Studies on the biology of the brown hare (Lepus europaeus) with particular reference to behaviour

Holley, Anthony J.F.

How to cite:

Holley, Anthony J.F. (1992) *Studies on the biology of the brown hare (Lepus europaeus) with particular reference to behaviour*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/6135/

Studies on the Biology of the Brown Hare (*Lepus europaeus*) with particular reference to behaviour

Anthony J. F. Holley

A Thesis submitted to the Faculty of Science
University of Durham
For the Degree of
Doctor of Philosophy
1992

ACKNOWLEDGEMENTS

I remember with warm gratitude my first supervisor, the late Dr. Paul Greenwood, for his inspiration and encouragement and I am deeply grateful to his successor Dr. John Coulson for much guidance, encouragement and support.

For comments upon drafts of some of the Chapters, my sincere thanks to Dr. Jonathan Adams, Dr. Richard Barnes, Dr. Tim Caro, Dr. Nigel Dunstone, Dr. John Flux, Dr. Jeff Graves, Dr. Tim Guilford, Dr. Ray Hewson, Dr. Hugh Kolb, Dr. David Macdonald, Dr. Neil Metcalfe, Dr. Pat Monaghan, Dr. Alun ap Rhisiart and Dr. Stephen Tapper.

For invaluable assistance with statistical analysis and presentation, I am indebted to my brother-in-law Dr. Thomas Hayton and also to Dr. Pat Monaghan and Dr. Neil Metcalfe.

I am very grateful to Jan Sweeney for the illustrations forming Figures 3 and 7 in Chapter 9 and to Stephen Tapper for the photograph at Figure 4 of Chapter 2. I am also pleased to acknowledge support and facilities provided by the Game Conservancy.

Many thanks to Cheryl Hicks who meticulously typed every word of each version of the thesis, to her mother Mary who assisted greatly in the preparation of the Figures, to my secretary Joy and finally to my sons Mark and Daniel for their interest and encouragement.

ABSTRACT

Behaviour of the brown hare (Lepus europaeus) was studied on the Somerset levels, U.K., between 1977 and 1987. The hare is exclusively nocturnal when nights are longest and part-diurnal when they are shortest but the transition is not smooth. There is a linear dominance hierarchy between bucks. The nearer a doe is to oestrus, the higher the rank of her escort. Some pre-partum does monitor the prospective birthsite. They are only occasionally escorted by bucks. In contrast, a non-monitoring pregnant doe was regularly escorted. Does lie up within 250m of their litters but take a more circuitous route when visiting them and detour when foxes are encountered. Four Autumn litters were suckled for between six and nine weeks. Sucking leverets usually sniff-noses when meeting up, followed by a short period of locomotor play after which they go quietly to the nursing point. Some weaned leverets continued to meet up. The principal component of locomotor play is 'streaking' - running top speed back and forth down a familiar route. Leverets disperse after nursing to a daily increasing extent. Leveret distress screams were audible from a distance of 550m. As a visible signal, the buck's white tail flag seems to serve no purpose. The doe uses her tail flag to lead her litter. Only does shake their tails which they do exclusively in the near presence of bucks; the bucks then sniff the ground underneath. Hares were not observed to signal to each other by body postures or to use their ears for purposes other than acoustic. Does convey a threat to bucks by flattening their ears and lifting their muzzles. Adults, particularly bucks, sniff a partner's nose for olfactory information as an alternative when the ano-genital region is inaccessible, but are frequently threatened when so doing. All chin-marking was by bucks of which 80% were solitary. Hares approached in the open by foxes stand bipedal when, on average, the fox is about 30m distant. The relevance of the behaviour patterns are discussed.

CONTENTS

CHAPTER 1

INTRODUCTION

The hare has been a subject of interest and, in some cases, reverence to man since the earliest times, depicted from paleolithic cave art onwards and across most cultures the world over. References to hares abound in the literature from the fables of Aesop to the Naturalis Historia of Pliny and the poems of Robert Burns. On the hare as an object of the chase, many chapters and whole books have been written. Yet, remarkably little of the behaviour of the genus has been understood, leaving a host of unanswered questions. Of the brown hare (Lepus europaeus), only 20 years ago those questions would have included - Are they crepuscular or nocturnal in their activity? Are they solitary or social animals? Do they have a ranking order? Why do they go mad in March? When do hares box each other and which sexes are involved? Why do they sometimes squat in a circle facing two in the centre? Do does drop their leverets singly or together? When do they suckle them and are the leverets then together or dispersed? Do does defend their leverets? Is the white undertail used for signalling and, if so, what is the message? Do they signal with their ears? How do they react to foxes? In the interval, Broekhuizen & Maaskamp (1980) have revealed much of the nursing behaviour of does and leverets. Schneider (1976, 1977a, 1977b, 1981, 1990) has addressed questions concerning social and reproductive behaviour and communication but his methodology, based primarily on cine and still photography, can cause interpretational errors - for example in identifying as a stereotyped display or signal-giving posture what is nothing more than the upward stretch of a newly risen hare. Lindlof (1978) and Monaghan & Metcalf (1985) revealed dominance hierarchies at artificial feeding stations and the latter also demonstrated that benefits attached to group vigilance. Of related species, Parker (1977) touched on aspects of behaviour of adult and leveret arctic hares and Aniskowicz et al. (1990) reported in detail on nursing behaviour of the species. Aspects of behaviour of the mountain hare were included in Flux (1970) and Hewson (1990) reported on social and reproductive behaviour including hierarchies and also behaviour of leverets. Lemnell & Lindlof (1981) and Bayfield & Hewson (1985) gave data on the daily activity period of the mountain hare. On the snowshoe hare, there were studies of nursing behaviour by Rongstad and Tester (1971) and of social organization by Graf (1985). Reviews of the literature on behaviour in the genus are to be found in Flux (1981) and Cowan & Bell (1986).

At the beginning of their book "The Leaping Hare", Evans & Thomson (1972) quote a fourth generation Suffolk gamekeeper, of forty years experience himself, saying - "we don't know the hare because we haven't observed it enough". In the final chapter of their book they say -

> "At the beginning of this book we suggested that the hare had not been studied enough; and at the end of our search, after listening to dozens of experts, it still appears that owing to its shyness and lonely habits and, at times, its inaccessibility it has not been sufficiently and precisely observed in its natural setting.... There is still many a gap in our catalogue of the hare's behaviour; and filling each of them would not be an easy undertaking. Yet it might be possible, after the various kinds of hares had been observed systematically over a long period, to clear up the contradictions and ambiguities that still exist in the various interpretations of its behaviour.... Traditional observation has not been evidence of a sufficiently full kind simply because there was not enough of it and by its very nature it was sporadic: neither the gamekeeper nor the ordinary countryman had the leisure or the incentive to make a detailed observation, over a long period, of any one animal, much less of such a difficult creature as the hare".

The study upon which this thesis is based has been entirely observational without involving any disturbance of the subjects, even that of catching and marking them. Field study of the brown hare is not easy. The animal has a large home range, usually involving a number of fields, with no central base or den. Its senses are sharp and its wariness extends to humans. When approached by the observer, it simply slips into the next field. In the first part of the breeding season all activity takes place during the long nights. In the later part of the season, hares are active by daylight but place themselves in longer vegetation. Many of these difficulties can be overcome by employing the methods used in this study of a fixed elevated observation point coupled with high powered optical instruments - and a lot of time. By these methods I have attempted to answer some outstanding questions and to point towards answers to others.

CHAPTER 2

STUDY AREA AND METHODS

Study Area

The study area comprised approximately 65ha of land, divided between 17 fields (Fig. 1) in the north western sector of the Somerset levels, close to Brent Knoll NGST 326527 (51^{o} 16' N, 2^{o} 58' W). The fields were predominantly pasture meadows, many of them unimproved, with a few of the improved fields being ploughed in rotation for cereal growing (Figs. 2 & 3). There were few hedges, fields being divided by drainage channels, the minor ones referred to as ditches and the major ones as rhynes (Fig. 4). Improved grassland fields were mown for silage and a crop of hay was taken from most of the remaining meadows. From April to early December young beef and dairy stock and some sheep were put onto those meadows which were not growing on for silage or hay.

Methods

Observations of the behaviour of brown hares within the study area were made during the period September 1977 to September 1987. For most of that time the population of the district was estimated at 10 hares/km^2. However, during the winters of 1980 and 1981 a

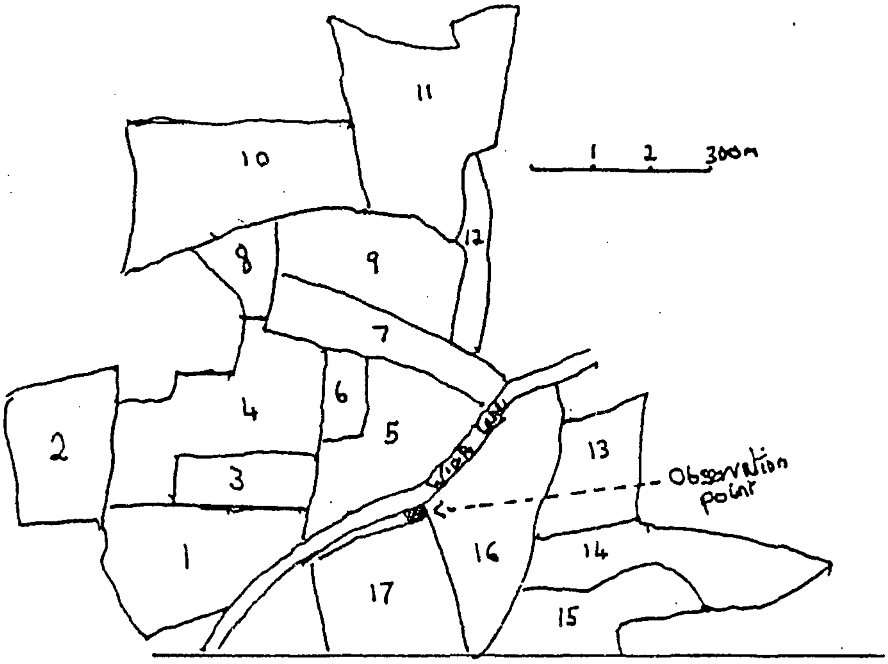


Figure 1. The 17 fields of the study area. Showing also the position of the author's house, the observation point.

Figure 2. Part of the study area including parts of fields Nos. 5, 7, 9, 11 and 12. Photograph taken from first floor.

Figure 3. Another part of the study area including parts of field Nos. 5, 6, 7, 8, 9 and 10. Photograph taken from roof conversion.

total of 30 foxes were shot for their pelts in the immediate vicinity and by 1982 the hare population had doubled. From 1983 onwards, the population dropped back to its former level.

All observations were made from my home, "Ferndale House", lying within the study area (Fig. 1). From 1981 to 1983, they were made from swivel windows on the first floor about 5m above ground level. From 1983 onwards, observations were from the specially converted roofspace of the house, at a height of about 9m. Figures 2 and 3 show photographs of portions of the study area which were taken respectively from the first floor and from the roofspace. One of the advantages of this method of study was that it involved no disturbance of the subject animals.

The optical equipment employed consisted of 7x50 binoculars, 15x80 tripod-mounted binoculars and a Zeiss Jena 20/40x80 binocular telescope. To that was added in 1980 a Celestron 8 inch catadioptic astronomical telescope, converted for terrestrial use, giving magnifications in excess of 100x. This instrument when coupled with a Canon AE1 was also used as a telephoto lens giving focal lengths of 2000mm and, with an extension tube, 2500mm. The photographs at Figure 1, Chapter 3, were taken using in one case the 50mm lens of the AE1 and in the other the 2000mm lens of the Celestron. In 1984 the Celestron 8 was replaced by a Celestron 11 with special terrestrial mounting (Fig. 5) and the AE1 by a Canon F1. The focal length of that combination was 2800mm and, with the extension tube, 3500mm. The very large objective lens of the Celestron enables a bright image to be obtained notwithstanding low light conditions. Observation was mainly during the earlier and

Figure 4. Drainage rhyne dividing fields 1 and 5. Gardenia jumped this rhyne each evening on her way to suckle her litter. (See Chapter 6).

Figure 5. Celestron 11 astronomical telescope on special terrestrial mounting.

later parts of the day which are the least affected by heat tremor, a problem encountered with the more powerful telescopes during the summer months. For photography, it was necessary to use fast film, 400ASA pushed up one or two stops. All photographs of hares reproduced in this thesis were taken through one or other of the Celestrons. Electronic night viewing equipment was not used, but with experience I was able to observe hares for up to 90 mins after sunset and up to 60 mins in the winter and for comparable periods before sunrise. I also observed them at night by moonlight and on snow. A spotlight was used on only one occasion, to observe the prolonged suckling of a leveret in October and November 1981 (see Chapter 6).

Following the acquisition in 1980 of the Celestron 8 telescope with its increased magnification and light transmission, I became able to identify individual animals either on a permanent basis or for at least part of a season. More than 60% of adult hares frequenting the study area over the period had ear damage in the form of permanent scars or tears or pieces missing. Examples of these appear in Figures 6, 7, 8, 9 and 10. Where possible, a permanent record of the individual in the way of a photograph showing the damage was obtained. In a few cases, where the individual was only frequenting a more distant part of the study area so that a detailed photograph could not be obtained, I prepared an ear damage diagram from inspection through the telescope at high magnification (Fig. 11). A few individuals, whilst lacking ear damage, were nevertheless distinctive by physiological features, such as particularly long tail or blunt ears or broad muzzle. The remaining occupants of the study

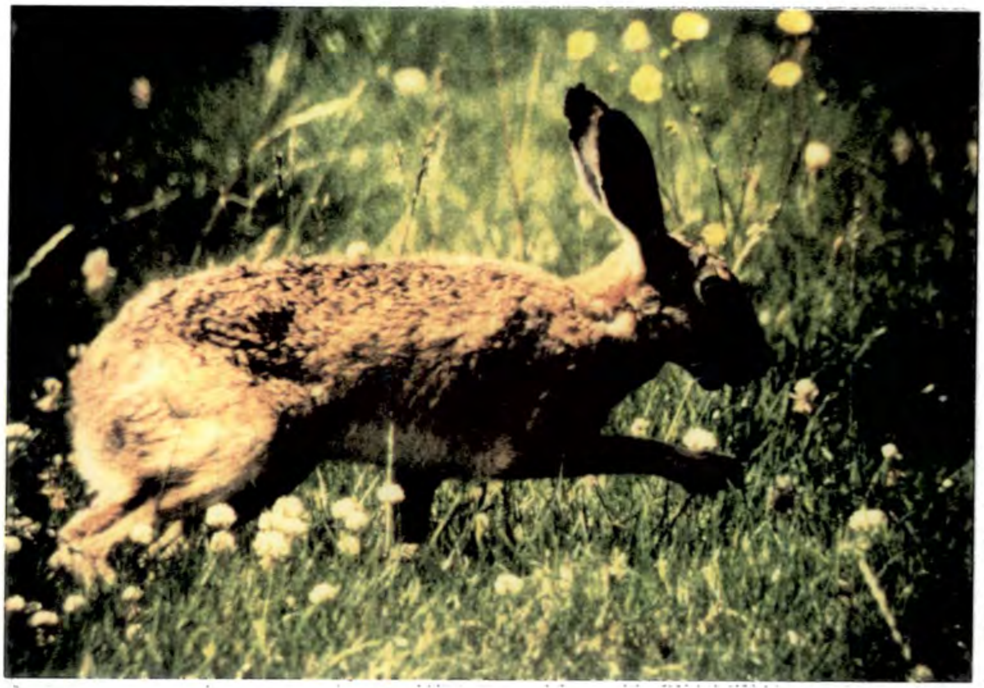


Figure 6. Bolingbroke, an alpha buck occupying the study area 1981-1984. Identified by piece out of left ear tip.

Figure 7. Cadet, young buck showing left ear tear, his masculinity and facial moult.

Figure 8. Euripides, subordinate buck showing left ear damage.

Figure 9. Falstaff, middle-ranking buck showing right ear damage.

Figure 10. Doe, Fuchsia, under observation 1985-1988. Distinguished by thin slice out of right ear tip.

Figure 12. The prominent nipples of Fuchsia, when lactating.

area could be identified during at least part of the year from the stages of their moults, which varied from individual to individual. Between 1981 and 1987 a total of 26 hares were recognized as individuals on a permanent basis. They could be sexed from inspection of the genitals and nipples. Individuals were named. Those first recognized in 1981 were allotted names beginning with the letter B, in 1982 the letter C, in 1983 the letter D and so on. The does were named after flowers. In good conditions, named individuals could be identified by telescope at distances of up to 600m.

In the case of some of the named does, it was possible to keep a record of their reproductive cycle through the later part of the breeding season. Pointers towards the approach of oestrus were the visibly advancing stage of a doe's pregnancy, coupled in some cases with an increase in the degree of attention paid to her by the bucks. The teats of a doe which are normally scarcely discernible, suddenly become clearly visible if not prominent when she starts suckling (Fig. 12). Birth of the litter usually precedes oestrus by a few days only. If copulation was not itself seen, the day of oestrus was marked by a peak of consort and satellite attendance by bucks (see Chapter 4 for definition) with frequent agonistic interactions between them, by the consort buck persistently approaching the doe to test by smell her state of readiness and, very often, by him attempting to mount and being threatened by the doe. A clear sign that oestrus is over is a dramatic drop in the degree of attention paid by bucks to the doe. Observation suggested that oestrus normally does not last for more than six hours.

Between September 1977 and September 1987, I spent

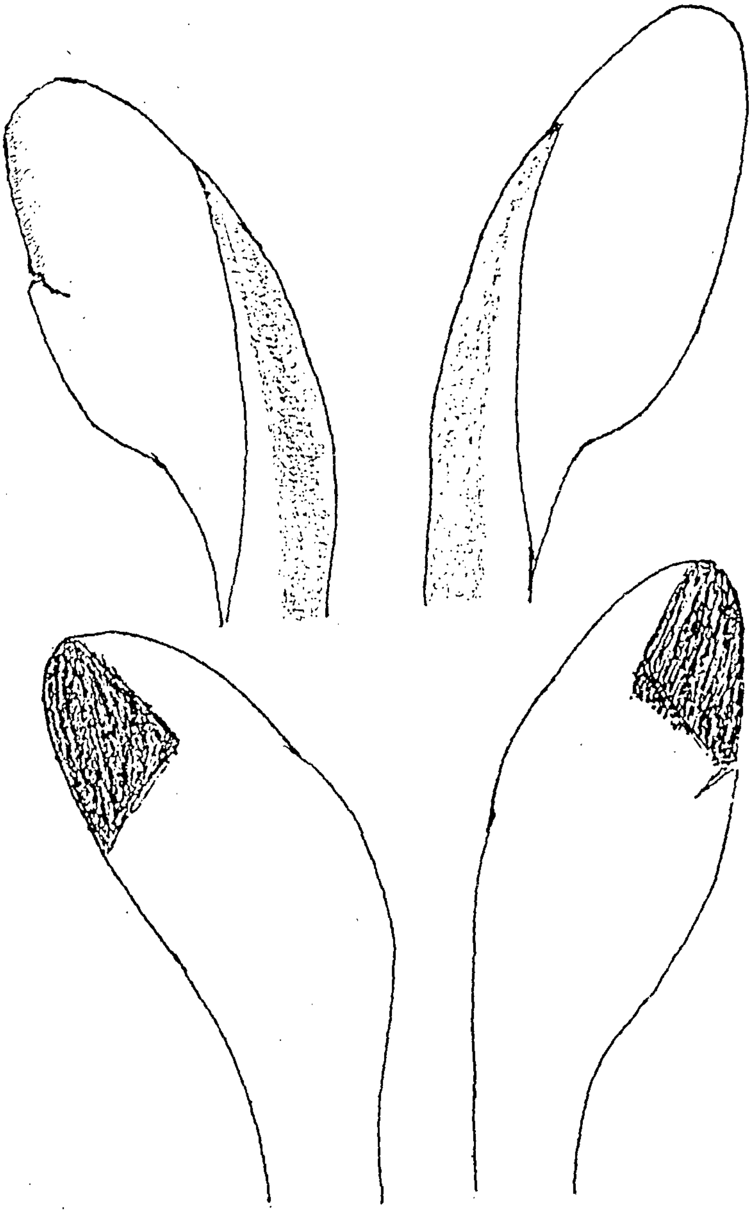


Figure 11. Ear damage chart of doe, Escalonia.

approximately 5000h observing hares in the study area divided as to approximately 60% of the time in daylight, 30% in twilight (defined as the first hours after sunset and before sunrise) and 10% at night. Both note taking and tape recording were employed in recording behaviour. Data collection was on an all occurrences or continuous recording basis, divided roughly equally between ad libitum and focal sampling (Martin & Bateson 1986). For timing the duration of suckling, a stopwatch was used. When conditions permitted, photographs were taken of behavioural components. During observation periods, the positions of individual hares were marked on 1/10000 charts of the study area. Distances between animals and between animals and observer were estimated. Fields were of small size and of known dimensions which assisted towards the accuracy of such estimates. Greenwich Mean Time was used for all records throughout the year.

CHAPTER 3

THE DAILY ACTIVITY PATTERN

Introduction

Many animals cycle between periods of activity and inactivity with circadian rhythmicity. The precise time and duration of these alternating periods is the result of natural selection on the individual species (Meddis 1975, 1983; Johnson & Hastings 1986). There has been no research on the circadian cycles of free living brown hares with the exception of Matuszewski (1981), who studied the daily movements during March and April of a population occupying a Polish forest by day and emerging to feed in nearby open fields by night. Of other species, activity cycles have only received attention in the mountain hare (Bayfield & Hewson 1975; Lemnell & Lindlof 1981) and the snowshoe hare (Mech et al. 1966).

