds seemed to be breeding two years in a row (being both pregnant and lactating) only 36% would have done so at Wareham.

So there is a large discrepancy revealed between the fecundity estimates from these two avenues of investigation. It is possible that the field data is biased by incorrect identification of calves and small yearlings and it is also likely that the post-mortem sample is inadequate for a valid representation of the true situation.

However, shooting stops at the end of January so these details take no account of still-births, abortions, late winter calf death and neo-natal mortality. Staines (1978), writing about a declining population of red deer in Glen Dye in Aberdeenshire, reports that between 29% and 44% of foetuses and calves are lost between mid-pregnancy and two months post-partum; a period not assessed here by the cull data. Guinness et al. (1978) report that on the Island of Rhum 18% of new calves died before the end of September and a further 11% (making 27% overall) died during the winter and early spring. Both these findings support the total calf mortality estimate (derived from seasonal changes in the observed population structure ratios) of 30% in the Frame herd. Thus, with a high late winter mortality (expected, but not proven) plus an inevitable bias in field data, the discrepancy may be partially explained.

Mitchell (1973) considers the yeld red deer hind to be symptomatic of nutritional distress. He also suggests that whereas hinds clearly are capable of calving every year in some environments, a large proportion of Scottish hinds fail to do so and often take a full year to recover from producing and rearing a calf. When they do reproduce again, yeld hinds are in better condition than those that reproduced recently. Hinds in good condition achieve a high pregnancy rate and might be expected to be more successful with their calves (Mitchell et al. 1976).

No yeld hinds were shot at Wareham where the shooting pressure is reported to have been quite severe in the last few years (E. H. Masters, pers. comm.). In this area the population was found to be too low to yield an adequate number of sightings on the driven transects for habitat use to be meaningfully described. This was reinforced by the scarcity of faecal accumulation data collected in the same area for it could have been argued that the dense nature of the vegetation was concealing many of the animals. In the New Forest the observed deer density was high (between 290 animals per 1,000ha during the rut and 226 per 1,000ha outside) and here 11% of the hind cull was yeld. Red deer densities in Scotland are reported at between 28 and 153 individuals per 1,000ha (Mitchell 1973). The shooting pressure on sika deer in the New Forest has been relatively light recently (J. Ealing, pers. comm.) and coupled to this high density of animals are stresses caused by the competition for feed from the New Forest ponies (as was discussed earlier). It is possible therefore, that here the population has reached the carrying capacity for the area and population growth is reduced. This has manifested in yeld hinds shot in Hampshire and an apparent calf mortality equivalent to that found in Scotland where winter conditions are much harsher and a higher value might be expected. The overall fecundity at Wareham is higher than in the New Forest (92% and 84% respectively) but both these values are much higher than the 40 calves per 100 hinds generally accepted for red deer in Scotland (Mitchell 1973). Coincidentally this is the fecundity calculated from observations of the Frame population.

It is proposed that the Wareham sika deer are healthier and are breeding more rapidly than those in the New Forest as a result of intensive culling (undoubtedly supplemented by poaching which is very difficult to control in the more extensive plantations: R. McKinley, pers. comm.).

Finally, one should note that all these ideas are speculative and that wide variations are noted in the fecundity and mortality of red deer populations from one year to another (Mitchell and Lincoln 1973, Guinness et al. 1978) and a totally different interpretation might be revealed from the examination of data collected over the next four years. It also seems to be rather strange that, if the New Forest sika really are under stress, they seem not to be spreading into other areas.

8. The sika deer in southern England

Until recently the only major ecological research work carried out on the Japanese sika deer in Britain was that by M. T. Horwood on the animals in the Poole Basin in Dorset. Findings were variously reported (Horwood 1969, 1971 and 1973, Horwood and Masters 1970, 1981) and the work has been referred to extensively in these pages.

The result of the more recent, and more intensive research reported here is that some of the points raised by Horwood and Masters can be extended or contested and it is proposed to review these briefly.

a. Diet

The most commonly discussed finding of Horwood and Masters was that sika deer in the New Forest were described as browsers and the Dorset animals as grazers. In the report of the work (Horwood 1971), the (admittedly) shaky evidence from six stomachs culled from the Frame herd one February is offered against evidence from the macroscopic examination of two hundred rumina collected over several years in Dorset.