The brown hare's day and that of most other leporids is divided into two distinct periods. One such period, comprising all or a large part of the daylight hours, is spent crouched in its form or resting place. This will be referred to as the inactive period. During much of the other, which will be referred to as the active period, comprising principally the night-time supplemented by some daylight hours the hare travels, feeds and interacts socially with conspecifics. These activities are, however, interspersed with shorter and less formal periods of rest. The combination of the clear cut distinction between active and inactive periods and the exclusively above ground lifestyle of the brown hare make it one of the best candidates of the smaller mammals for direct observational field studies of its circadian cycles. In this Chapter I report the result of such a study.

Methods

For all hares observed settling into or leaving their forms, records were kept of the time of entry or departure. Although all entries and departures whenever observed were included in the data, the majority of them were obtained during observation periods mounted for that purpose. These commenced and closed at least an hour before and after the earliest and latest expected entry or departure as the case might be. At certain times of the year it was possible to record six or more entries or departures in the same observation period. There were in the study area a number of forms which were occupied regularly but not continuously and not always by the same hare. Difficulties could arise when a hare appeared to be entering a new form because it might, on the other hand, be merely taking a rest before moving on. In those cases I checked back after all other hares were in their forms and only counted it as an entry if the hare in question was still in occupation. For departures, where there was any doubt, I only included those hares which had been observed in occupation of the form before noon on that day. Generally, on any particular day hares were noted either entering or departing their forms, but not both. These will be referred to as "different" hares. In some cases, which will be referred to as "same" hares, I recorded on the same day both the time a hare entered its form and the time it departed. "Same" hare data were collected particularly intensively in March.

On occasions hares leave their forms temporarily and sometimes they even switch forms during the day. A frequent cause of does leaving their forms in the early part of the day is harassment by bucks which are still abroad prospecting for females. Another cause of departure is disturbance by cattle or by agricultural operations. Finally, towards the end of the day hares sometimes leave their forms to have a brief snack - they do not normally feed from within the form itself (personal observation). Such temporary departures were disregarded. On the other hand, at some times of the year hares tend to stay feeding close to their forms for a period after emerging, and in the event of disturbance or perceived danger they will slip back into their forms (personal observation). In those cases it was the time of the original exit which was recorded.

Apart from the instances of temporary departure mentioned, hares did not normally leave their forms before evening. The only exception arose when a doe was very close to oestrus, when the bucks could be active throughout daylight. In the late winter and throughout the spring a large part of the population occupied forms on relatively open ground which were not difficult to locate from an elevated position (Figs. 1 & 2). A smaller number occupied open ground forms in the autumn (Fig. 4). During the summer months

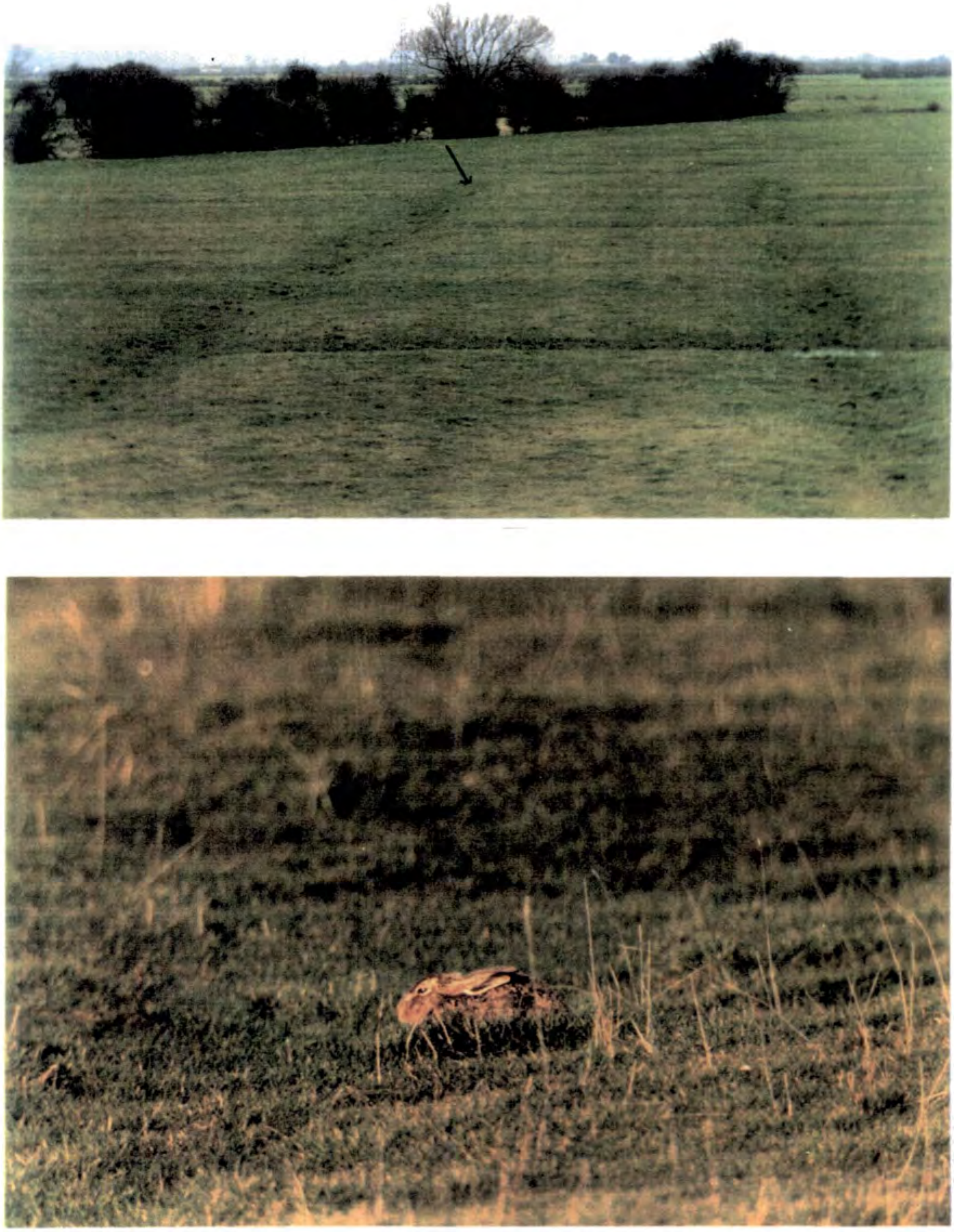


Figure 1. Buck. Bolingbroke, in regular form March 1982.

Figure 2. Photographs taken 12 April 1982.
Upper - buck Cavalier in form which he had occupied regularly, but not daily, for two months.
Lower - at 1601h Cavalier stretching, having just emerged from form (sunset 1902h).

Figure 3. Doe, in regular form August 1981.

Figure 4. Bolingbroke, in regular form October 1981.

most hares lay up in hay or cereal fields or other tall vegetation (Fig. 3). As many of these were out of sight to me, it may be that they did leave their forms more freely during the middle part of the day, as some woodland frequenting hares do (Stephanie Wray pers. comm.). For the hares which I observed, however, the interval between entering and departing forms could be regarded as the daily period of inactivity. Likewise, the period between departing and entering was defined as the nightly activity period with no consideration of periods of inactivity which might have occurred throughout the night.

For more than 10 months in the year hares entered and left their forms either in daylight or close to sunrise and sunset presenting no problems to me in observing the event, employing standard optical equipment. When nights were longest, they were entering their forms long before sunrise and it was not possible to observe the earlier entries in the absence of moonlight. Because of this problem I mounted special watch, between 15 December 1985 and 6 January 1986 on one form, which was being occupied regularly by the same hare, with the principal object of recording entry times.

The "different" hare data was collected throughout the study, the "same" hare data being collected during the second five year period. The annual population of the study area ranged between 10 and 20 adult hares. No individual hare was seen in more than four successive years. These factors in combination will go some way towards confounding the obvious possibilities of bias arising from the observational constraints of the study.

In analysing the data, the observed times of entry into and emergence from *forms* of different hares have been differenced from the day's sunrise/sunset values, averaged for each day and then averaged over the pertinent week. Those results having indicated a cyclic behaviour, harmonic functions were fitted to the a.m. and p.m. weekly mean differentials and thus provide an overall perspective of the pattern of shifting exit and return times. The fitted curves have the form

$$y = A.\cos(wx) + B.\sin(wx) + C$$

where $w = 2\pi/T$. $T = 52$, the period in weeks of the differential function in hours, y, and $x = 1,2,3,\ldots,52$, the weekly determinator. A, B, C, are the constants to be determined by a Least Squares fit. The constant C will be the long run average of the variable y. The resulting function will be a harmonic curve, of period T, of amplitude $\sqrt{A^2 + B^2}$, and phase arctan (B/A). A test of statistical significance can be carried out on $(A^2 + B^2)$ by an approximate F test with 2 and N-3 degrees of freedom (N = number of weekly observations, somewhat less than 52). The choice of positive and negative for the differentials was arbitrarily decided and is recorded in Table I. These analyses omitted the relatively few "same" hares, thereby enabling comparison to be made between the two groups.

Results

Altogether 814 entries and exits were recorded, 242 entries and 572 exits. Of the total there were 180 from "same" hares, leaving 152 entries and 482 exits from "different" hares. The number and relative frequency of these spread over the year are shown in Figure 5, divided between "different" hare entries, "different" hare exits and "same" hares. As the study involved regular observation throughout

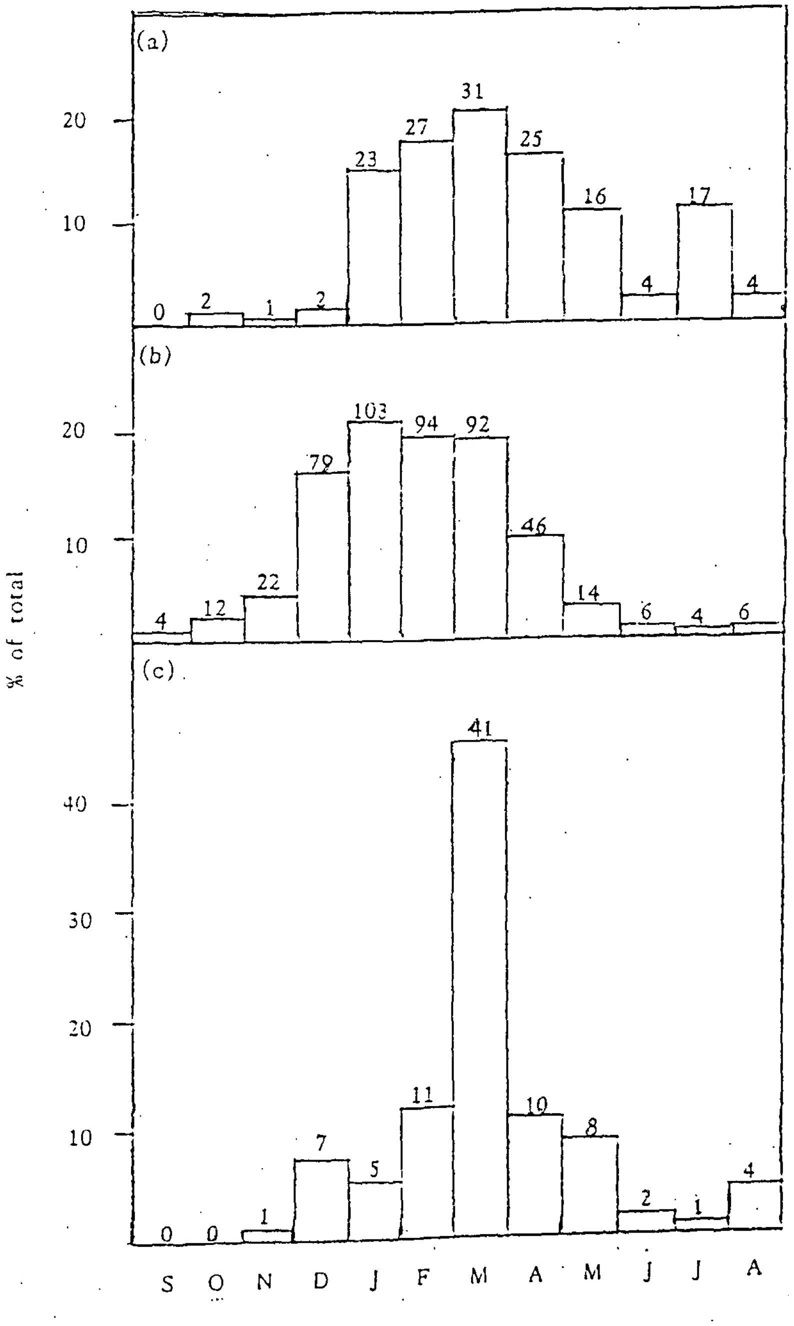


Figure 5. The number, above the bars, of observed (a) entries into forms of different hares, (b) exits from forms of different hares and (c) entries and exits of same hares, divided between the months of the year. Seasonal variations reflect primarily detectability of the forms except for peak of same hares in March, which reflects application of additional observer time - see text.

the year the relative frequencies of observed exits (Fig. 5b) can be taken as a rough indication of the frequency of use of open, easily visible, forms compared with concealed forms. On that basis the use of open forms decreased from a peak, which held throughout the first quarter of the year, by 50% in April and 85% in May.

Set out in Table I are the weekly means of the differentials between, respectively, entries and sunrise and exits and sunset. In the case of entries, a positive value represents entry (end of activity) before sunrise and a negative value entry after sunrise. In the case of exits, positive values represent departure (commencement of activity) after sunset and negative values departures before sunset. Table II lists respectively the values of the fitted harmonic functions for the entry and exit differentials and also the values of the summation of both differentials. The weekly average duration of true night (sunset to sunrise) and the values of the harmonic function fitted to those data appear in Table III together with the weekly values of the harmonic function of the activity period, being the value of true night duration minus the value of the summed entry and exit differentials. The statistics of harmonic functions appear in Table IV, followed in Table V by the tests of statistical significance.

The curves of the fitted harmonic functions in Figures 6, 8 and 9 can be regarded as the major components of the data. In Figure 6 the constants of sunrise and sunset are shown separately with the curves of the functions of entries and departures respectively. Also shown are the scattered observations of "different" hares from which the curves have been constructed and, for comparison, the excluded "same" hare data averaged for each week. To illustrate the pattern

Table I. Weekly means of a.m. and p.m. differentials. Hours are shown in decimal fractions. Positive values for entry before sunrise and exit after sunset; negative values for entry after sunrise and exit before sunset.

ENTRY		EXIT	
Week	Hours	Week	Hours
1	.702	1	.429
2	1.19	2	.094
3	.293	3	.2264
4	- .262	4	.044
5	.247	5	.2518
6	.239	6	.974
7	.1833	7	- .031
8	-1.22	8	.59
9	- .075	9	- .51
10	- .1475	10	- .269
11	- .911	11	- .495
12	- .0993	12	- .423
13	.1175	13	- .576
14	- .218	14	-1.776
15	-1.548	15	-1.772
16	-1.7	16	-1.298
17	- .43	17	-2.169
18	-1.966	18	-1.863
19	- .673	20	-1.837
22	-2.843	24	-3.38
26	-3.22	25	-2.56
27	-2.93	26	-3.698
28	-3.51	27	-3.18
29	-1.683	28	-2.328
30	-4.55	29	-2.45
31	-2.937	30	-2.862
32	-2.68	31	-1.675
43	.04	32	-1.79
46	.02	36	- .75
52	.77	37	- .78
		38	- .2
		40	.12
		42	.145
		43	- .185
		44	.23
		45	.168
		46	.35
		47	.304
		48	.415
		49	.467
		50	.4434
		51	.437
		52	.379

Table II. The values of the fitted functions for a.m. and p.m. differentials and, in the fourth column summation of the differentials computed from the sum of the separate harmonic functions.

Week	A.M. Differentials	P.M. Differentials	Summation
1	.54707	.668326	1.2154
2	.565423	.607435	1.17286
3	.558391	.524084	1.08248
4	.526076	.41949	.945566
5	.46895	.295178	.764128
6	.387845	.15296	.540805
7	.283945	-.005	.278855
8	.158765	-.176666	-.0179017
9	.014129	-.359269	-.34514
10	-.147852	-.550233	-.698085
11	-.324818	-.746775	-1.07159
12	-.514187	-.946028	-1.46022
13	-.713198	-1.14509	-1.85829
14	-.918949	-1.34105	-2.26
15	-1.12844	-1.53106	-2.6595
16	-1.33861	-1.71234	-3.05096
17	-1.54641	-1.88226	-3.42867
18	-1.74879	-2.03833	-3.78712
19	-1.94282	-2.17827	-4.12109
20	-2.12565	-2.30006	-4.42571
21	-2.29463	-2.4019	-4.69653
22	-2.44728	-2.48233	-4.92961
23	-2.58139	-2.54015	-5.12154
24	-2.695	-2.57454	-5.26953
25	-2.78644	-2.58498	-5.37143
26	-2.8544	-2.57133	-5.42573
27	-2.89787	-2.53379	-5.43166
28	-2.91622	-2.4729	-5.38912
29	-2.90919	-2.38955	-5.29874
30	-2.87688	-2.28495	-5.16183
31	-2.81975	-2.16064	-4.98039
32	-2.73865	-2.01842	-4.75707
33	-2.63475	-1.86037	-4.49512
34	-2.50957	-1.6888	-4.19837
35	-2.36493	-1.5062	-3.87113
36	-2.20295	-1.31523	-3.51818
37	-2.02599	-1.11869	-3.14468
38	-1.83662	-.919436	-2.75605
39	-1.63761	-.720377	-2.35799
40	-1.43186	-.524413	-1.95627
41	-1.22237	-.334405	-1.55677
42	-1.01219	-.153121	-1.16531
43	-.804396	.0167944	-.787602
44	-.60201	.172865	-.429145
45	-.407986	.312812	-.0951748
46	-.225153	.434596	.209443
47	-.0561765	.536442	.480265
48	.0964789	.616864	.713343
49	.230588	.67469	.905278
50	.344195	.709076	1.05327
51	.435642	.71952	1.15516
52	.503598	.705872	1.20947

Table III. True night durations and total night activity. In the second column, weekly night (sunset to sunrise) duration averages calculated from data supplied by the Science and Engineering Research Council. In the third column, the result of fitting the harmonic function to the weekly averages. In the fourth column, total night activity being true night duration minus the sum of the fitted a.m. and p.m. differentials from Table II.

Week	True night duration	Fit of the harmonic function	Total night activity
1	15.983	15.812	14.5966
2	15.817	15.6772	14.5044
3	15.533	15.4847	14.4022
4	15.233	15.2372	14.2916
5	14.867	14.9383	14.1742
6	14.483	14.5925	14.0517
7	14.05	14.2047	13.9258
8	13.633	13.7806	13.7985
9	13.167	13.3264	13.6716
10	12.717	12.8488	13.5469
11	12.267	12.3546	13.4262
12	11.8	11.8511	13.3113
13	11.35	11.3457	13.204
14	10.883	10.8456	13.1056
15	10.45	10.3583	13.0177
16	10	9.89069	12.9416
17	9.55	9.44975	12.8784
18	9.15	9.04185	12.829
19	8.767	8.67296	12.794
20	8.4	8.34843	12.7741
21	8.067	8.07302	12.7696
22	7.817	7.85073	12.7803
23	7.617	7.68481	12.8063
24	7.467	7.57767	12.8472
25	7.417	7.53088	12.9023
26	7.433	7.54512	12.9708
27	7.533	7.62018	13.0518
28	7.733	7.75497	13.1441
29	7.95	7.94752	13.2463
30	8.267	8.19503	13.3569
31	8.6	8.49388	13.4743
32	8.967	8.83971	13.5968
33	9.367	9.2275	13.7226
34	9.783	9.65157	13.8499
35	10.217	10.1057	13.9769
36	10.667	10.5834	14.1016
37	11.1	11.0776	14.2223
38	11.55	11.5811	14.3371
39	12	12.0865	14.4445
40	12.467	12.5866	14.5428
41	12.917	13.0739	14.6307
42	13.367	13.5415	14.7068
43	13.85	13.9824	14.77
44	14.217	14.3903	14.8195
45	14.633	14.7592	14.8544
46	15	15.0838	14.8743
47	15.35	15.3592	14.8789
48	15.65	15.5815	14.8681
49	15.867	15.7474	14.8421
50	16.033	15.8545	14.8013
51	16.117	15.9013	14.7462
52	16.117	15.8871	14.6776

Table IV. Statistics of the harmonic functions. A is the coefficient of the Cos term, B is the coefficient of the Sin term and C is the constant term, the long run average.

Differentials	A	B	C	Amplitude (hours)	Phase Shift		Days from year end
					Radians	Weeks	
A.M.	1.679,00	.462,20	-1.175,40	1.74	+.2686	-1.07	-10.99
P.M.	1.638,60	-.212,36	-0.932,73	1.65	-.1289	+2.22	+19.04
A.M. + P.M.	3.327,60	.249,84	-2.108,13	3.33	+.0782	+.622	+ 7.84
True Night Duration	4.170,98	-.370,44	+11.716,10	4.19	-.0886	-.733	- .863
Activity Period - estimated	0.853,38	-.620,28	+13.824,23	1.05	-.6292	-5.21	-39.97

the daily activity pattern

Table V. Tests of statistical significance.

1. Amplitude = $\sqrt{A^2 + B^2}$	F-statistic	Degrees/freedom	P-value
A.M. Differentials	88.9	2 & 27	< .001
P.M. Differentials	285.8	2 & 40	< .001
2. Phase Shifts	**Approx. z-test**	**-**	**P-value**
Difference of B values (A.M.-P.M.)	2.522	-	< .01

of an individual separated from that of the population, at Figure 7 are shown exit date collected from one buck, Bolingbroke, over a two year period. The divergence between the entry and exit curves in Figure 6, which are significant (Table V), justifies their separate treatment. The fit between both sets of data ("different" and "same" hares) and the curves is visually clear. There are indications in midsummer that the activity period at both ends of the day may be longer than the curve predicts and also that from week 31, the first in August, onwards until the end of October activity, both morning and evening, is shorter than predicted. The latter period coincides both with the end of the breeding season and also with the relatively sudden and dramatic reduction in vegetation levels brought about by haymaking and harvesting. During August there is to the observer a noteable change in the behaviour of the hares, marking the commencement of what I refer to as the "shy period". Set out below are descriptive diary notes 1984-1987:-

> "p.m. 7 August 1984. In general, at the moment it is amazing how very little activity there is prior to sunset and how sudden it has been"
>
> "a.m. 8 August 1987. It looks as though the shy period has started"
>
> "p.m. 10 August 1986. Generally, I have the impression that suddenly the tempo of the hares' activities has died down and they are retreating from the light".

The scattered observations from both "different" and "same" hares in Figure 6 show outliers. The two from "different" hares in weeks 19 and 34 have been excluded from the computations. For week 19 there were only two recorded exits of "different" hares and both emerged exceptionally late. The hares concerned were a doe in

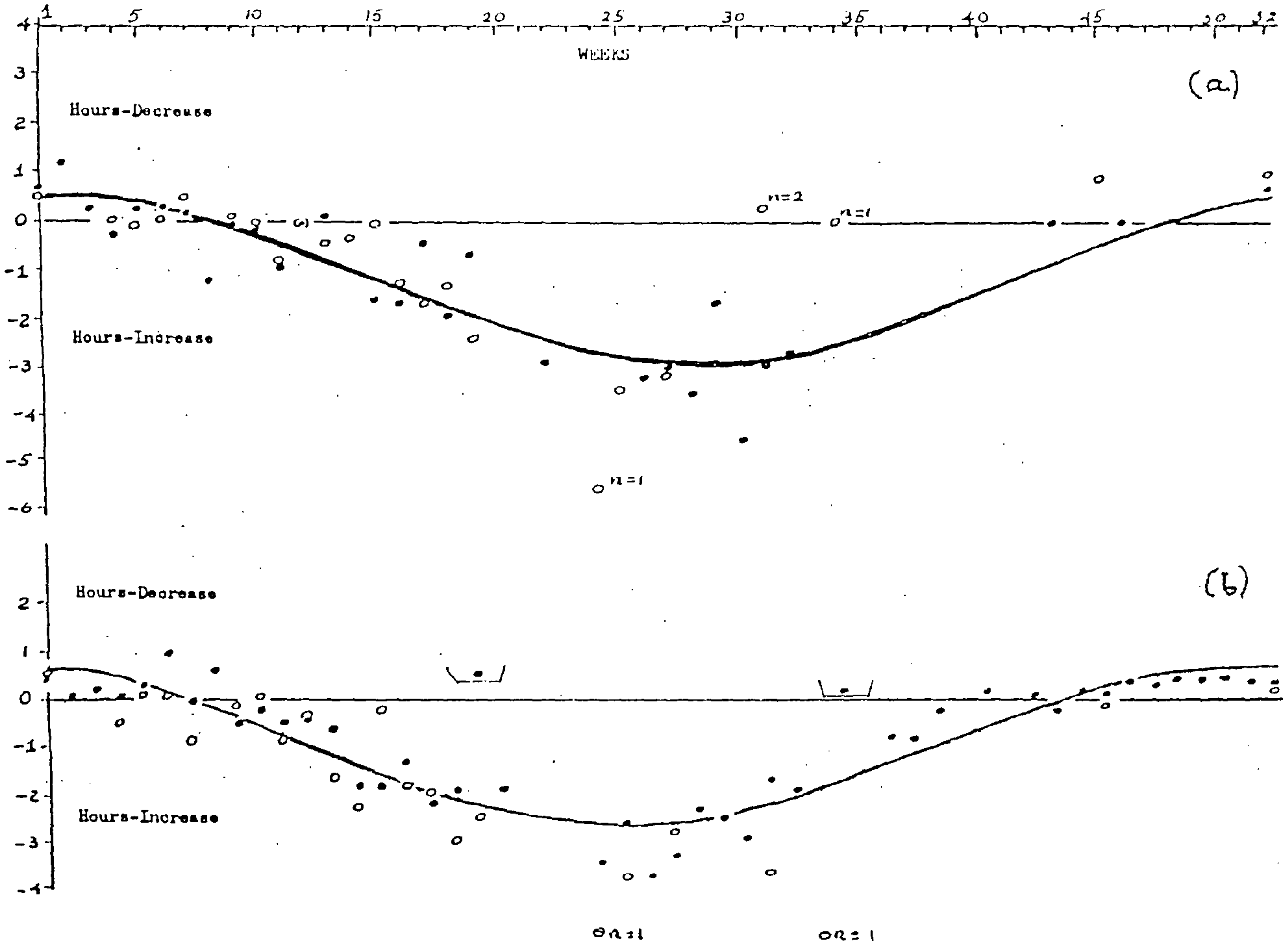


Figure 6. Night duration differentials. The constants at (a) and (b) are respectively sunrise and sunset with the curves of the harmonic functions of entries into and departures from forms throughout the 52 weeks of the year. Shown (·) the scattered observations of "different" hares from which the curves have been constructed including two outliers (see text) and (o) the excluded "same" hare data averaged for each week.

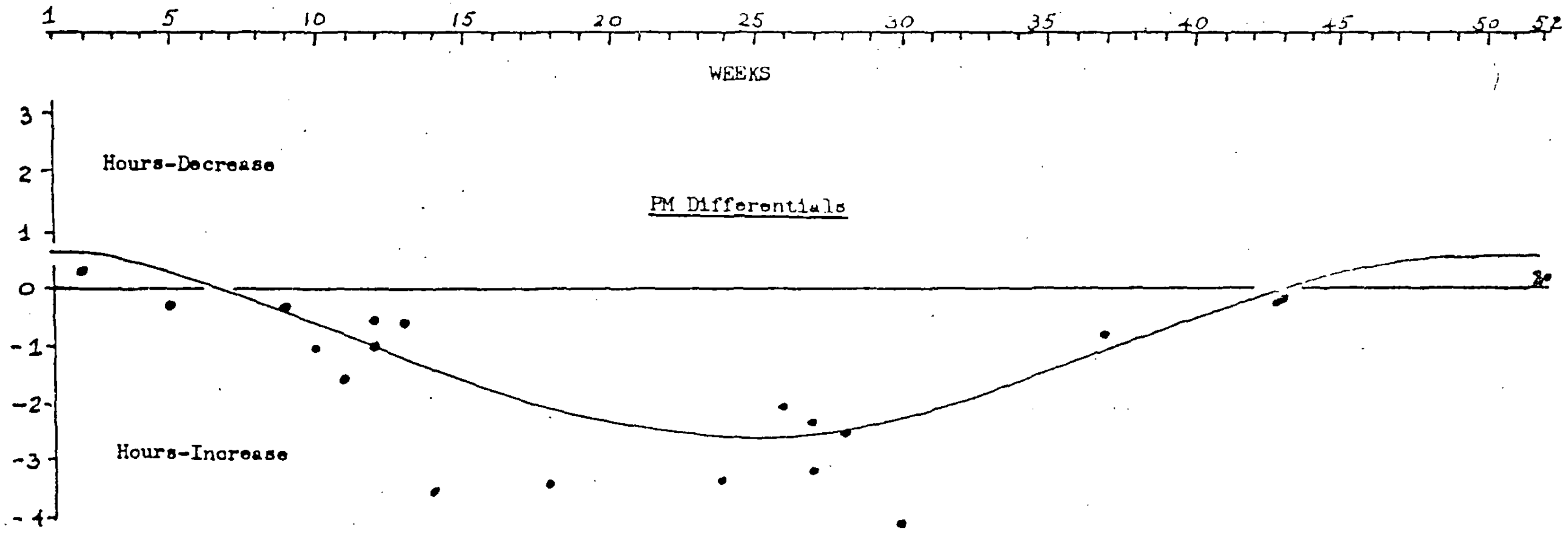


Figure 7. The curve of the harmonic function of exits from forms and (•) the times of each exit of the buck Bolingbroke as recorded over a two year period.

1985 and a buck in 1986. The doe was lying up in a hayfield and for more than an hour prior to departure was feeding apparently from her form, which is most unusual and may therefore represent an instance of observer error. The reason for the buck's late departure was, simply, exhaustion. He had been involved throughout the morning in competitive interactions with other bucks as a doe came into oestrus, followed by the high intensity events of the oestrus itself. For that week, departures were recorded from three "same" hares and it will be seen that the average from these conformed to the general pattern (Fig. 6). The "different" hare outlier for week 34 depended, again, upon only two recorded exits. These were from unidentified hares and the circumstances are not therefore known, but they occurred in the shy period during which, as previously mentioned, hares were emerging later than the curve predicted. The few outliers for "same" hares related to single animals, with the exception of week 31 where the records were from a doe being mate-guarded by a buck on 3 August at the very end of the season. The single animal shown for week 24 was the doe Bluebell on the day of parturition when she spent only six hours in her form (see Chapter 5). It will be noted that the "same" hare outliers for weeks 31 and 34 which entered their forms particularly early also left them early, suggesting a limiting factor operating on the length of the inactive period.

Figure 8 shows the curve of the sum of the separate morning and evening differentials. The values of that curve when deducted from the values of true night duration produce the curve of the activity period or adjusted night duration appearing, with the curve of

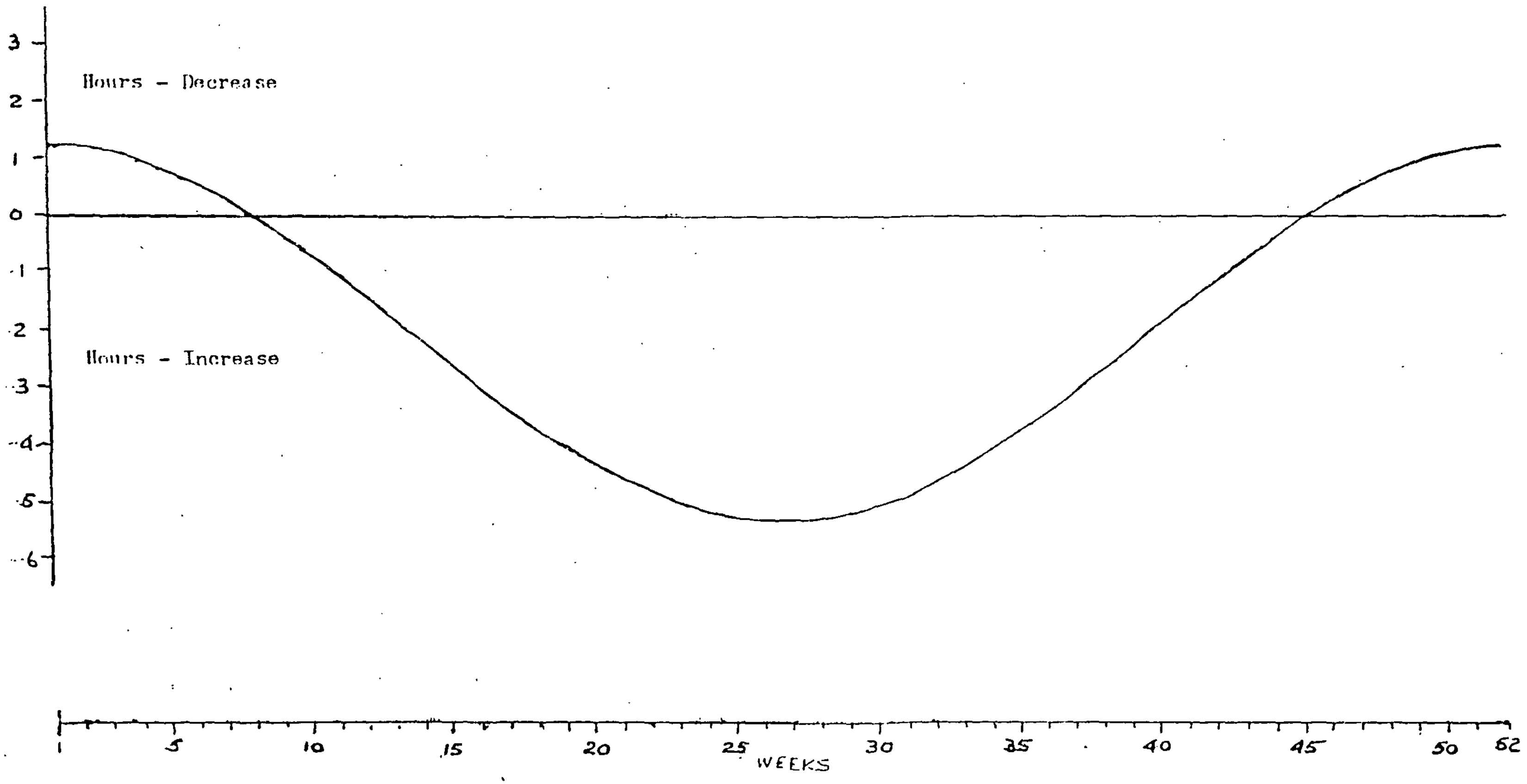


Figure 8. Summation of night duration differentials, showing the curve of the sum of the separate morning and evening differentials. The values of the curve when deducted from the values of the true night duration produce the curve of the activity period or adjusted night duration.

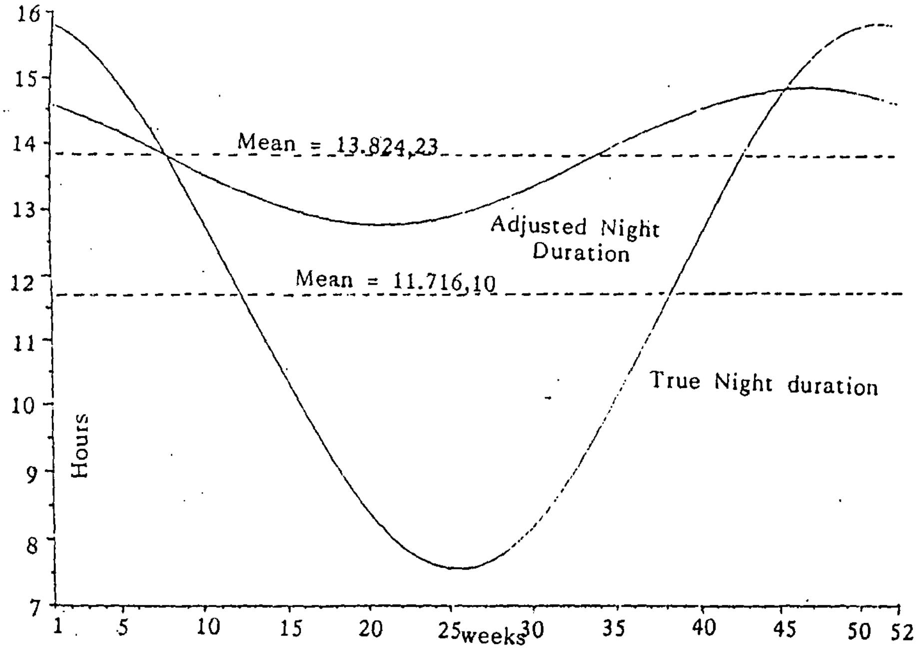


Figure 9. Impact of night duration differentials. The curve of adjusted night duration represents the activity period.

true night duration, in Figure 9. Results from the curves reveal a mean nightly activity period of 13.8h, compared with a mean night duration of 11.7h. At peak night duration of more than 15.5h the activity period occupies less than 14h. At lowest night duration, in mid-summer, of less than 8h it occupies some 13h of which more than five are in daylight.

Is the transition from exclusively nocturnal activity in the earlier part of the year to a part daylight regime in the Spring and Summer a smooth one? That question is addressed in Figures 10 and 11. The former shows, in relation to sunset and also to night length, the weekly mean time of departure from forms for the period from the end of October to the beginning of May, based on a total of 496 departures of both "different" and "same" hares. Whilst in general the slope of earlier departure matches that of declining night duration, there is a period between weeks 8 and 12, inclusive during which night length reduces from 13.6h to 11.8h, when there is an arrest in the progression of earlier departures. For those five weeks, the mean time of departure hovers between 5 and 25 mins/pre-sunset. Then suddenly in week 13, the last in March, the mean departure time jumps to just over an hour pre-sunset and thereafter the progression resumes. Figure 11 is constructed exclusively from "same" hare data which, by recording both the entry and departure times of an individual hare, define both the inactive period and, by deduction, the active period also. From the first 18 weeks in the year, I have taken those weeks for which I have four or more "same" hare data and in Figure 11 have shown the mean activity period duration against the mean duration of night. The number of records for weeks 12 and 13

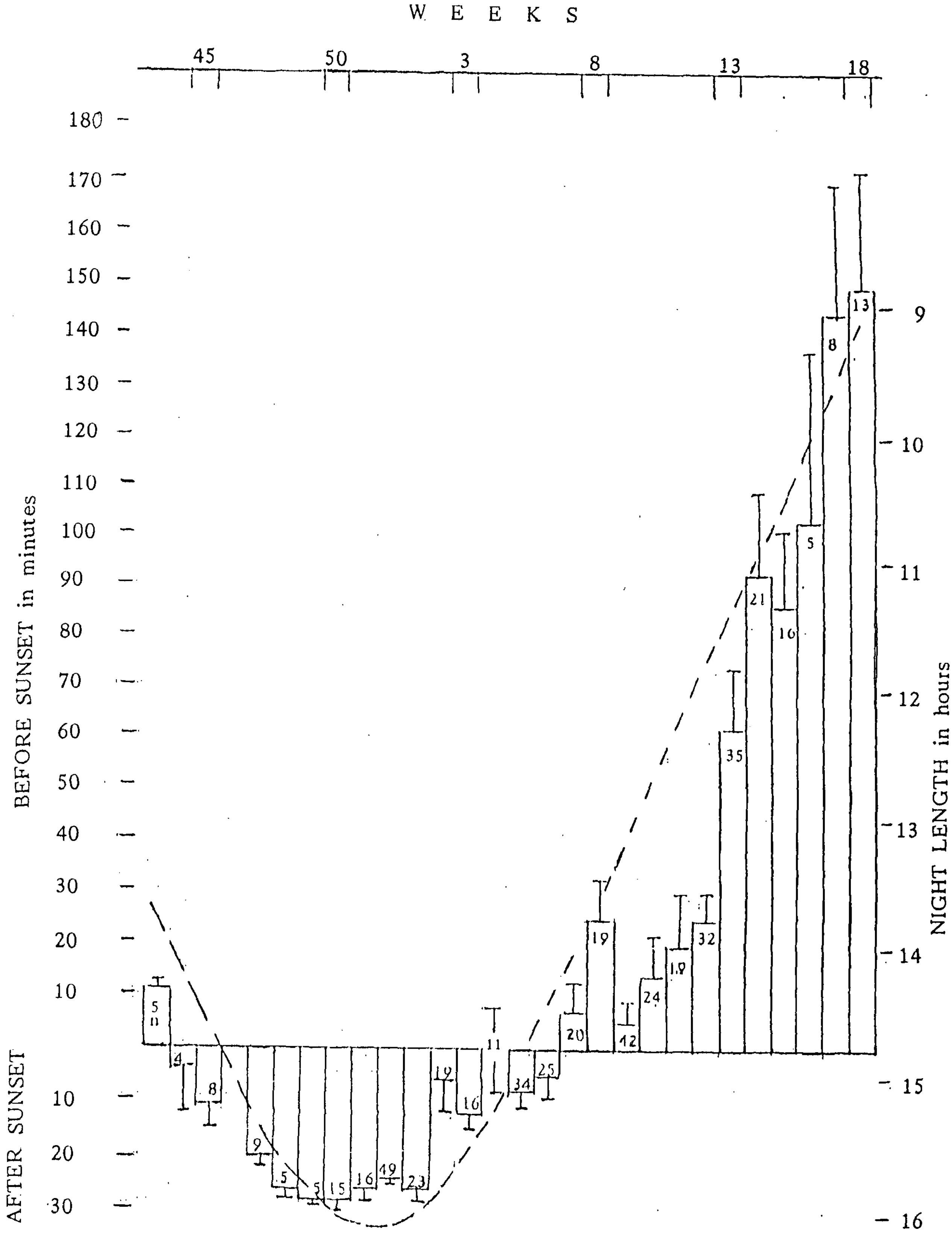


Figure 10. The times $(\bar{x} \pm SE)$, in relation to sunset, of 496 exits of hares from their forms, commencement of activity, during 28 weeks from the end of October to the beginning of May. Also showing, by the intermittent line, the change in hours of darkness over the period.