In the recent work sixty two rumina were collected from three winters of animals culled at Wareham and the contents were examined under low magnification. The composition of the contents was described volumetrically. One hundred and twelve rumina were collected over four winters from the New Forest and in both areas the annual diet was described from microhistological analysis of regularly collected faeces. The definition of the Dorset animals as grazers is vindicated, with the further detail that _Calluna_ provides an important food supply throughout the year. Pine needles are taken by the Poole Basin animals, but in low quantities and only in the winter.

In the deciduous woods in Hampshire the diet changes seasonally and in February these deer do indeed feed upon coniferous browse to a considerable extent; 23% of faecal content in February 1980. However, in the spring and summer, grass comprises around 50% of the intake and these animals cannot be classified as browsers on the strength of that; better to classify them as "opportunists" as has Hofmann (1982).

b. Social organisation

The social organisation of the New Forest sika seems to be based upon the unit of the hind and calf, frequently with a yearling; much as is reported in the red deer. This is in direct contradiction to Horwood's assertion (1971) that the "normal group of hind, yearling and calf were not seen..." When working at Purbeck in the present study this family grouping was again not observed. Bearing in mind the considerable distances over which observations were collected at Purbeck, the poor visibility and the difficulty experienced in separating hinds and calves, it is not surprising that family groups were not distinguished; particularly when recalling that most of Horwood's observations and many of mine, are derived from large feeding aggregations found in the fields. In this situation one would not expect to see family units as they tend to become merged with the feeding assemblies and only separate out when the larger groups disintegrate. The ideal habitat in which to observe these social units is prethicket or oakwoods where visibility is adequate for observations to be collected, but vegetation density, or forage distribution are such as to inhibit the formation of bigger groups of animals.

c. Social behaviour

Unfortunately, due to factors entirely beyond one's control, neither the Purbeck nor the Wareham survey studied the rutting season effectively. In the New Forest some details were investigated quite rigorously during two seasons and a set of very inconclusive findings was produced.

No evidence was found to compare with the rutting stands and territory markings that Horwood and Masters report for the Poole Basin deer, nor were many stag fights reported. The rut in the New Forest seems to be a "low-key" affair lasting for a couple of months and with a gradual decline as stags are heard calling until the middle of January.

Stag home ranges were plotted from sightings of individuals and although some were shown to occupy relatively limited areas, others clearly did not. Several of these "home ranges" overlapped and wallows seemed to be common property. Horwood and Masters (1970) suggest that the stags in the Poole Basin do not feed and that they remain in the compartments for the duration of the rut, emerging to feed in the fields at the end. One cannot be certain, bearing in mind the dense nature of the vegetation, (prethicket in Horwood's day, dense thicket now) that the males do not feed. During the earlier work there would have been more forage available within the compartments than there is now and anyway the majority of records were collected on an average of one circuit per week "...usually completed well before midnight.." On the basis of a more extensive survey with circuits conducted more frequently and covering all 24 hours, it is suggested that stags may well emerge later than the hinds. It is also possible that the males are able to acquire sufficient digestible forage from within the plantations; at least, for the duration of the rut. This would neatly parallel the segregation of red deer stags and hinds onto different feeding grounds where this different feeding ability is exploited (Staines et al. 1982). Stags were found feeding during the rut in the New Forest although the effectiveness of these feeding bouts is difficult to assess. Even the red stags in Scotland, who lose up to 20% of their body weight over the rut (Mitchell et al. 1976) feed for some brief periods during the rut; 5% of the 24 hours as against the more usual 50% (Clutton-Brock and Albon 1978).

It is clear that considerable gaps remain in the knowledge of the ecology and, particularly, in the social behaviour of the sika deer. It is also not certain to what extent the situation in the south of England may be extrapolated to that rapidly developing in Scotland where the formulation of an informed management policy for these animals must soon receive high priority.

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