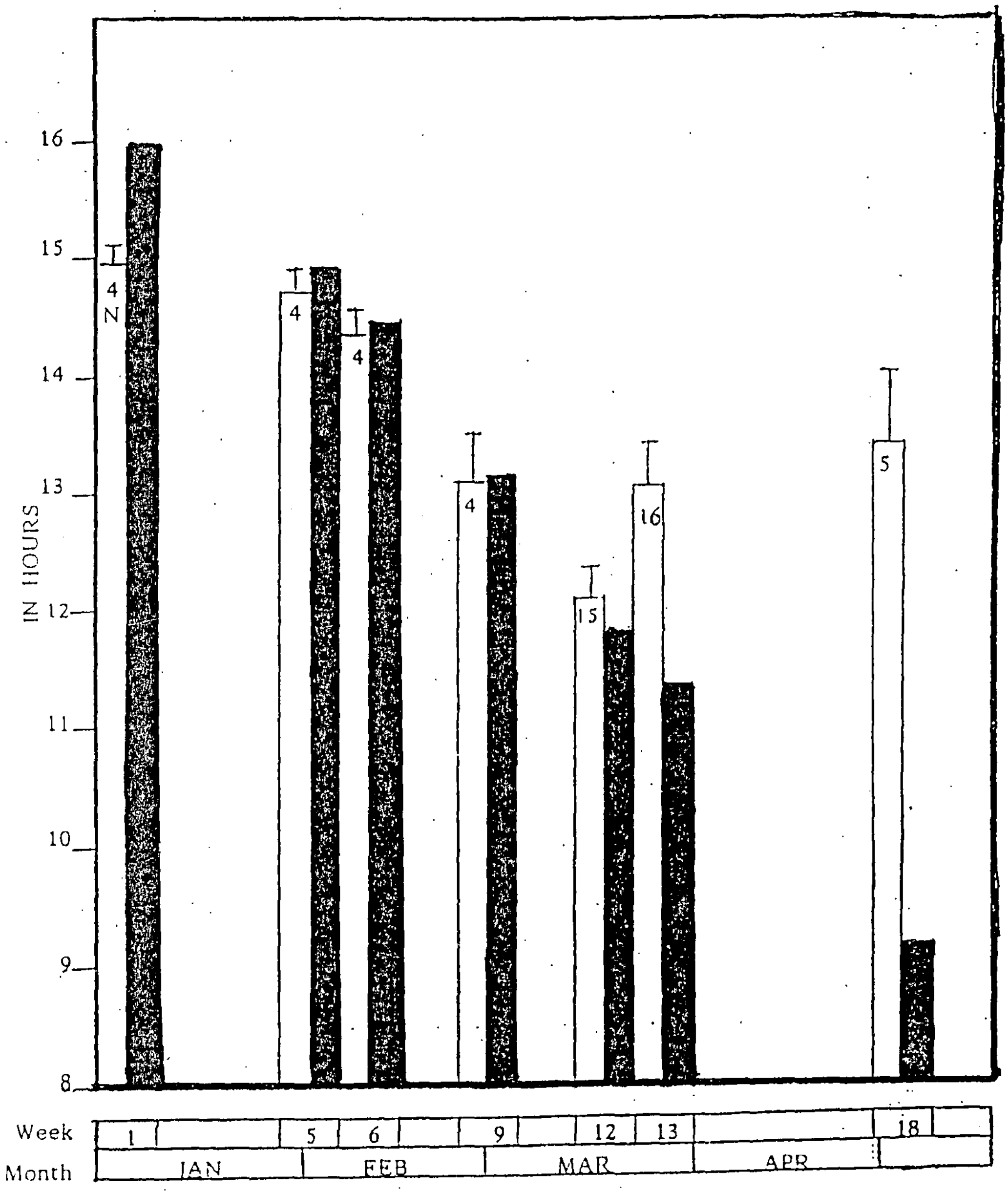


Figure 11. Unshaded columns - the daily activity period, length of time out of forms ($\overline{X} \pm$ SE). Shaded columns - the average night length, between sunset and sunrise, during 7 of the first 18 weeks of the year.

reflect the particular attention given to that period as mentioned in Methods. From a peak of nearly 15 hours in week 1 the mean activity period duration declined to a minimum of just over 12h in week 12, the third full week in March, mirroring the decline in duration of the night hours. That decline was reversed in week 13, when the mean activity period increased to 13.1h and exceeded night duration by more than 1.6h. By week 18 the mean activity period had increased to 13.4h and exceeded night duration by more than 4h. The results appearing in Figures 10 and 11 demonstrate that the transition is not a smooth one.

In December and early January, when the night hours are longest, hares are almost totally nocturnal. They enter and leave their forms in darkness. The time of emergence is consistent both within and between individuals, being generally no more than 30 mins. after sunset (Fig. 10). The time of morning form entry was more variable and, as mentioned in Methods, was sometimes so early that darkness prevented me from observing the event. In Figure 12 are the results of observation of one form, which was being occupied regularly by the same hare, during the 23 days between 15 December 1985 and 6 January 1986. The form was occupied by the hare on 17 of the 23 days. On 11 of those days I observed the emergence of the hare at times ranging between 19 and 36 mins, with a mean of 26.8 mins, post-sunset. On only two of the days was I able, by moonlight, to observe the hare entering the form at respectively 83 and 56 mins pre-sunrise. On another six days when it was too dark for me to see the moment of entry I recorded the time when I could first discern the hare in the form. Those times ranged between 46 and 96 mins

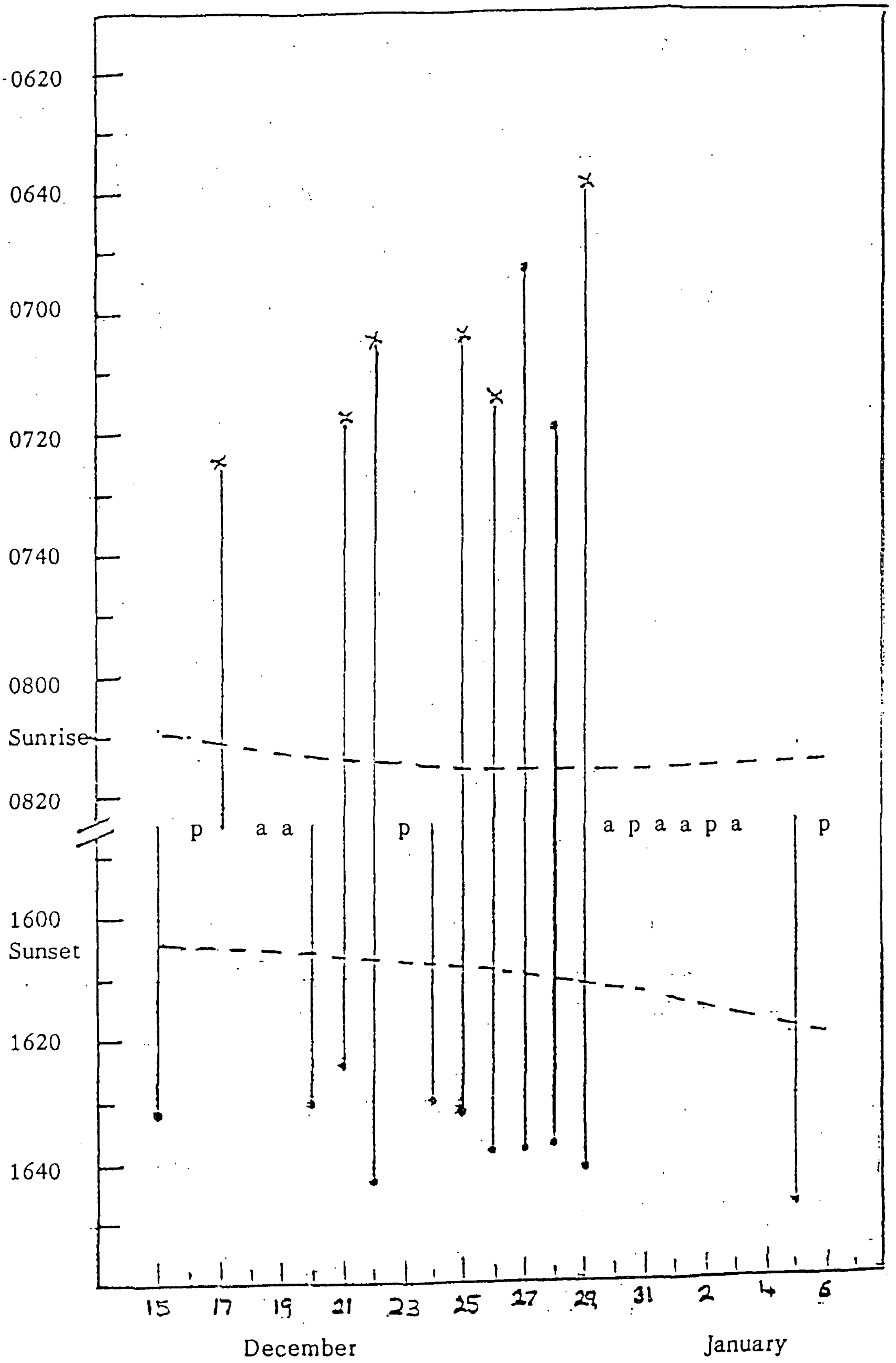


Figure 12. Observed occupation of one form by the same hare during 23 days, 15 December 1985 to 6 January 1986. Form entry or exit (•), earliest sighting of hare already in form (x), hare present in form on the day but arrival and departure not observed (p) and hare absent that day (a). Vertical lines denote continuous occupation and the part of the day during which observation was mounted.

pre-sunrise. On none of the eight days was the hare in its form later than 46 mins pre-sunrise. On five of them it entered more than an hour and on one more than an hour and a half before sunrise.

Discussion

The results of this study demonstrate that the brown hare is essentially a nocturnal animal. Given sufficient hours of darkness, the whole of the activity period lies within them. During the few weeks when there is a marked excess of darkness hours over activity hours, hares consistently emerge from their forms, commence activity, within 30 mins after sunset and the excess is reflected in the time they enter their forms, cease activity, which can be as early as one and a half hours before sunrise. When the night hours are insufficient the activity period overlaps into daylight at either end of the day.

In the study area the duration of night, sunset to sunrise, cycles seasonally between a maximum of 16 and a minimum of 7.5h, a range of 8.5h. The activity period of the hares varies between a maximum of just under 15h in mid-winter and a minimum of just over 12h in the third week of March, a range of less than three hours. When almost totally nocturnal in mid-winter the activity period averages about 14.5h. Although it reduces to just over 12h by late March, nevertheless that low point is of short extent and the mean duration of the activity period taken throughout the year is likely to be close to the value of 13.8h of the harmonic curve in Figure 9. Personal observation, however, suggests that certain individuals, such as pregnant and nursing does and alpha bucks, require activity periods of up to 16h or more.

The activity period follows a seasonal cycle, the duration of the period generally reducing as the hours of daylight increase. This produces the surprising outcome that the daily activity period is substantially longer before the breeding season commences in late December than it is in the peak months of March to June inclusive. Why should the daily activity period be shorter in the peak of the breeding season than before the season commences? Why does it cycle at all? The answer appears to lie in the nocturnal preference, or daylight aversion, of the brown hare. Assuming an optimal activity period of around 14h, it would be expected that the transition from a totally nocturnal activity period to a part diurnal one, as the night hours dropped below 14, would be smooth. That, however, is not the case. The duration of the activity period in fact declines from nearly 15h in the first week of January to a minimum of just over 12h in the third full week of March, mirroring and keeping just within the duration of the night hours (Figs. 10 and 11). Then, suddenly in the fourth week of March the activity period increases to 13.1h and exceeds night duration by more than 1.6h. By week 18, the activity period is 13.4h, and exceeds night length by more than 4h. This pattern of events suggests first that some inhibitory factor is preventing smooth transition from a totally nocturnal to a part diurnal regime and secondly that there is a point, at roughly 12h of duration, beyond which the activity period cannot easily be contracted. When examined against the reduction of activity hours from January to March, keeping just within the declining night length, the conclusion must be that the inhibitory factor is daylight itself. Another probable manifestation of the factor is in the variation between the harmonic curves for the times of form entry and departure. In the spring the departure curve crosses the sunset line into daylight two weeks before the entry curve crosses the sunrise line. In the evening after spending the day in its form a hare will be hungry and is likely to be less shy of daylight than a well fed one returning to its form in the early morning. Although hares once they are regularly active by day rapidly extend the duration of daylight activity, none the less the inhibitory factor is still operating to the extent that the duration of activity remain shorter than during the totally nocturnal regime. There are indications of a relatively sudden withdrawal from daylight activity at the end of the breeding season in August, mirroring the emergence into daylight activity late March. The suddenness of the latter event, which throws the hares out onto the daylight stage, brings a finer focus upon the explanation of the March hare phenomenon given by Holley & Greenwood (1984) - the "mad" interactions between hares observed in March take place with equal regularity during the months January to July inclusive but between January and March occur at night and from March onwards occur by day in longer vegetation.

Previously, the only field study of brown hare circadian activity was of a population in Poland lying up in a forest by day and emerging to feed in the nearby open fields by night (Matusewski 1981). The study, which was conducted during March and April, recorded the times hares entered and left the forest and not their forms. There was some feeding to be had in the forest and the times of entering and leaving it cannot be taken as defining the activity period. The times of first emergence onto the fields from the forest increased, however, from 20 mins pre-sunset at the end of February to 80 mins pre-sunset at the end of March. Throughout March and April almost all hares re-entered the forest during the 40 mins before sunrise. The author comments that the faster morning movement was probably caused by disturbance, mainly humans and dogs. Mech et al. (1966) studied 5 radio-collared snowshoe hares in Minnesota USA from mid-January to May. Again, they did not have the times of entry and emergence from forms. Onset of activity was considered to be the first movement of 2^{o} or more (usually 50-200 feet) recorded on the automatic radio tracking system, and cessation was extrapolated on a similar basis. Their results showed that seasonal changes in both onset and cessation of activity followed the trend of changing sunrise - sunset times. Generally, the study animals began moving each day shortly after sunset and ceased activity before sunrise. In the case of one doe, sufficient data were available to show a high correlation between seasonal changes in periods of daily inactivity and seasonal changes in length of daylight. The doe's nightly activity decreased from about 13h in January to less than 9h in May. Costa et al. (1976) observed black-tailed jackrabbits in enclosures of natural vegetation in the Mojave Desert California (Lat. 35^{o}N) reported a mean activity period of 12.3h in March, 10.3h in July/August and 13.2h in December. In general, they said jackrabbits became active within 30 mins of sunset and returned to daytime forms between dawn and sunrise, regardless of season. Lemnell & Lindlof (1981) studied by radiotelemetry, involving automatic signal recording, the activity pattern of 9 mountain hares during periods throughout the year in Sweden.

Again, they did not observe hares entering and leaving forms but their equipment was sufficiently sensitive to define ambulatory and feeding activities as such, without depending upon the degree of movement away from the resting site. The hares were almost entirely nocturnal in winter and daylight activity gradually increased up to 50% in summer when the nights were very short. The authors suggest that mountain hares are basically nocturnal but increase their daylight activity due to the short nights in summer. The results of two of the four works reviewed above fit the pattern disclosed by this study. In the case of the work of Mech et al. (1966) on the showshoe hare, it must be a possibility, however, that the constraints of the methodology employed in that study have suggested a difference which is not real. The forms of brown hares during the summer months are generally in concealing long vegetation. When the hares emerge they tend to spend the remaining daylight hours feeding in the area of their form. After nightfall they move to feeding grounds which are more in the open and which they leave again before dawn (personal observation). If snowshoe hares behave similarly, then the study animals involved may well have been entering their forms later and leaving them earlier than the methodology suggested, and have been feeding close to their forms during the intervening period. As to the black-tailed jackrabbits, the study area was the most southerly of the four and therefore the differential duration of night hours between winter and summer would be the least. It seems that the hares could accommodate the differential within a strictly nocturnal regime.

I have shown that the optimum activity period for the brown hare is in the region of 14h, but can extend to 16h, and that there is resistance to it being reduced below 12h. This leads to the question whether there is any lower limit on the duration of the inactive or resting period - on which there is as yet no data. Historically, the inactive or sleep period of an animal was thought to provide only an energetically restorative benefit to it. More recently, it has been suggested that it functions to afford animals protection during a period of the daily cycle when they may be vulnerable to predation (Webb 1975; Meddis 1977, 1983). This hypothesis implies that resting or sleep sites should be selected to provide the animal with maximum security during its immobility state, which should itself be at those times when the animal is least adapted to survive. (Meddis 1975). The daily inactive rest period in its form of the brown hare seems to fit the recent hypothesis, but study of a closely related species, the arctic hare, might provide the means of testing it. Arctic hare does in the 24h summer daylight of the Canadian far North suckle their litters at intervals of approximately 19h instead of every 24h, as in the brown hare (Aniskowicz et al. 1990). One of the possibilities must be that the does are condensing their day into a 19h cycle, in which event there must be reductions in either the active or inactive period, or both. The lactating doe, suckling a litter of up to 8 leverets, will face high energetic demands. Can she therefore reduce the hours she spends feeding between nursings? If not, then perhaps she is able to reduce substantially the normal inactive or resting period, in which event the recent hypothesis would be strongly supported. Observational research should be able to provide the answer to that question.

CHAPTER 4

HIERARCHY OF BUCKS: DOMINANCE STATUS AND ACCESS TO OESTROUS DOES

Introduction

The home range of a brown hare overlaps that of a number of conspecifics of both sexes (Broekhuizen & Maaskamp, 1982). As a result each hare will inevitably become familiar with the other individuals inhabiting it. Competition for any resources which are scarce can therefore be anticipated. Such resources could include food and, for males or bucks, oestrous females or does.

Each doe is pregnant for most of the long breeding season, from late December to August. Broekhuizen & Maaskamp (1981) found that between February and August 88% of all does over 12 months old were pregnant. Oestrus which follows parturition by a few days only (Lincoln 1974) is normally of very short duration, copulation activating ovulation (Stieve 1952). The operational sex ratio is highly biased in favour of bucks and keen competition between them for oestrous does would be predicted. Such competition has indeed been recorded both anecdotally and in the scientific literature (Schneider 1976; Holley & Greenwood, 1984).

There is an important distinction between competition where the contestants have never met before and competition where the opponents have interacted previously and as a result have prior information with which to make an assessment. In the latter category animals will be more likely to use asymmetries to settle contests without indulging in costly fighting (Maynard Smith, 1982). The most frequent high intensity interaction between bucks competing for a doe takes the form of one buck chasing another to a greater distance from the doe without any physical contact between them.

Competition for a resource will normally give the opportunity to measure social dominance between individuals, reflected by differences in their resource-holding power (Parker, 1974). However in a number of species it has been found that individuals respect 'ownership' of a resource so that an animal in possession will not usually be supplanted from the resource by another whatever their respective status. Respect of ownership is perhaps most strikingly demonstrated in a territorial context but also extends to certain kinds of feeding sites and to receptive females. In a study of olive baboons Packer (1979) found that dominant males would defer to subordinate males while the latter were consorting with oestrous females. Male lions are conspicuous in the extent to which they respect another's temporary ownership of a female (Packer & Pusey, 1982). In general, respect of ownership seems to occur in species where the risks of injury during a one-on-one fight are high (Packer & Pusey, 1985).

Although the question was not specifically addressed, it seems that respect of ownership was not evident in two studies of brown hares at artificial feeding sites (Lindlof, 1978; Monaghan & Metcalfe, 1985) both of which produced strong evidence of hierarchies within the hares visiting the sites. The object of this study was to look for a dominance structure in the breeding season relationships of brown hare bucks and, in the absence of respect of ownership, for any correlation between dominance status and access to oestrous does.

Methods

The study area comprised fields 16 and 17 totalling approximately 10ha being unimproved pasture used for cattle grazing. During the period of this study, which ran from 1 May to 31 July 1982, the area was under observation for a total of 176h in 100 separate periods on 78 out of the 92 days. Observation periods were for the most part during the first two hours after sunrise and the last two hours before sunset. A record was kept of all hares seen in the area distinguishing between known and unknown individuals. A total of seven known hares were recorded in the area, two does and five bucks. Unfamiliar individuals were only occasionally seen and escorting of either of the known does by strange bucks was never observed. Records were kept of all chases and their outcome, of all consortships (defined as one hare consistently keeping within 10m (and often much less) of another) and of all satellites (defined as any hares consistently accompanying and keeping within 50m of a consorting pair). It is not unusual for chases to be repeated many times as the animal which has been pursued keeps returning to the area from which it has been chased. When such repeated chases occurred during any observation period they were counted as two chases only, no matter how many repeats there were. Commencement of oestrus of each of the two does was observed, that of Celandine on 11 July and that of Clover on 25 July. Celandine's previous oestrus had been on 23 May in field 5, just across the lane from the study area.

Results

Table I shows by name the known individuals and the number of days, out of the possible total of 78, on which they were observed within the study area. Cicero was seen on only 5 days. Chestnut was noted the most frequently - on 46 days. Cadet disappeared after 19 June and was not seen again either inside or outside the study area.

During the study, 31 chases between bucks were recorded (Table II). These were made up of 10 repeated chases and 11 single chases. In five of the single chases the presence of a doe in the immediate area was not detected but as does are more secretive than bucks it is quite possible that some were overlooked. In the remaining single chases and all the repeated chases there was a doe in the immediate area. The outcome of chases between the two individuals was always the same and was not affected by respect of ownership of a doe. Two chases involved the supplanting of a consorting buck by another, in one case on the day of the doe's oestrus. Nor did it make any difference with which of the does the bucks were seeking to consort. For example, of the five chases by Bolingbroke of Cavalier, two were when Bolingbroke was consorting with Celandine, two were when he was consorting with Clover and one was when he supplanted Cavalier from Clover. To test for a hierarchy it is only reliable to use the data from those chases involving the three hares each of which contested with the others, namely Bolingbroke, Cavalier and Chestnut. The chases involving Cicero all took place on one day and there were no interactions with Cavalier. Cadet who

Table I. Occupation of the study area by known individuals during 78 days of observation 1 May - 31 July 1982. *Cadet disappeared after 19 June

Name	Sex	Number of days on which seen	% of total
Bolingbroke	buck	20	26
Cicero	buck	5	6
Cavalier	buck	27	35
Chestnut	buck	46	59
Cadet	buck	16*	21
Clover	doe	32	41
Celandine	doe	22	28

disappeared halfway through the study only interacted with Chestnut, losing all eight chases. That leaves the 15 chases or contests involving Bolingbroke, Cavalier and Chestnut. Using the binomial formula the probability of obtaining no reversals where Bolingbroke is dominant to Cavalier who is dominant to Chestnut = $(0.5)^{15}$, $P<0.001$. These three hares formed a highly significant hierarchy.

Table III, by reference to days before oestrus and the time of first sighting in any observation period (commencing with day 35), shows all 38 occasions when one of the does was seen to be escorted by bucks, distinguishing between consorts and satellites. During the period neither of the does was on any occasion escorted by an unknown or unrecognized individual. Using the respective rankings of 1, 2 and 3 for Bolingbroke,

hierarchy of bucks

Table II. The outcome of 31 chases or contests between bucks.

Loser	Winner Bolingbroke	Cicero	Cavalier	Chestnut	Cadet	Totals
Bolingbroke		0	0	0	-	0
Cicero	4		-	-	-	4
Cavalier	5	-		0	-	5
Chestnut	6	4	4		0	14
Cadet	-	-	-	8		8
Totals	15	4	4	8	0	
% Won	100	50	44	36	0	

Cavalier and Chestnut, and excluding the one occasion when Cicero was consort, as his ranking is not clear, it is possible to calculate a mean ranking score for the consort for each day. As Figure 1 shows there was a highly significant increase in the ranking of the consort the closer a doe was to oestrus.

hierarchy of bucks

Table III. Escorting by bucks pre-oestrus. * - consort buck. S - satellite buck

	Days before oestrus						
Celandine	33	22	5	3	2	1	0
Bolingbroke				*	*	*/S	/*
Cicero							*/S
Cavalier			/*		*/S	/*	
Chestnut	*	*	*/S	S	S/	S	S
Cadet		S					

Clover	23	22	19	18	17	16	12	11	10	7	6	3	1	0
Bolingbroke										*/				*
Chestnut			*	*/S	*			S						
Cavalier	*		*	/*		*	*	*	*	S/*	*	*	*	S

Discussion

This study revealed a highly significant dominance hierarchy among the bucks of a small local population. In a total of 31 chases or contests between bucks, there were no reversals and this applied even when the loser was supplanted as consort of a doe. There was no respect of ownership. No fighting or boxing between bucks was observed during the period, in contrast with boxing between does and bucks which was seen on several occasions. Neither the weights nor the ages of the bucks were known, nor was the basis upon which the hierarchy was est-

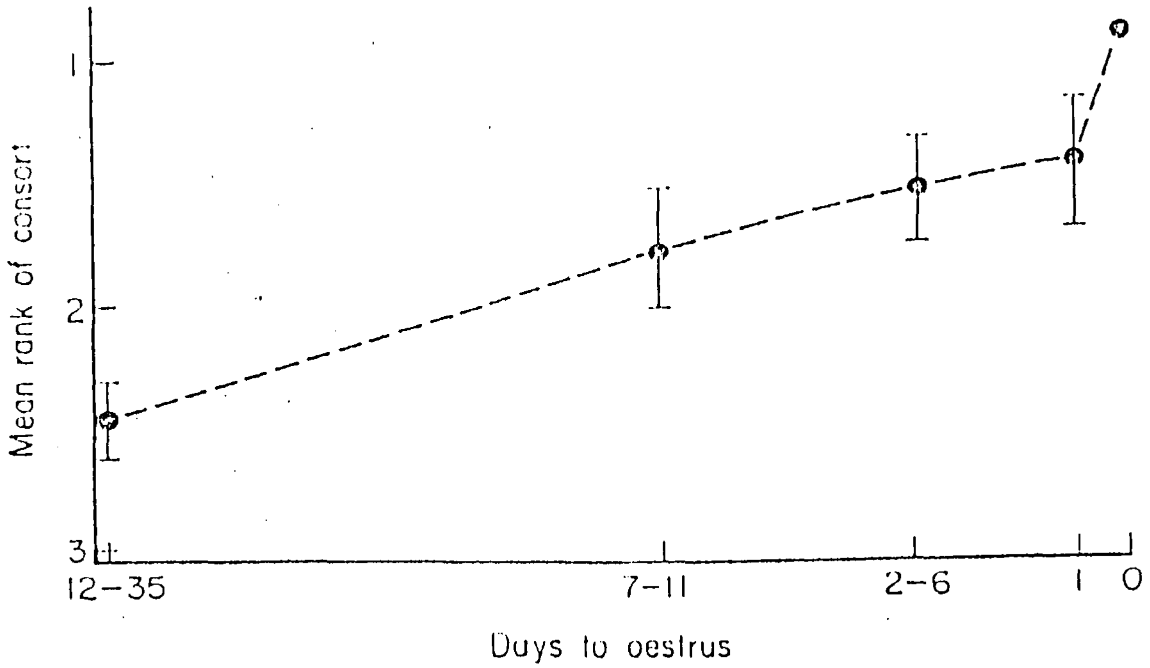


Figure 1. Mean dominance rank of consort (+S.E.) in relation to days to oestrus, $r_S=0{\cdot}701, n=37, P<0{\cdot}001$. Analysis is based on original observations shown in Table III without grouping them into time periods.

ablished. The contests were observed during the latter part of the breeding season at a time when there would perhaps be the least uncertainty between the bucks as to their place in the rank order. Lindlof's (1978) results, however, seem to indicate male dominance rankings as being equally well established considerably earlier in the season. His observations, made between mid-March and mid-April, were of competitive interactions between individuals of both sexes at an artificial feeding site in Sweden. In the total of 172 interactions or contests there were 38 reversals where the subordinate ranking animal won the contest. Lindlof did not separately analyze and compare between-sex contests and within-sex contests. Looking at his data, there were significantly more reverses in between-sex encounters $x^2=11.03$, $P<0.001$. 1 d.f. Out of 124 between-sex contests, there were 36 reversals, whereas out of 48 within-sex contests there were only two reversals, and these were between does.

Throughout the breeding season, bucks visit does and consort with them for variable periods of time. It will be noted from Table I that the number of days on which each of the three bucks tested for dominance, namely Bolingbroke, Cavalier and Chestnut, were observed in the study area was in inverse order to their dominance ranking. That suggests that a dominant buck has a larger home range than a subordinate one which personal observation confirms. In this study, the nearer a doe was to oestrus the higher the rank of any consort was likely to be. Because at oestrus many does are escorted by a consort and also one or more satellites, consortship is unlikely to guarantee copulation but only to give an advantage.

CHAPTER 5

BEHAVIOUR OF PRE-PARTUM DOES

Introduction

Hitherto there has been no study of the behaviour of wild does pre-partum. As oestrus usually occurs within a few days post-partum (Lincoln 1974) and nursing of litters continues for about four weeks, does having their second or third litter of the season are likely to be suckling their preceding litter during the first half of the gestation period of 42 days (Broekhuizen & Maaskamp 1980). In the next Chapter I report that suckling does when away from their litter, which they visit for a few minutes only once in each 24h period, are to be found within 300m of the litter. This Chapter is concerned with the whereabouts and behaviour of does in the later stages of gestation. During the course of this study there were four cases where does which were known to have dropped a litter had been under observation for some time before that event (Table I). Although no births were seen, the date of birth could be estimated to a believed accuracy of ± 3 days based on the evidence set out in the Table. Although a small sample, comparison of the behaviour of the does indicates the possibility of at least some of them having the choice of two behavioural strategies for determining the

Table I. The pre-partum does

Doe	Estimated date of parturition	Estimate dased on
Bluebell	13 June 1981	suckling of day old leveret
Clover	24 July 1982	development of prominent nipples and observation of post-partum oestrus
Fuchsia	2 Aug. 1985	development of prominent nipples and estimated age of suckling leverets
Fuchsia	5 Sept. 1987	development of prominent nipples and estimated age of leverets she was visiting nightly, although suckling was obscured from view

eventual birthsite of the litter. Leverets are born in the open, their only protection from predators being their immobility and their crypticity in relation to their surroundings. For the first few weeks of their lives they are only familiar with and therefore restricted to a very small area of ground. Accordingly it is of importance that the prospective birth place and its surroundings should be so chosen as to optimize the leverets' chances of survival and I will be suggesting that the does' strategies are linked to this imperative. I also examine a possible example of pre-partum defence of the prospective birthsite.

The four pre-partum does

pre-partum does

(1) Bluebell. 24 May - 18 June 1981. This doe was first described on 24 May 1981 on taking up occupation in field 17, 20 days pre-partum. The field, comprising 4.37ha of unimproved pasture, immediately adjoined Ferndale. Vegetation at the time was thin, but some of the grasses were flowering and many thistles were growing. The field was used throughout the season for rough grazing and on 24 May there were 12 bullocks in it. To them 30 sheep were added on 2 June. On average, there were three hares including Bluebell in the field each day. Regulars were two bucks, Boris and Barnum.

Bluebell was under observation on 17 out of the 20 days pre-partum for a total period of more than 30 active (out of form) hours divided as to 11.5h spread over seven days, during the first 10 days of the period and as to 18.5h spread over each day of the second 10 day period. Sunrise to sunset was around 0400 to 2020h. The most frequent time of observation was 1900/2000h but there were regular checks at 0800 and 1730h (Table II).

The assumed birth place of Bluebell's litter is marked in Figure 1 and was at the junction of two field drains. From there the day-old leveret emerged to be suckled on 14 June. Also marked are the focal areas occupied by Bluebell two hours before sunset on each of the observation days. The two points near the centre of the field are those occupied on days 20 and 19 pre-partum. Apart from those two days, the location of the doe in the morning was never more than 50m from the position occupied by her in the evening. During observation periods she generally moved no more than was necessary to continue to graze. It can be seen that in the last 10 days pre-partum the doe frequented areas within a radius of 40m of the birth place. She was

pre-partum does

Table II. Bluebell pre-partum. Periods of observation, divided as to solitary and escorted

Date	Observation period/s		Solitary(h)	Escorted(h)
24 May 1981	1800-1900		1	
25	1945-2045			1
26	1800-2100		3	
27	1730-1815	1915-2030	1.5	0.5
28	1720-1750	1845-2015	0.5	1
1 June	1800-1900		1	
2	1830-2000		1.5	
3	1900-1930		0.5	
4	1900-2100		2	
5	1900-2000		1	
6	1800-1900		1	
7	1800-2000		1.5	0.5
8	1830-2000		1.5	
9	1730-1830	1930-2030	2	
10	1730-1830	1930-2130	3	
11	1800-1900		1	
12	0845-0915	1900-2030	2	
	Brief checks 0800 and 1730 daily		2	
	total		27	3
	%		90	10

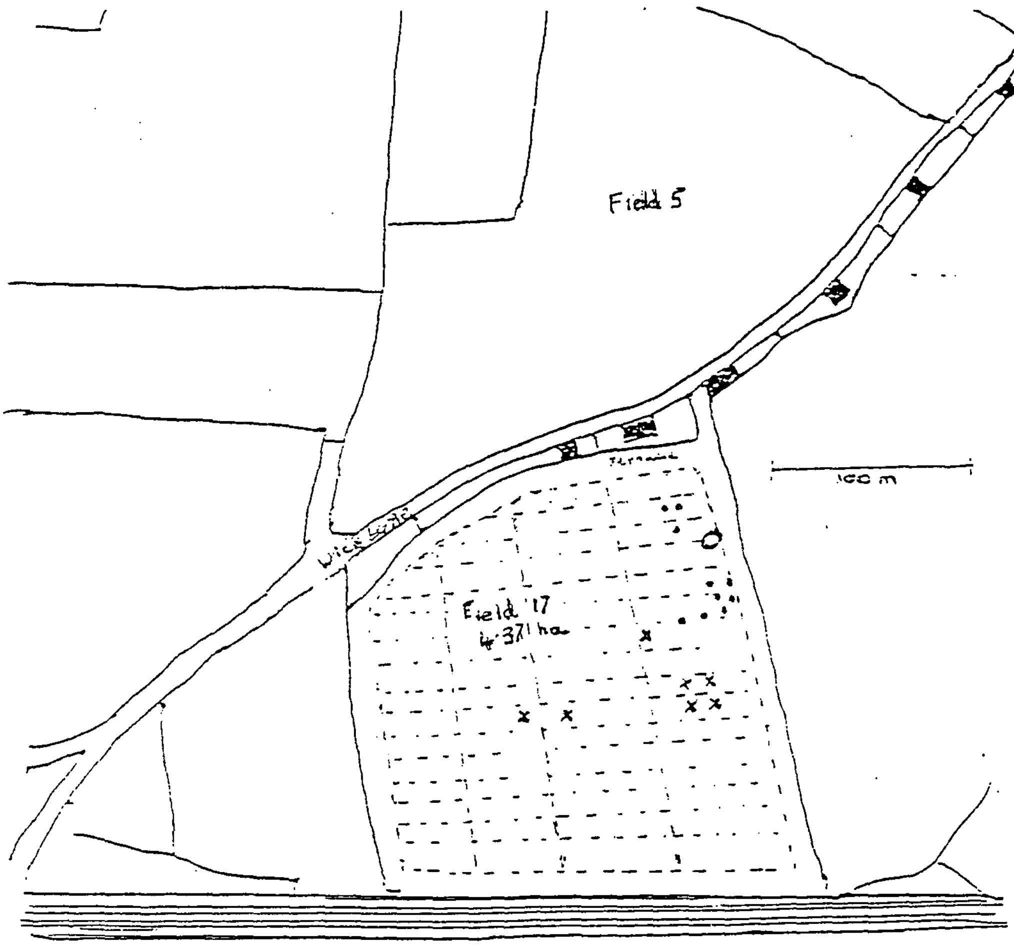


Figure 1. Bluebell pre-partum 24 May to 13 June 1981. Showing birthsite of the litter - 0 : location of Bluebell, two hours before sunset, on seven days between 20 and 11 days pre-partum -x and on each of the following 10 days -●. Also showing run of the field drains.

not, however, seen at any time either resting orgrazing at or within five metres of the birth place. The doe did not leave the area to lie up during the day but did so either in the thistle beds or, on some days, in the shelter of the ditch. Activity period - time out of form (see Chapter 3) - extended from before 1700 to after 0800h, i.e. more than 15h. On the day of parturition she went to her form at 0930h and emerged at 1530h - a lying up period of only six hours.

During the 29h of observation Bluebell was solitary for 26h and escorted by one or more bucks for three hours, representing 10% of the total. During the last seven days pre-parturition she was escorted for 0.5h (4%) out of 12.5h of observation (Table II). After parturition on 13 June Bluebell left the field only entering it after sunset to suckle and was not again seen in it during daylight hours until 17 July. Her post-partum oestrus took place elsewhere.

(2) Clover. 2 - 14 July 1982. This doe was first described on 21 May 1982 on taking up occupation in field 17. At that time she was post-partum, the daily increase in the prominence of her nipples suggesting that she had entered the field immediately following parturition. I was unable to locate the litter she was then suckling, but each evening around sunset she was leaving field 17, crossing the lane and ditch and entering field 5. Clover's regular occupation of field 17 ceased after 2 June but resumed on 2 July when she was an estimated 17 days pre-partum. As in 1981, field 17 was used in 1982 for rough grazing. There had been 15 bullocks in the field but these were moved out on 2 July and during the period in question the field was unstocked. Much of the vegetation had been grazed but some grasses were flowering and there were beds of thistles. Again as in

1981, there were on average 3 hares including Clover in occupation of the field each day. Another doe, Celendine, had her oestrus in the field during the period. Regular bucks were Chestnut and Cavalier.

Clover was under observation on 15 out of the 23 days pre-partum for a total period of more than 20 active hours. Sunrise to sunset was around 0410 to 2025h. The most frequent observation time was 1830/1930h. There were regular brief checks at 1700h but only one in the morning (Table III).

This doe dropped her litter out of the field. Following parturition she was again, as she had been late May, leaving the field around sunset and crossing the lane at the same place to enter field 5 to suckle a litter which was not located. Clover was later seen suckling her last litter of the season in that field. During observation hours pre-partum, Clover ranged all over the field. She was on the move for at least part of every observation period and during any such period never moved less than 50m. Although some of the movements were more than 200m she was not seen in any other field during daylight hours. The doe was regularly active in the field for more than 2.5h before sunset and was probably lying up there. The length of her activity period is not known.

During at least part of every observation period Clover was escorted by one or more bucks. Out of the total of 20.5h she was escorted for 14h, representing 68%. During the last seven days pre-parturition she was escorted for 6.5 (92%) out of the seven observation hours (Table III). After parturition Clover remained in field 17, had her post-partum oestrus there on 25 July and was still in regular occupation in August.

(3) Fuchsia. 17 July - 2 August 1985. This doe was first

pre-partum does

Table III. Clover pre-partum. Periods of observation, divided as to solitary and escorted

Date	Observation period/s		Solitary(h)	Escorted(h)
2 July 1982	1900-1930			0.5
3	1900-2000			1
6	1830-2100		2	0.5
7	1830-1930	2015-2115	1	1
8	1730-1930	2015-2045	2	0.5
9	1845-1945		0.5	0.5
13	1830-1930			1
14	1830-2030			2
15	2015-2115			1
16	1800-1930		0.5	1
17	1730-1800			0.5
18	0600-0630	1830-2030		2.5
19	1830-1930			1
22	1945-2045		0.5	0.5
24	1730-1930			2
		total	6.5	14
		%	32	68

described in March 1985. She took up regular occupation in field 5 on 17 July 1985, having spent the previous two weeks or more in the adjoining field 6. Field 5, comprising 4.25 ha of unimproved pasture, lay immediately across the lane from Ferndale. It was used throughout the season for rough grazing for 12 young heifers. Much of the vegetation in the field consisted of tall flowering grasses. There were no other hares regularly occupying it.

During the 16 days pre-partum there were 19 observation periods - at least one every day (Table IV). The doe was not seen on 19 or 20 July nor on 1 August. She was under observation for a total of 24.5 active hours on 13 days. Sunrise to sunset was around 0430 to 2005h. The most frequent observation period by me was between 1900/2000h. There were, however, three during the early morning.

The regular nursing point and assumed birth place of Fuchsia's litter is shown in Figure 2. As in the case of Bluebell, it was at the point of junction of two field drains on the periphery of the field. This junction was within 20m of the lane and within 25m of the nearest house. Also marked on the plan are the focal areas occupied by Fuchsia on 13 days pre-partum. The positions shown are all as at one hour before sunset with the exception of one, 12 days pre-partum, which is at 0630h. During observation periods the doe generally moved no more than was necessary to graze progressively. The focal points are seen to be grouped in an area 100-150m across the field, but opposite to, the assumed birth place. The doe was not leaving the area to lie up during the day but was doing so in field drains. Some days she was seen emerging at about 1730h. Her activity period totalled about 14h, 1730-0730h.

pre-partum does

Table IV. Fuchsia pre-partum. Periods of observation, divided as to solitary and escorted

Date	Observation period/s	Solitary(h)	Escorted(h)
17 July 1985	1800-2000	2	
18	1800-2000	2	
19	1800-2000		
20	1800-2000		
21	0515-0715 1800-2000		2
22	1900-2000	1	
23	0515-0715 1830-2030	1.5	0.5
24	1900-2000	1	
25	1830-2030	2	
26	1830-2000	1.5	
27	1730-2000	2.5	
28	1730-2000	2.5	
29	1800-2000	2	
30	1800-2000	2	
31	0615-0645 1830-2000	2	
1 August	1800-2000		
	total	22	2.5
	%	90	10

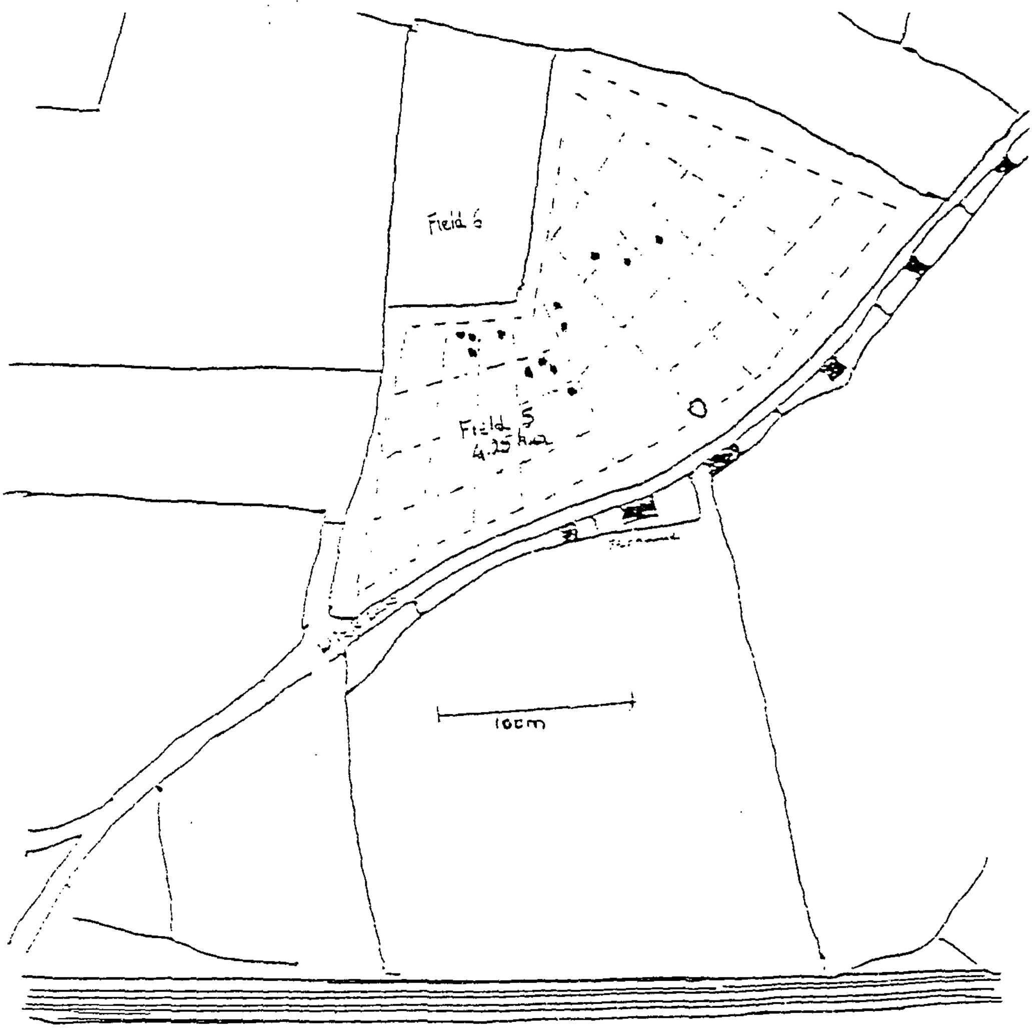


Figure 2. Fuchsia pre-partum 17 July to 2 August 1985. Showing birthsite of the litter - 0 : location of Fuchsia on 12 out of the 16 days pre-partum one hour before sunset and on one of the remaining days at 0730h -•.

pre-partum does

During the 24.5h of observation Fuchsia was solitary for 22 and escorted, by a single buck Ebenezer, for 2.5h - 10% of the total. During the last seven days pre-partum in 12.5h of observation she was solitary throughout. After parturition on 2 August Fuchsia was in field 5 during the evening of the following day and again during the evening of 6 August. After that she was not seen in the field except after sunset to suckle her litter of three.

(4) Fuchsia. 22 August - 3 September 1987. Twenty minutes after sunset On 22 August 1987 Fuchsia was seen emerging from a field drain in field 9. This field comprised 4.25ha of unimproved pasture and had been grown for hay which was mown at the end of July. It was unstocked at the time but eight Friesian bullocks were put onto it on 27 August. She may well have been occupying the field before 22 August unknown to me because observation had been concentrated on another part of the study area. There were no other hares in regular occupation of the field. When first seen I suspected, wrongly as it turned out, that Fuchsia was already nursing a litter. With a view to studying nursing behaviour, observation was focussed upon her during the hour immediately following sunset on 10 out of the next 13 days. There was also one period of observation around dawn making a total of 12 hours.

The area in field 6 in which Fuchsia's litter was dropped on or about 5 September is shown on the plan at Figure 3. Field 6 comprised one hectare of unimproved pasture which had been mown for hay at the beginning of August. It had not subsequently been stocked and was the only unstocked field in the area at the time of parturition. Also shown on the plan at the south end of field 9 is the approximate birth

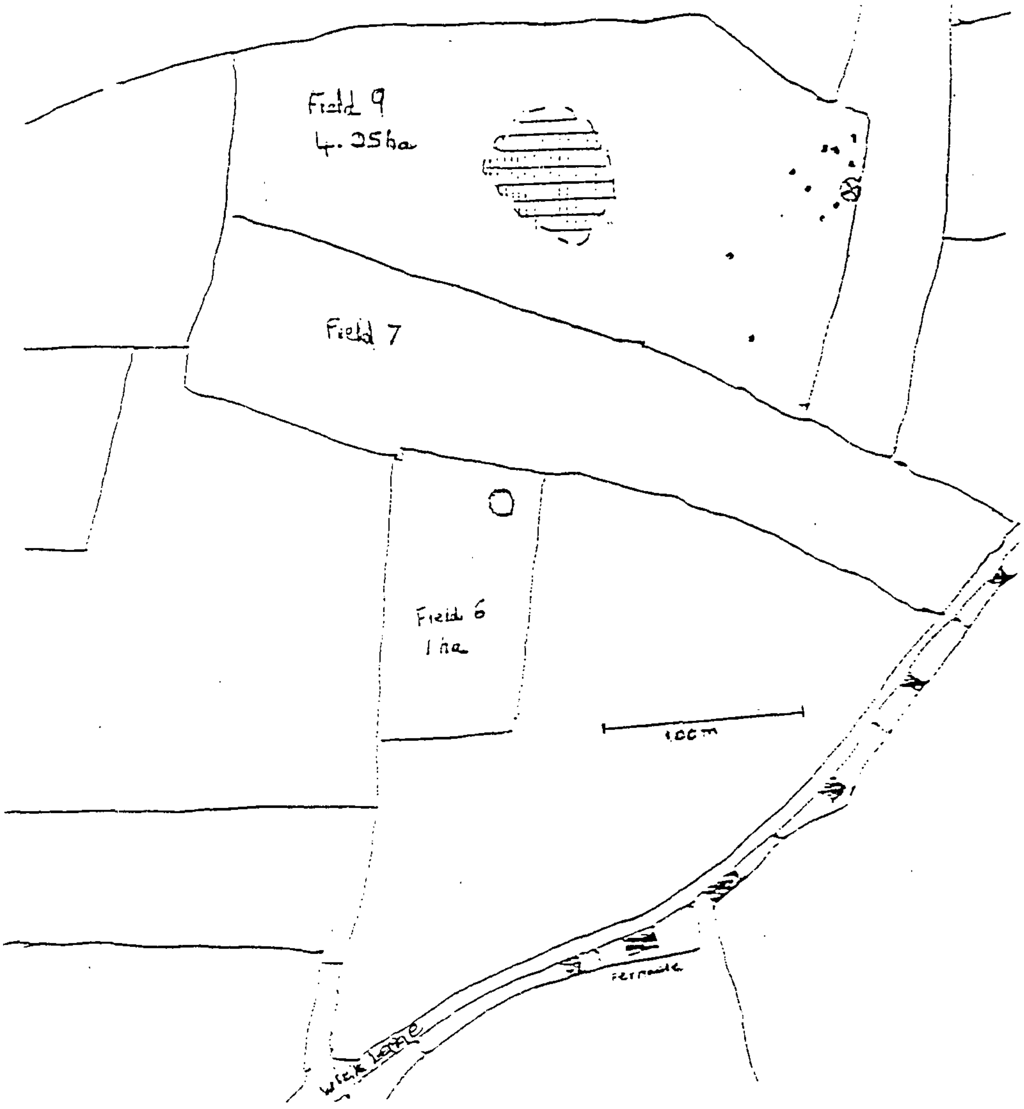


Figure 3. Fuchsia pre-partum 22 August to 5 September 1987. Showing birthsite of the litter - 0 : birthsite of Fuchsia's last litter of 1986 - ⊗: location of the doe on the 10 observation nights at 50 mins after sunset -•. Also showing, hatched, the area in which she was lying up by day.

place of Fuchsia's last litter of 1986, born on or about 8 September - (see Chapter 6). Finally, there are shown the general area in which Fuchsia was lying up during the day and her approximate position on each of the 10 nights of observation pre-partum at 50 mins after sunset, being the mean time at which Fuchsia had commenced suckling previous litters. It will be seen that Fuchsia's positions at that time were grouped around the area in which the last litter of 1986 was born. It consisted of the edge of a drainage ditch where there was a considerable quantity of live and dead vegetation which had not been reached by the mower. Initially the doe was moving down to that end of the field soon after sunset, but after the bullocks had been put in she arrived later, nearer to what would be nursing time. Her nipples were not showing and by extending the length of the observation period I found that she was not in fact suckling on those occasions. During five out of the last six observation periods pre-partum the bullocks were at the extreme south end of the field when Fuchsia arrived. Also they had consumed much of the ditch edge vegetation. These factors may have contributed to a change of plan on the part of the doe who dropped her litter somewhere in field 6.

Fuchsia was lying up during the day in field drains in the central area of field 9 as shown on the plan. She was not escorted by bucks during any of the observation periods. After 5 September Fuchsia continued to lie up in field 9 for another 10 days. Following sunset she no longer went down to the south end of the field but made off in the direction of field 6.

Does and carrion crows

During the 10 years of the study I saw 10 instances of hares actively chasing birds, all corvids. There was one chase each of jackdaws

pre-partum does

Table V. Chases of crows by hares

	Hares			
Date	Sex	Name	Approx. days pregnant	Chase repeated
26 April 1985	doe	Unnamed		Yes
16 April 1986	doe	Glory	8	Not recorded
3 May 1987	doe	Unnamed		Yes
23 Aug 1987	doe	Fuchsia	31	Yes
25 Aug 1987	doe	Fuchsia	33	Yes

and rooks, three of magpies and five of crows. At least two and probably all chases of magpies were triggered by the birds sidling up and trying to take a peck at the hare, in two cases a buck and in the remaining case a doe. The chase of rooks was by a buck which had just settled in its form in the early morning when a party of eight rooks landed in the area immediately around it. The buck charged out of its form scattering the rooks which re-grouped and were then again scattered by the buck. In contrast, the chases of crows were unprovoked. The latter are analysed in Table V. All of the chases were by does. Four out of five were repeated and three of the five were by does known to be pregnant at the time. A typical example - at 0500h on 23 August 1987 Fuchsia, then 31 days pregnant, chased a crow at full speed over a considerable distance. At 0540h there was an even more frantic chase. The crow flew ahead of the hare at a height of about a metre and was chased north up the field and then back south, a distance of at least 200m. The chase of jackdaws was in May 1984 by Escallonia, a doe then approximately 23 days post-oestrus. During a period of 10 mins there were 12 chases by her of members of a pair of jackdaws which were frequenting the same part of the field as her, but which were in no way interfering with her.

Discussion

The observations on pre-partum does reported in this Chapter were made at locations where and at times when hares could be studied by the conventional methods employed. Accordingly, excluded from study were areas too densely vegetated to permit detailed observation, such as well grown hay and cereal fields. The results, therefore, do nothing to define the environments preferred by pre-partum does. Likewise, there is no information as to behaviour of the animals during the hours of complete darkness, of which there were about seven per day.

What does emerge from the results is that during the latter part of their pregnancy some does spend much and perhaps all of their time, both active and inactive, within 150m and often much less of the spot where they will drop their litter. Their presence in the area is discreet, in the sense that they move around very little and are only infrequently attended by bucks. Bluebell 1981 is the most extreme example of the behaviour described. She first appeared within the natal area 20 days before parturition. For the final 10 days she was not seen outside a radius of 50m from the birth place of her litter. She was escorted by one or more bucks for 10% of the total time under observation. Post-partum she left the field and had her following oestrus elsewhere.

pre-partum does

Fuchsia in 1985 when 16 days pre-partum took up residence in an area in the same field as, but between 100 and 150m away from, the presumed birth place. This was very close to the road and also to occupied dwellings, which may have caused her to keep further away. Like Bluebell, she was escorted by bucks for only 10% of the time and post-partum she left the field and had her following oestrus elsewhere. For her last litter of 1987, two years later, Fuchsia was occupying unstocked field 9 at least 15 days pre-partum. Each evening, at the time when she would have been nursing if her litter had already arrived, she was visiting the south end of the field, being the same location as that in which she had nursed her last litter of 1986. In the outcome, and probably due to the introduction of cattle into field 9, Fuchsia dropped her litter in field 6, the only unstocked field in the area. In contrast to the other does, during her 16 days pre-partum Clover in 1982 occupied a field separated from the birth place by firstly hedges or fences, then gardens of houses, then the width of the lane and finally a ditch. She did not confine herself to one part of the field but ranged widely and frequently over it maintaining an overt, rather than a discreet, presence. She was escorted by one or more bucks for 68% of the total time. Post-partum she remained in the field and had her following oestrus there. The litter of the brown hare is dropped in one place in the open. The relatively precocious young disperse to an increasingly greater distance, commencing the second or third day after birth, and only re-gather once every twenty-four hours soon after sunset, at the original birth place, to be suckled by the doe. Nursing by the doe takes less than ten minutes, after which she leaves and the leverets are believed again to disperse (Broekhuizen & Maaskamp 1980). This behaviour in its various elements is highly cryptic with the function of avoiding the attention of potential predators to the presence of the litter. Why then should a doe, by her consistent presence in a small area prior to giving birth, run the risk of drawing attention to the area? The answer appears to be that the choice of the birth place and subsequent nursing point of the litter is of importance and that the suitability, or otherwise, of a possible site can only be established either by expensive trial and error or by constant monitoring on site. Such monitoring may show that the possible birth site is on the regular beat of a farmer and his dogs, or of a fox or is the favoured gathering place of the local livestock. It would also bring to light any environmental shortcomings for the litter, such as inadequate shelter in adverse weather conditions. Normally, monitoring would take a passive form but it could also be active. An apparant example of the latter is the behaviour of Fuchsia in August/September 1987 when, following the introduction of cattle into field 9, she commenced arriving at the prospective birth site at the precise time at which she would be arriving to suckle - and found the cattle gathered there on five out of six nights. It is difficult to interpret these nightly visits in any other way than as trial runs.

The ultimate proof of a well chosen birth place and nursing point will be the successful rearing of a litter from it. If a site has been successful once then unless the environment has changed, for example by a crop on it having been harvested, it should stand a better than average chance of being successful again. Assuming that the monitoring strategy does carry some costs, it might then be more beneficial for a doe which has reared a successful litter to use the same birth place a second time, but on this occasion to abdicate monitoring and to keep away from the site until dropping her next litter. That strategy may have been adopted in 1982 by Clover which, whilst frequenting field 17, appeared to have dropped three successive litters across the lane in field 5. In her case the monitoring strategy could not have been employed because field 5 was out of view from field 17. Only the outcome of her last litter of the season is known in that she was seen suckling a single leveret in field 5 in October. That leveret would have been the product of her oestrus observed in field 17 on 25 July.

From a sample of four it is impossible to be in any way definitive. The two strategies, the one of residential monitoring of and the other of keeping away from the projected birth place of the litter, may be complementary or alternative or may be only some of a greater number of strategies. It is, however, a sufficiently regular feature of the breeding season to find does unobtrusively keeping to a restricted area for periods of several weeks to suggest that the strategy of monitoring is frequently employed. It may also be employed by does of other species. The home range of a radio tagged snowshoe hare doe contracted from 32 to 8 acres for the eight days prior to parturition and in her next litter the range again reduced from 29 to about 8 acres prior to birth (Rongstad & Tester 1971). Flux (1970) showed that the average daytime range of mountain hare does contracts substantially during the breeding season.

The effect of monitoring by does is to disperse part of the population. The monitoring does will be as dispersed as the prospective birth places of their litters. Not only will they be dispersed, but from the results of this study and also from general observation they are likely to be solitary. Of the study does which would have at least one more oestrus that season and thus be of interest to bucks, the monitoring Bluebell in 1981 and Fuchsia in 1985 were escorted by bucks for only 10% of observation time, whereas the non-monitoring Clover in 1982 was escorted for a massive 68% of the time. The differences became even more accentuated when comparing the extent of time spent solitary and escorted during the last seven days pre-partum (Fig. 4). Bluebell and Fuchsia were solitary for respectively 96% and 100% of observation time against only 8% for Clover. Bluebell and Clover were occupying the same field in successive years and in each case the field was also occupied regularly at the time by two bucks. That females have the means to encourage or discourage male attention is considered in detail in Chapter 8, but I am suggesting here that the difference in the extent of escorting by bucks, in the same way as the maintaining of a discreet or an overt presence by the does, is the result of the employment of differing strategies by the latter.

During the study I recorded all instances of hares chasing birds. There was a total of 10, all of which were chases of corvids. Three of magpies and one of rooks were prompted by provocation or disturbance. The remaining five chases of crows and one of jackdaws were unprovoked and were all by does. In the only case involving a doe escorted by a buck the doe chased a crow repeatedly, but the buck did not. Four of the five chases of crows and the chase of jackdaws were repeated a number of times. Three of the chases of crows were by does known to be pregnant at the time. Fuchsia chased a crow more than once when 31 days pregnant and was seen chasing a crow again two days later. These chases were in field 9, the prospective birth place of Fuchsia's litter. I have seen a leveret less than one week old killed

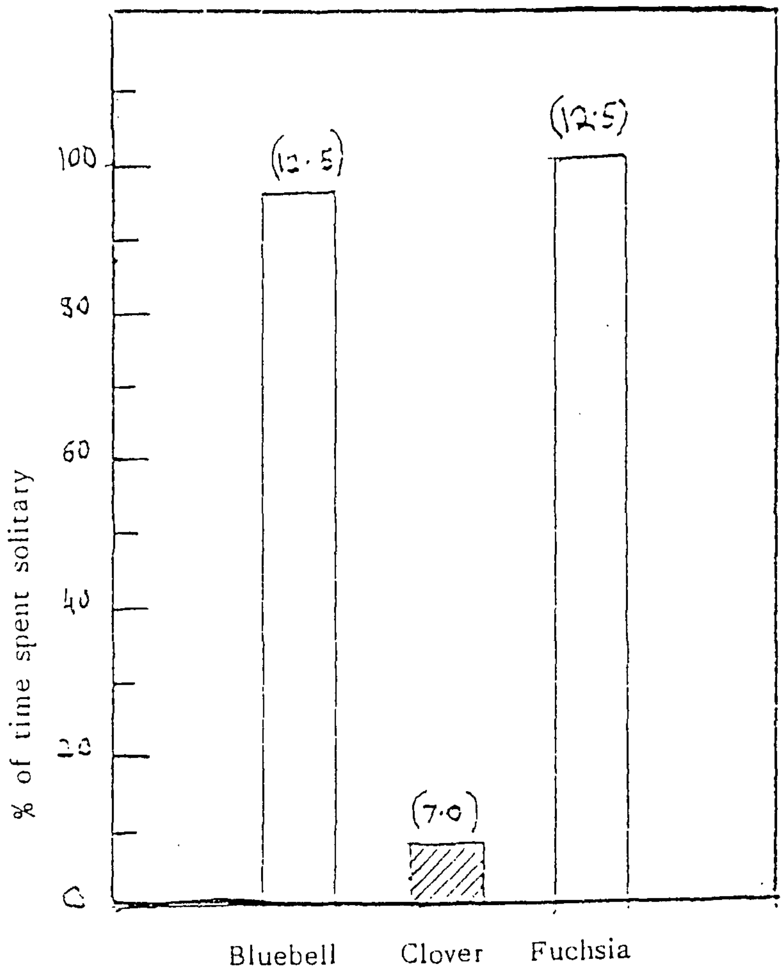


Figure 4. Percentage of observation time spent solitary by three does during the last seven days pre-partum. Unshaded columns for monitoring does (see text): shaded column for non-monitoring doe. The number of observation hours is shown in parenthesis.

by a pair of crows. Predation by hooded crows on young hares was observed on Southern Sweden (Erlinge, Fryelstam et al. 1984) These observations suggest that pre-partum does have a propensity to chase crows away from their own vicinity, which is also likely to be the vicinity within which they will be dropping their litters. The doe leaves the area after parturition, but perhaps the effect of past chases confers some protection on the litter by deterring crows for the first few vital days.

CHAPTER 6

BEHAVIOUR OF NURSING DOES

Introduction

During the past 20 years work in the Netherlands has revealed much information on the nursing behaviour of does and leverets. The latter, which are born fully coated and sighted, are dropped together by the doe. Within two or three days the litter commences dispersing and progressively move further from the birth place. The litter, however, regathers at the birth place each evening to be suckled by the doe. Leverets start grazing and can digest vegetable matter by their thirteenth day and usually are weaned at about one month old. However, at least some of the final litter of the breeding season are suckled for up to 10 weeks. Apart from the brief daily visit to suckle, the doe keeps herself at a distance from the litter (Broekhuizen & Maaskamp 1980). Similar nursing behaviour has been reported of the snowshoe hare (Rongstad & Tester 1971) and the arctic hare, but in the perpetual summer daylight of the high North the intervals between nursings of the latter were reduced from 24 to between 18 and 19 hours (Aniskowicz et al. 1990).

In the case of the brown hare doe, attention has previously been focussed upon the short period surrounding her arrival and subsequent interaction with her litter at the nursing point. In this Chapter I present data first on the whereabouts of does when away from their litters and of the time of, and factors affecting, their journey to the litter and then I compare data on the time and duration of sucklings of litters on my study area with those from the Netherlands. I report some observations on the behaviour of the doe after suckling and also after she has lost her litter and finally two instances where protection of the litter by a doe might have been involved.

Daytime distance from the litter

No births were observed during the course of this study. It is not known, therefore, how long does remain close to the birthsite after parturition. It is clear, however, that within the space of a few days, probably within 24 hours, they place a considerable distance between themselves and their litter by day and only return to it after sunset to suckle. In the case of five does I was able to observe, during part of the nursing period of their litters, their daytime locations and those of the litters. In addition, the courses taken by the does when visiting the litters were determined (Table I). Figure 1 shows the routes taken by four of the does, the fifth being in another part of the study area. In all five cases the direct distance between the doe and her litter in daytime was less than 300m although some does, by taking a circuitous route, were travelling much longer distances when visiting the litter to suckle (Table I). The distance of the does from their litters was not limited by the extent of their home ranges. Both Celandine and Fuchsia could have been a further 250m from their litters during the daytime

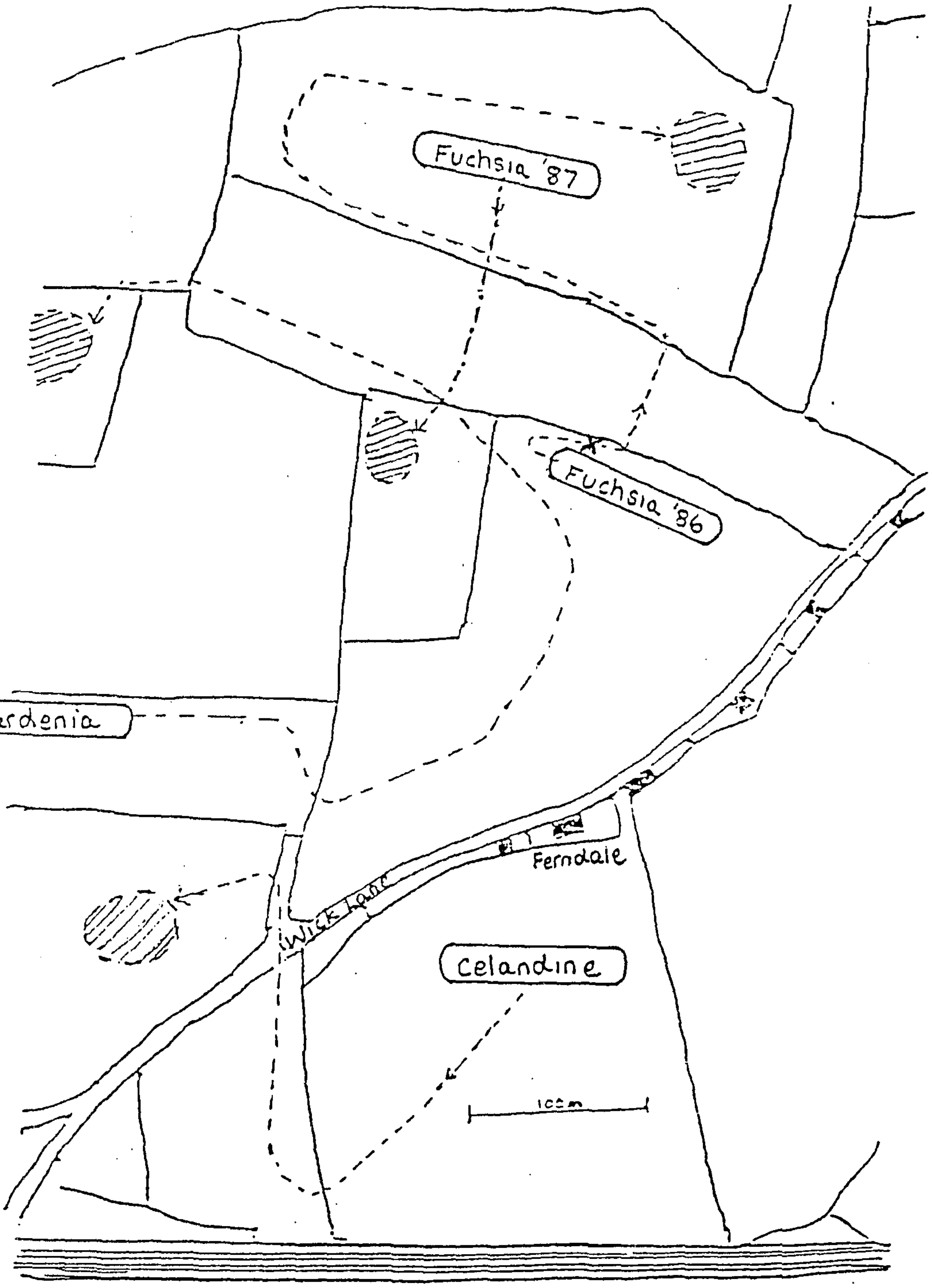


Figure 1. Showing ▭ the daytime lying up areas of four named does and the routes taken each evening to suckle their litters in the hatched areas. Also showing at X the spot from which Fuchsia was able to watch her litter gather before suckling.

nursing does

Table I. Daytime distances - to nearest 50m - between does and their litters, and distances travelled to suckle

Year	Doe	Age of litter (days)	Distance travelled doe/litter (m)	Direct Distance doe/litter (m)	Journeys observed (n)
1982	Celandine	2-6	500	250	4
1986	Gardenia	18-23	800	250	5
1986	Fuchsia	11-23	600	200	6
1987	Fuchsia	2-12	200	200	5
1987	Glory	6-13	300	250	4

and still have been well within their respective home ranges. Except for Gardenia's detour to monitor a fox (see post) does took the same course on each occasion.

Onset of daily visit to the litter

For most of the season does are out of their forms and active in the evening for a considerable time, it can be several hours, before they start the journey to suckle (see Chapter 3). During that time, much of which is spent feeding, they may move around the field in which they have been lying up. For that reason I treated a doe as commencing the journey to suckle when she left the field in which she had been lying up, although in practice she may well have been on the move for ten minutes or more before that. For three does with litters at a known distance, I was able to collect a sequence of departure times. The data for two of them set out in Table II (refer to Figure 1 for the

Table II. The time, in relation to sunset, of departure for their litters of nursing does from their daytime lying up fields and the distances of travel. Also, for Fuchsia, the times of her arrival at the vantage point in parenthesis and of first appearance of her leverets

Date	Departs field	Leverets appear	Age of litter (days)
	(mins after sunset)		
	Celandine - 300m		
6 July 1982	1	-	2
8	17	-	4
9	8	-	5
10	4	-	6
	$\bar{x}$ 7.5 SD ± 6.95		
	Gardenia - 600m		
17 May 1986	6	-	18
18	10	-	19
19	27	-	20
21	21	-	22
22	17	-	23
	$\bar{x}$ 16.2 SD ± 8.42		
	Fuchsia - 550m		
30 Sept 1986	(27) 37	21	14
3 Oct	(23) 31	26	17
9	(35) 39	37	23
15	(20) 35	-	29
	$\bar{x}$ 35.5 SD ± 3.42		

course taken) suggest a departure from the daytime area of around sunset. The circumstances of the third doe, Fuchsia, were unusual in that, from a vantage point on the edge of the field within which she was lying up during the day, she was able to overlook the area of the nursing point about 160m distant. Squatting behind and looking over the top of a small ditchside bush, the position of which is shown on Figure 1, Fuchsia observed her two leverets appear and meet up prior to suckling. It will be seen from Table II that, although she had approximately 500m to travel Fuchsia was leaving her lying up field about 20-30 mins later than the other two does.

Escort on the visit

In total I observed 24 departures from the lying up area and 59 arrivals at the nursing point by does. In Table III these are divided into two groups according to the time of year, those before and those after 18 August: it is exceptional for a doe to come into oestrus after that date. The data presented in Table III tends to show, as would be expected, that does travelling to nurse are more likely to be escorted when pre-oestrus than when post-oestrus, but the difference is not statistically significant ($x_1^2 = 3.66$). That does not, however, shed any light on the important question whether more does leave their lying up areas escorted than arrive escorted at the nursing point. Whilst escort on the early part of the journey might be no disadvantage, as does are at pains to visit the nursing point unobtrusively it would be expected that they would prefer to do so unescorted. Of the five nursing does observed to leave their lying up areas escorted by bucks the two which were post-oestrus separated from their escorts during the early part of the journey. Does are adept at shaking off following bucks at times

nursing does

Table III. Extent of escorting of does leaving lying up areas to suckle and also when arriving at the litter, divided as to journeys before and after 18 August - see text. In parenthesis, does known to be nearing oestrus

Before 18 August		After 18 August	
Escorted	Unescorted	Escorted	Unescorted
	leaving to suckle		
5(3)	5	1	13
	arriving to suckle		
1(1)	8	0	50

when they wish to be unaccompanied (personal observation) and these appeared to be examples of such behaviour.

The three cases where a pre-oestrus doe was observed to leave for her litter escorted by a buck all related to the doe Celandine and occurred on the evenings of 6, 8 and 9 July 1982 (Table IV). The circumstances are looked at in detail because they are the only example of events which some does must undergo when they are suckling a very young, totally dependant, litter and at the same time are nearing oestrus and becoming an increasing target of male attention. Celandine came into oestrus on 11 July. Her previous oestrus on 23 May was also observed and she would have dropped her litter from that on or about 4 July. The route she took to suckle is shown in Figure 1. It was only possible to keep her under observation during the first 300m of her journey owing to obstruction from foreground objects, but on all three days her escort remained with her throughout that distance. On

Table IV. Celandine post-partum and pre-oestrus. Consort and satellite bucks in the lying up area and escorts on her evening journey to suckle. Dominance ranking of bucks - Bolingbroke (alpha), Cavalier (beta) and Chestnut (gamma)

Date	Days to oestrus	Days post-partum	Evening consort	Satellite/s	Escort to suckle
6 July 1982	5	2	Cavalier	none	Cavalier
8	3	4	Bolingbroke	Chestnut	Bolingbroke
9	2	5	Bolingbroke	Cavalier Chestnut	Bolingbroke
10	1	6	Cavalier	Bolingbroke Chestnut	none

6 July she was escorted by Cavalier, the second ranking buck. She was not in the field on the following day. On 8 and 9 July she was escorted to suckle by Bolingbroke, the alpha buck. The couple were not accompanied by satellite bucks on any of the three occasions. On 9 and 10 July, Celandine was mate guarded (see Chapter 4) all day in her form by Bolingbroke. It was surprising, therefore, to note that on emerging from her form on the evening of 10 July, within 24 hours of her oestrus, Celandine was guarded by Cavalier with Bolingbroke and Chestnut, the third ranking buck as satellites. At 2100h, about the time she normally started her journey to the litter, Celandine was unguarded. Cavalier had left her side and he and Bolingbroke were 20m and 50m from her. Celandine then moved off following her usual route to the litter and this time none of the bucks accompanied her. There were no other does in the area to explain this change from pre-

vious behaviour. The following morning, Celandine was back in the same part of the field with Bolingbroke guarding her against strong competition from three satellites. I observed her oestrus commence during the early afternoon.

Of a total of 59 observed arrivals of does to suckle only 9 were during the period before 18 August. One of that group was the only doe to be escorted and she was pre-oestrus (Table III). At 2155h 45 mins after sunset, on 25 July 1987 she arrived at the nursing point escorted by a buck and there they were joined by the week old single leveret. Almost immediately, but very suddenly, the doe raced off through the long vegetation pursued by the buck. She soon shook him off and four minutes later returned unaccompanied to suckle.

Predators and the visiting doe

On more than 10% of occasions there was a fox in the vicinity as a doe approached the nursing area. In such cases the doe delayed her visit and, by active monitoring, ensured that the fox had cleared the area before she went on to her litter. Two examples of such monitoring follow:-

(a) At 2120h, 20 mins after sunset, on 18 May 1986 Gardenia was following her usual northerly course on the way to nurse her litter. Normally she would have continued along the path shown on the plan at Figure 2. On this occasion she turned and travelled back south in the direction from which she had come. At 2125h she was seen to be tracking behind and parallel to a fox which was moving south close to the border in the adjoining field. Soon after 2130h Gardenia entered the adjoining field by the gate and watched the fox out of the area before again taking a course to the north (Fig. 2). In monitoring the fox she had detoured by some 400m.

(b) At 1920h, 32 mins after sunset on 5 October 1986, Fuchsia was moving south in field 9 towards her two leverets when she spotted, at a distance of 100m, a fox moving north close to the border in the immediately adjoining field. She stopped for the next seven minutes, watching the fox closely as it moved away north, before she ran south to suckle the leverets.

Direction of arrival

The doe may arrive at the immediate nursing area consistently from the same direction, or she may vary the direction from day to day so that it is unpredictable. In the former event the waiting leverets are likely to move towards the doe in anticipation of her arrival with the result that the nursing point, at which the doe meets and suckles them, moves progressively in that direction. Where, however, the doe arrives each night from an unpredictable direction the nursing point is likely to remain constant. For an example of the latter behaviour refer to Table V where, whenever conditions permitted, the direction of arrival of a doe was recorded during the extended nursing period of her last litter of the season. Although the leveret was of an age to be highly mobile, suckling took place in the same part of the field each night. That the same doe can employ either strategy was demonstrated by Fuchsia. Between 11 August 1985, when her three leverets were 9 days old, and 19 August, Fuchsia visited the litter from varying directions and each night they were suckled at exactly the same nursing point. On the other hand between 27 September 1986 when her two leverets

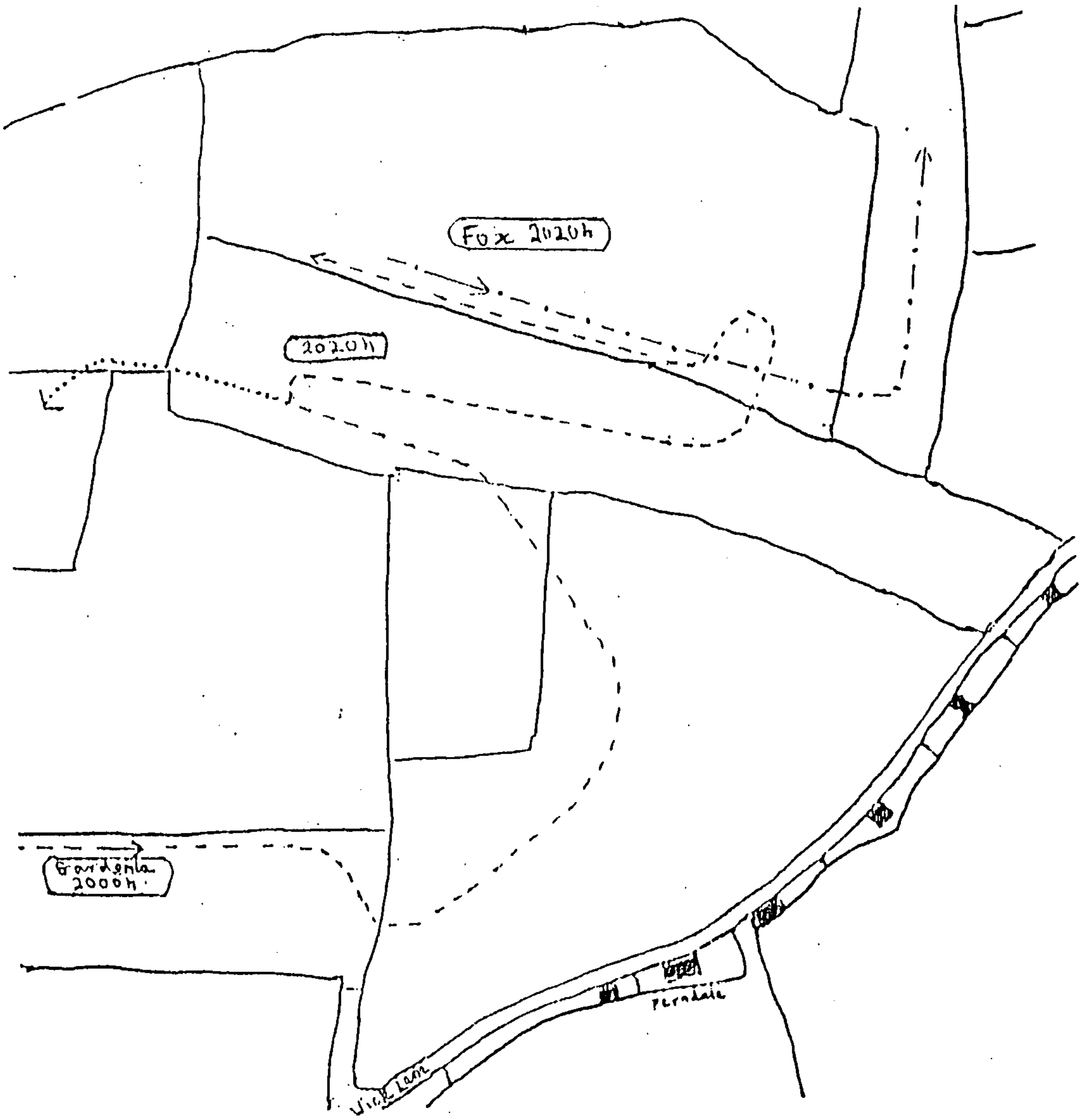


Figure 2. At 2020 h Gardenia, travelling to suckle, spots a fox in the adjoining field. She turns about and, following, monitors the fox out of the area before resuming the journey to her litter. Also showing (..........) the course she would have taken had she not detoured.

Table V. Direction of arrival at the nursing point (NP) of two does, and effect upon position of NP

Doe A

Date	Litter age (days)	Direction of doe's arrival	NP moves - direction (m)
18. Oct 81	31	SE	
19	32	NE	0
20	33	W	0
21	34	NW	0
23	36	NW	0
25 Nov	38	W	0
1.11.	45	SE	0
8.	52	NW	0
		Total	0m

Doe B

Date	Litter age (days)	Direction of doe's arrival	NP moves - direction (m)
28 Sept 86	12	N	
30	14	N	N 25
1 Oct	15	N	0
3	17	N	N 10
4	18	N	N 10
5	19	N	0
6	20	N	N 7
7	21	N	0
9	23	N	N 10
		Total	N 62m

were 11 days old and 9 October she visited the litter consistently from a northerly direction and during that period the nursing point moved north approximately 62m (Table V). Figure 1 (top) shows the probable explanation for her consistent arrival from the north. Each night she entered the field at the easiest and safest point, under the only gate, the field otherwise being surrounded by ditches. If she had then approached the litter direct she would in time have drawn them ever nearer to the gateway and even, possibly, into the adjoining field.

Time of suckling

The arrival of the doe and the commencement of suckling was observed on 49 occasions spread over 10 litters (Table VI). Of those occasions the majority, 27, was in October with nine in August, four each in July, September and November and one in June. The earliest commencement of suckling was 35 mins after sunset on 5 October 1984 and the latest, a doe on the last night of suckling her litter, 88 mins after sunset on 26 July 1988. The mean time of commencement of all observed sucklings was 48 mins after sunset. In the case of the doe Fuchsia I was able to compare times of suckling of litters in successive years - a litter of three, probably the penultimate litter of that year, born about 2 August 1985 and a litter of two, probably the last of that year, born about 16 September 1986 (Table VII). In 1985 the mean time of commencement of suckling ($n = 9$) was 49 ± 4.7 SD mins after sunset and in 1986 ($n = 10$) was 51 ± 6.0 SD mins after sunset showing a close agreement between the two years.

Length of suckling period and duration of a suckling

Of a total of 16 suckling leverets under observation, 10 disappeared, presumed taken by predators, prior to weaning. In consequence,

Table VI. The 10 suckling litters observed 1979 - 88

(a)	(b)	(c)	(d)	(e)	(f)	(g)	(h)	(i)	(j)
1		11 Oct 1979	48	62	1		1	4	
2	Bluebell	14 June 1981	1	1	1	1		1	
3		18 Oct 1981	31	59	1		1	11	9
4	Clover	17 Oct 1982	41	43	1		1	3	2
5		29 Sept 1984	29	51	2		2	7	2
6	Fuchsia	11 Aug 1985	9	17	3-1	2		9	2
7	Glory	6 Sept 1985	3	7	2	2			
8	Fuchsia	27 Sept 1986	11	23	2	2		10	4
9	Glory	31 July 1987	13	13	1	1		1	1
10		24 July 1988	22	24	2-1		1	3	
		Totals			16-2	8	6	49	20

(a) Litter number
(b) Doe - where known
(c) Date first seen
(d) Estimated age *
(e) Age at last observed suckling
(f) Litter size and any reduction during period
(g) Litter probably lost - doe but not leverets at nursing point
(h) Litter probably survived
(i) Timed arrivals of doe (n)
(j) Timed suckling duration (n)

* < 3 weeks ± 3 days
\> 3 weeks ± 7 days

Table VII. Times of arrival of the doe Fuchsia to suckle two litters in successive years. Ages of litters on first arrival nine and 11 days respectively

1985 Date	1985 Doe arrives (mins post-sunset)	1986 Date	1986 Doe arrives (mins post-sunset)
11 August	48	27 Sept	62
12	47	28	52
13	48	30	49
14	43	1 Oct	46
15	47	3	50
16	52	4	41
17	49	5	45
18	48	6	52
19	60	7	57
		9	52
	$\bar{x}$ 49.1 SD ± 4.7		$\bar{x}$ 50.6 SD ± 6.0

the results produced no data as to the length of the suckling period of litters during the main part of the breeding season but the leverets in all four litters from the Autumn, probably the last of the does' breeding season, were suckled for at least 43,51, 59 and 62 days (Table VI).

Sucklings, which are terminated by the doe jumping away from the litter, were timed. All but three of these were from Autumn litters receiving prolonged suckling (Table VIII). Between the second and the eighth week the duration of the average suckling bout had halved. Particular attention was paid to the suckling of a leveret estimated to be about one month old on 18 October 1981. Between that

Table VIII. The duration of 20 timed sucklings, divided into weeks of age of the litters. Separate weekly columns for litters. Showing * sucklings of the litter referred to in the text. Also giving the number and peak of sucklings timed by Broekhuizen & Maaskamp (1980): their results for weeks 5 to 9 were not subdivided.

Age of litter	Timed sucklings			Broekhuizen & Maaskamp	
(weeks)	(mins/s)			n	peak (mins)
2	3-30	3-06		29	3-5
		3-37			
3	2-20	3-11		59	3-4
	1-45				
4	2-40			57	3-4
5	2-30*				
	2-15*				
	2-00*				
6	2-00*	2-00	2-30		
	2-10*	1-40			
7	1-55*	2-20			
	1-40*				
8	1-45*				
9	1-30*				

date and 15 November suckling was observed on 12 occasions and timed on nine of them (Table VIII). During the period the duration of suckling reduced progressively from 150s to 90s.

Interference with suckling

Interference by conspecifics occurred only twice, on successive evenings during the extended suckling period of the leveret mentioned in the preceding paragraph. On the first evening another hare was at the nursing point when the doe arrived and on the second evening another hare came up to the nursing point 30s after suckling had started. On both occasions the doe vigorously chased off the intruder. Interference with suckling by cattle was also observed twice, both of them during the suckling of Fuchsia's litter of August 1985. On the first occasion at 2120h, 43 mins after sunset, Fuchsia was joined by the three leverets at the usual nursing point but was immediately disturbed by inquisitive cattle nearby. The family party moved several times but eventually were suckled at the usual spot at 2132h. Two evenings later cattle had settled at the nursing point, one cow lying over the spot where the leverets usually waited for the doe. Nevertheless the leverets gathered close by. At 2125h Fuchsia arrived in the field drain behind the cow and started to suckle the leverets. The cow got up and went over to investigate whereupon Fuchsia jumped away and loped off, showing a lot of white tail flash, followed by the leverets. Shortly she stopped in another field drain and suckled.

Post-suckling behaviour

In the absence of artificial light, observation of the doe after suckling was generally impossible. However, I used a spotlight in the case of the doe with one leveret which was still suckling in the late Autumn of 1981. On five nights between 21 October, when the leveret was approximately 34 days old, and 8 November the doe remained within 25m of the nursing point for periods between nine and 15 mins and averaging 13 mins after suckling. On at least three of the nights the leveret, which usually followed the doe and rejoined her after she jumped away, was seen to be moving away from the doe before she left in the opposite direction. On the last occasion I observed suckling, when the leveret was an estimated 59 days old, the doe and leveret stayed together in the area for approximately 30 mins after suckling and then left in close company. Another doe and leveret in the Autumn were observed to commence leaving the area of the nursing point in company after suckling when the leveret was approximately 54 days old, 8 days before the last observed suckling.

During periods spent near the nursing point after suckling, does have been seen grooming themselves. On one occasion in good light I was able, from a distance of only 40m, to watch Fuchsia thoroughly grooming her nipples immediately after suckling her three 12 day old leverets.

Protection of litter

During the course of the study there were no unequivocal examples of litter protection, but there were two cases where the circumstances pointed in that direction. These were:-

(a) Some time on 13 June 1981 the doe Bluebell dropped her litter at the junction of two field drains on the periphery of field 17. The 12 bullocks and 30 sheep in the field went through the area of the birthsite many times during that day. On one occasion, Bluebell moved swiftly towards the advancing cattle and settled in front of them in the exact spot from which the day old leveret was observed to emerge the next night to be suckled. I have not seen another case of a hare going towards and settling virtually at the feet of advancing cattle.

(b) At 2030h, 13 mins before sunset, on 7 May 1981 a pair of magpies were seen harrassing a very small leveret which was running away from their aerial attacks and emitting the loud distress scream. An adult hare which had been about 30m away moved over and interacting with the magpies appeared briefly to disperse them. A pair of carrion crows then descended, scattering both the magpies and the hare. Within three minutes the crows had killed the leveret and were beginning to consume it. The hare did not intervene again.

Loss of litter

I had the opportunity to observe the behaviour of Bluebell after the loss of her day old leveret some time on the 14 or 15 June 1981. On 15 June, after arriving at the nursing point at the usual time, she remained within 20m for at least an hour. She returned at the same time the following evening but not subsequently. The notable features of behaviour whilst within the nursing area were:-

(a) Frequent high intensity listening from a stationary position, followed by moving a short distance and then listening again.

(b) The tail carried up and pressed back along the back displaying the white flash of the underside to the full.

In all the other four litters which disappeared before weaning the doe was observed to visit the nursing point at suckling time on one or more occasions after the disappearance.

Discussion

It was known from the studies in the Netherlands (Broekhuizen & Maaskamp 1980) that, except when suckling, does keep at a distance from their litter. One of the effects of that would be to eliminate any possibility of association by potential predators of the presence of the doe with that of her vulnerable litter. Another effect would be to remove from the vicinity of the litter all the high intensity, and visually prominent, interactions (see Chapter 4) attendant upon the post-partum oestrus of the doe. It was not known, however, at what distance does kept themselves from their litters. The results of this study, involving five litters from four does, reveal daytime direct distances of between 200 and 300m between doe and litter. Such distances are less than half those at which in good conditions the human ear can detect the distress screams of leverets (Table VI Chapter 7). The possible relevance of this is discussed in Chapter 7 but if does were to respond immediately to the distress screams of their leverets then, at the distances mentioned, they could, by taking the direct route and assuming a maximum speed of 70 kilometres per hour (MacDonald 1984), be with their litter within 20s. The distance from her litter at noon of one radio-tagged showshoe hare doe, whose position was logged on 8 of 28 days post-partum, was on average 161m (range 30-213m) from her litter and that of another, logged on 8 of 23 days post-partum, was 211m (range 116-335m) (Rongstad & Tester 1971). An arctic hare doe is described as spending "most of the time between nursing bouts alternately feeding and resting several hundred metres from the litter" by Aniskowicz et al. (1990).

Nursing does start their nightly journey to their litter around sunset and arrive about 50 mins later. The approach is a slow one allowing the doe to be watchful throughout. In the one unusual case where a doe could, from a vantage point in her daytime lying up field, see her leverets meet up in the nursing area she commenced her visit considerably later than other does. This suggests that does normally allow a margin of time during the course of their travel from lying up areas to cover unexpected contingencies.

Such is the intensity and concentration of their reproductive effort during the breeding season that most does will experience their next oestrus whilst they are still nursing the previous litter and often within a few days of parturition. During the height of the season from February to the end of May, Broekhuizen & Maaskamp (1981) found an average of 87% of the healthy females to be pregnant in the Netherlands. Hewson & Taylor (1975) show a similar percentage for females in Scotland. If the interval between successive gestations was spread evenly over the population it would therefore be 42/0.87 = 48 days, giving an interval between parturition and the following conception of six days. When approaching oestrus does are the target of highly interactive and competitive attention from the bucks (Chapter 4). There is an evident conflict between the high profile of that attention and the extreme circumspection with which does have all contacts with their litters. How that conflict could be resolved was therefore of some interest. Results from this study throw some light upon the question. The indications are that does will not tolerate the proximity of another adult whilst they are suckling. They rid themselves of such unwanted company either by guile, leading the other hare away from the nursing point and then shaking it off, or, more directly, by chasing it away. Events surrounding the post-partum and pre-oestrus doe Celandine were particularly interesting despite her litter itself being out of sight. During the six or seven days between partum and oestrus she was the centre of attention of three or more competitive bucks. She was mate-guarded by day and on three out of the four observed visits to her litter she was escorted first by the beta buck and on the second and third visits by the alpha buck. Why was it, therefore, that on the fourth visit, with her oestrus following the next day, she left unescorted, the three bucks remaining behind in the lying up area? It must be concluded that the bucks had learnt that it was in some way unprofitable to accompany the doe. That may have been because they had discovered that she would return and the round trip was for them a waste of energy, or because of whatever tactics the doe employed to ensure that she was on her own when she reached the litter.

This study supports the expectation that, when visiting their litters, does would be vigilant for potential predators and would react, if any were detected, so as to protect the litter. The results show that when encountering foxes on the journey to their litter does monitored the fox until it was well clear of the area before resuming their journey. Broekhuizen et al. (1986) report delay of nursing by a doe on two successive evenings on account of a barn own hunting in the area of the nursing point.

Broekhuizen & Maaskamp (1980) appear to state that nursing does approaching their litters generally arrive from the same direction on successive evenings, and this is the interpretation made by Aniskowicz et al. (1990). I believe, however, that Broekhuizen & Maaskamp were saying that in some cases does do consistently approach from the same direction, and that in those cases there is a tendency for the nursing point to move progressively in the direction from which the doe will arrive. The results of this study show that does often use the same route from their daytime lying up area to the general area of the litter. Once there, not all of them consistently approach their litters from one direction. Indeed, individual does can vary the method of approach between one litter and another. The behaviour of arctic hare does approaching their litters seems to be identical to that of the brown hare (Aniskowicz et al. 1990).

Broekhuizen & Maaskamp (1980) collected extensive data on the time of commencement of suckling, which starts immediately upon arrival, from a total of 47 litters spread over the whole of the period from February to November during which lactating females are regularly encountered. On average, nursing started 63 mins after sunset. They did not break down the average on a month by month basis, but it is evident from their Figure 3 that there were some variations and in particular that during September and October nursing started nearer to sunset than in the three preceding months. In this study the mean time of the start of 49 nursings from 10 litters was 48 minutes after sunset. As the majority (63%) of the records were obtained in September and October, and the sample of litters was small, it is unlikely that there is any substantial variation in the time of nursing in relation to sunset between the study area in Somerset and that in the Netherlands.

Information as to the length of the period of maternal care, in the form of suckling in the wild, is limited to the data from 6 litters in the Netherlands given by Broekhuizen & Maaskamp (1980). The three litters born before 18 August were suckled for periods of 23, 32 and 33 days respectively in contrast with the three born after that date which were suckled for periods of 42, 57 and more than 67 days. Very few leverets are born in the Netherlands or in England after the end of September (Broekhuizen & Maaskamp 1981; Lincoln 1974). Hence any litter born after 18 August is likely to be the last of that doe's breeding season. Of the 10 litters observed in this study only four were born before 18 August. Three were predated or disappeared.

The fourth was not located until the leverets were about three weeks old but the age estimate was too approximate to provide useful data. Of the six litters born after 18 August two disappeared and the remaining four were suckled for at least 43, 51, 59 and 62 days respectively. Suckling of the first of the four litters probably continued after 43 days but could not be seen because thenceforth the doe and the leveret were meeting up behind, instead of in front of, a dividing hedge. From the results of Broekhuizen & Maaskamp (1980) and this study the indications are that customarily the last litters of the breeding season are suckled for an extended period of up to eight or nine weeks. That is approximately the same length as the suckling period of the arctic hare, which only has one litter per breeding season, but the latter effects more sucklings because, in the perpetual daylight of the arctic Summer, the doe suckles at intervals of approximately 18 hours instead of 24 hours (Aniskowicz et al. 1990). Extended nursing periods in the last litters of the season have also been reported for the snowshoe hare (Rongstad & Tester 1971), the european rabbit (Lockley 1973) and the swamp rabbit (Sorensen et al. 1972) and may be characteristic for all lagomorphs. Referring to litters born in the main part of the breeding season Broekhuizen & Maaskamp (1980) report that the suckling period is terminated by the doe and not by the young which continue to gather at the nursing point for several evenings after the doe has ceased to arrive. In the light of the prolonged suckling of the last litter of the season it can be deduced that, were she not pregnant and facing the energy demands of production and subsequent maintenance of the next litter, a doe would not bring the suckling of earlier litters to an end after just over four weeks. Their prospects of survival could be enhanced by continued suckling but that would be at a cost to the next litter. This is an example of the difference between the best interests of the earlier litters and the best interests of the doe, that is to say, an example of parent-offspring conflict. According to Trivers (1974), conflict arises whenever parents should not invest so much in current offspring that it will jeopardise their ability to invest in future offspring. On the other hand offspring of polygynous species, such as the brown hare, are selected to demand more than their dam should invest since they are not as related to future young as she is. Even if the probability was that the doe's next litter would be sired by the same buck, there would still be conflict because any parent is only half as related to an offspring as the offspring is to itself. Therefore, the benefit of an act of parental investment for a parent is half the benefit of the same act to the offspring (Robinson 1980). The offspring will be favoured to stop seeking parental investment when, but not before, the cost of the investment is more than twice the benefit it receives.

In their detailed study Broekhuizen & Maaskamp (1980) recorded the duration of a total of 241 individual sucklings of litters. The duration of the 20 sucklings which I noted generally corresponded with their results with the exception of those from the last weeks of extended final litter suckling periods. Broekhuizen & Maaskamp, referring to data from two such litters, say that nursing lasted only about half a minute after the sixth week and that it was reducing rapidly prior to that. My data in Table VIII, particularly those from one such litter, show a very slow decline in the duration of suckling periods, with a duration of 90s being recorded in the ninth week. A similar slow reduction between five and eight weeks post-partum in the duration of suckling of the single litters per season of arctic hares on Ellesmere Island, which are weaned at eight to nine weeks, was reported by Aniskowicz et al. (1990).

By their sixth week of age a litter of arctic hare leverets usually followed their mother away from the nursing site after suckling. With increasing age they followed her for increasing distances until they accompanied her to feeding areas used by other hares. There they came into contact with other adults (Aniskowicz et al. 1990) In this study one leveret receiving an extended period of suckling in the late Autumn was observed on several occasions, from its fifth week onward, moving away from its mother before she left the nursing area. There was, therefore, an opportunity for it to stay longer in its mother's company than it chose to do. On the last occasion it was seen to be suckled, at an estimated age of 59 days, mother and leveret remained in the area of the nursing point for about thirty minutes and then left together. Another seven week old autumn leveret was seen regularly to leave the immediate area of the nursing point in company with its dam. In neither case was it known how far the pair went in company, but it may be that the brown hare also leads the older leverets of its final litter of the season to suitable feeding areas in the period immediately before weaning.

In the results I have included details of two possible instances of defence of the litter by does. As yet there are no records of maternal protection of the young in any leporids, although many of the species, including the brown hare, give high pitched distress calls or screams when captured by a predator (reviewed in Cowan & Bell 1986).

nursing does

This study reveals that does lying up in daytime are within areas from which they would be able to hear any such screams from their litter, and this highlights the question whether they may respond to such screams to which I return in Chapter 7.

I was able to observe at close quarters the behaviour of a doe visiting the nursing point of her two-day-old leveret which had disappeared since the last suckling. It would be expected that the absence of the leveret would bring to the fore those aspects of the doe's behaviour which serve both to detect the whereabouts of the leveret and also to advertise to the leveret her own whereabouts. The predominant activity of the doe was high intensity listening from a stationary position, mirroring the behaviour of a leveret awaiting its dam as described in Chapter 7. Whether the doe was listening for movement on the part of the leveret or for some other form of auditory advertisement is not known. From observations of Bouman & Overton reported in Broekhuizen et al. (1986), that may take the form of clicking of the incisors, to which other hares are stated to react up to a distance of 60m. The most obvious visual advertisement, and probably an olfactory one as well, by the doe was the display of her white tail flash to the maximum extent by pressing the upper surface of the tail forwards along her back. Display of the white tail flash by does is rarely seen - see Chapter 8 in which I suggest that its use as an advertisement to the litter, as here, is its primary function.

CHAPTER 7

BEHAVIOUR OF LEVERETS

Introduction

In common with ungulates (Geist 1971; Lent 1974) and most animals, hares are particularly vulnerable to predation during their first few weeks of life. Not only can they not run as fast or for so long as adults, but they are vulnerable to a greater range of predators as a result of their smaller size. The anti-predator strategy is hiding, relying on minimal activity to avoid detection by predators. Mothers and offspring are in contact for only brief periods when the leverets are nursed (Broekhuizen & Maaskamp 1980). Gradually, as herbivory commences, leverets' activity increases. Accounts of the behaviour of leverets have hitherto been limited to the extent to which they disperse, the times and places at which they converge for nursing, the times at which they are attracted to adults and other leverets and the duration of nursing (Broekhuizen & Maaskamp 1976, 1980; Broekhuizen et al. 1986). In this Chapter I report on and consider the functions of the behaviour of leverets as they converge for nursing and disperse afterwards and also their locomotor play and distress scream.

The daily convergence and dispersal of sucking leverets

Of the 10 litters of varying ages observed during the course of the study, five contained at the time a single leveret (see Table VI Chapter 6). Of the other five, one litter disappeared at seven days of age. Table I sets out data from the remaining four litters as to the times in relation to sunset of onset of evening activity, of siblings meeting, of siblings gathering at the nursing place (two litters only) and of nursing by the doe. It should be noted that in the case of onset of activity the times given are of first observed activity. In many instances the actual times of first activity may have been considerably earlier, because the furtive behaviour of the leverets and their general tendancy to keep to dips and hollows in the ground (personal observation) kept them out of sight. For litters 1 and 3 (Table I) onset of activity was observed before sunset, in some cases by two or three hours, whereas the other two litters were not observed to be active until after sunset. This difference may have resulted from topographical rather than behavioural causes. The nursing points of litters 2 and 4 were in pasture fields in which the grass was low, having been mown for hay or silage. The leverets were lying up by day either at the field verges or in the depressions of field drains. The nursing point of litter 1 was in a former cereal field that had undergone its first ploughing, leaving deep furrows in which the leverets were lying up. Litter 3 was in an unimproved meadow stocked at low density throughout the season in which there was a profusion of tall vegetation. This last field was closer to my observation point than the others, which assisted me in following the movements of the leverets in the vegetation. The earlier commencement of activity in that litter from 12 days of age onward coincided

Table I. Times and duration of meetings between litter mates prior to nursing showing also estimated age of litter at first observation in parenthesis and name of doe where known.

Date	Mins before (-) or after (+) sunset				Time together before nursing (mins)
	Earliest observed activity	Siblings meet	Siblings at nursing point	Nursing commences	
		Litter 1 (29)			
29 Sept 1984	- 42	-42		+34	76
30 Sept	- 30	-27		+32	59
6 Oct	+ 10	+ 8		+47	39
10 Oct	+ 19	+14		+36	22
		Litter 2 (22)			
24 July 1988	+ 38	+38		+60	22
25 July	+ 42	+38		+82	44
26 July	+ 46	+41		+88	47
		Litter 3 (10) Fuchsia			
12 Aug 1985	+ 19	+19		+47	28
13 Aug	+ 13	+16	+29	+49	33
14 Aug	- 67	+18	+33	+43	25
15 Aug	-105	+25	+35	+47	22
16 Aug	-113			+52	
17 Aug	-161	+11	+39	+49	38
18 Aug	-229	+31	+37	+48	17
19 Aug	- 87	+33	+33	+60	27
		Litter 4 (11) Fuchsia			
27 Sept 1986	+ 15	+24	+30	+62	38
28 Sept	+ 15	+22	+35	+52	30
30 Sept		+42		+49	7
1 Oct	+ 22	+34	+39	+46	12
3 Oct		+32		+50	18
4 Oct	+ 23	+28		+41	13
6 Oct	+ 15	+27		+52	25
7 Oct	+23		+42	+57	
$\bar{x}$ (± SD) litters 3 & 4 only		+25.9±8.3	+35.2±4.1	+47.1±13.0	

with the commencement of herbivory by the leverets.

I observed 21 meetings of siblings prior to suckling (Table I). There were three leverets in litter 3 and the time of meeting appearing in Table I is the time of first meeting of any two of them. Nineteen (90%) of 21 meetings were after sunset. The only exceptions were the first two meetings of litter 1, one of which was 42 mins and the other 27 mins before sunset. That litter, as mentioned earlier, was in a recently ploughed field and the absence of vegetation enabled the leverets to see each other as soon as they were active, notwithstanding their forms were about 70m apart. The two meetings of that litter observed 7 and 11 days later were both after sunset. The leverets of litter 3 were active for long periods, in one instance more than four hours, before they met. This was because each kept to its own sector of the field and, owing to intervening tall vegetation, would not have been able to see the others until, after sunset, they all moved towards the nursing point. Leverets did not normally meet at the nursing point but went in company to it at the appropriate time from the meeting place. As shown in Chapter 6, in some litters the location of the nursing point remained the same throughout the nursing period. In such litters, the leverets were likely to meet in the same general area each evening, (see Figure 1 for an example). In other litters, the nursing point moved progressively in the direction from which the doe arrived each evening and the meeting place of the leverets was less predictable.

In nine of the 21 meetings between leverets prior to nursing, I was able to record their behaviour (Table II). In seven cases (78%), the leverets sniffed each others noses. In five (56%), one of the leverets return-streaked and in four (44%), there was stotting by one or more (for descriptions of these behaviours see Table V post). The impression given was of excitement and exuberance, best illustrated perhaps by the two instances of one leveret jumping straight over the top of another. Excited behaviour persisted while the leverets were in the meeting area, a period which varied between five and 28 mins, depending upon the time of meeting. On only one occasion were leverets seen to go direct to the nursing point without first meeting away from it. On the preceding evening, one of the litter of three had been killed by a fox immediately after nursing while the doe and leverets were still together. The home range of the predated leveret ran between those of the other two. The next evening the two remaining leverets made their way direct to the nursing point and were there together at the time they would normally have been joining up at the meeting area. There were no litters close enough to each other to involve the possibility of intermingling, as reported by Broekhuizen & Maaskamp (1980). For comparison, leverets were also watched after weaning and some were seen to join company in the evening but at no other time. Such groups were of two only (Table III) and appeared to be of similar age, but in one dyad were of such dissimiliar appearance that they may not have been siblings. Upon meeting they showed the same excited behaviour as nursing leverets.

About 12 mins before the doe arrived, sucking leverets made their way, usually in company, to the nursing point. The time of this move did not depend upon the time the leverets met. As Table I shows,

Table II. Behaviour between litter mates when meeting prior to nursing.

Litter	Number in litter	Estimated age (days)	Behaviour on meeting
		29	sniff noses; one sniffs back of the other
1	2	36	sniff noses; one sniffs back of the other; stotting by one
		40	short chase; sniff noses; 4 return streaks by one which jumps straight over the other at end of first return
2	2	23	sniff noses
		11	return streak by one; stotting
		12	sniff noses; stotting; return streak by one
3	3	15	return streak by one
		16	sniff noses; return streak by one; one stott jumps over another
		17	sniff noses

when they met earlier than usual, they stayed longer at the meeting area. The behaviour of the leverets at the nursing point was markedly different from that on the meeting area. At the nursing point it was

Table III. The times when in company and behaviour of observed dyads of weaned leverets. * - dyad already or still in company as observation commenced or ceased.

Date	Estimated age (weeks)	Time		Behaviour noted
		Sunset	In company	
27 Aug	6	1910	1920 - 1925	
11 Sept	8	1937	1835*- 1850*	sniff noses; stotting
28 July	6	2006	2015 - 2027	stotting; frequent physical contact
4 Aug	7	1955	2000*- 2035*	sniff noses; one sniffs back of other; frequent stotting
30 July	7	2003	1900*- 1915	stotting
5 Aug	8	1953	2015*- 2030*	
18 Aug		1929	1936 - 2000*	nose sniffing; 3 return streaks
19 Aug	10	1927	1935 - 1945*	
7 Sept	12	1846	1910 - 1930*	

subdued. They squatted up close together always within a metre of, but more often physically in contact with each other. For some of the time they groomed themselves and each other, but for most of it they remained almost motionless, watching and listening for the doe. When she arrived they rushed to meet her. During the hour or so after sunset, leverets would also rush towards other adult hares which passed in their vicinity (Table IV). This applied irrespective of the sex of the stranger. When approached, some adults rejected and chased away the leverets. In some cases, however, the leverets appeared to break off the contact. Not all adults reacted aggresively. At 40 mins after sunset on 25 July 1988, two 23 day old leverets awaiting their doe approached a buck which had come near. Each leveret ran up to him more than six times. Sometimes he turned quickly to face them and sometimes he jumped over them. However, on more than 11 occasions he followed and rejoined the leverets when they had moved on. He also chased each of them distances of a few metres more than 10 times. It appeared to be an example of an adult, other than the doe, playing with youngsters. I have seen similar behaviour between adults and weaned leverets but in those cases have not known whether or not the adult was their mother.

I have no quantitative data as to how soon after nursing leverets move away from each other and from the nursing place. However, on three evenings between 25 October and 1 November 1981, when observing a doe nursing a single six week old leveret, the leveret remained with the doe close to the nursing point for between five and 10 mins after sucking and then moved away from the area before she did. As to the distance to which leverets disperse, I was able in August 1985 to observe closely one litter of three leverets (litter 3 Table I) between the ages of nine and 16 days. They were in a lightly stocked, unimproved meadow with tall vegetation. The leverets were active before sunset (see Table I) giving the opportunity to assess the areas within which they were ranging (Figure 1). At nine days old that

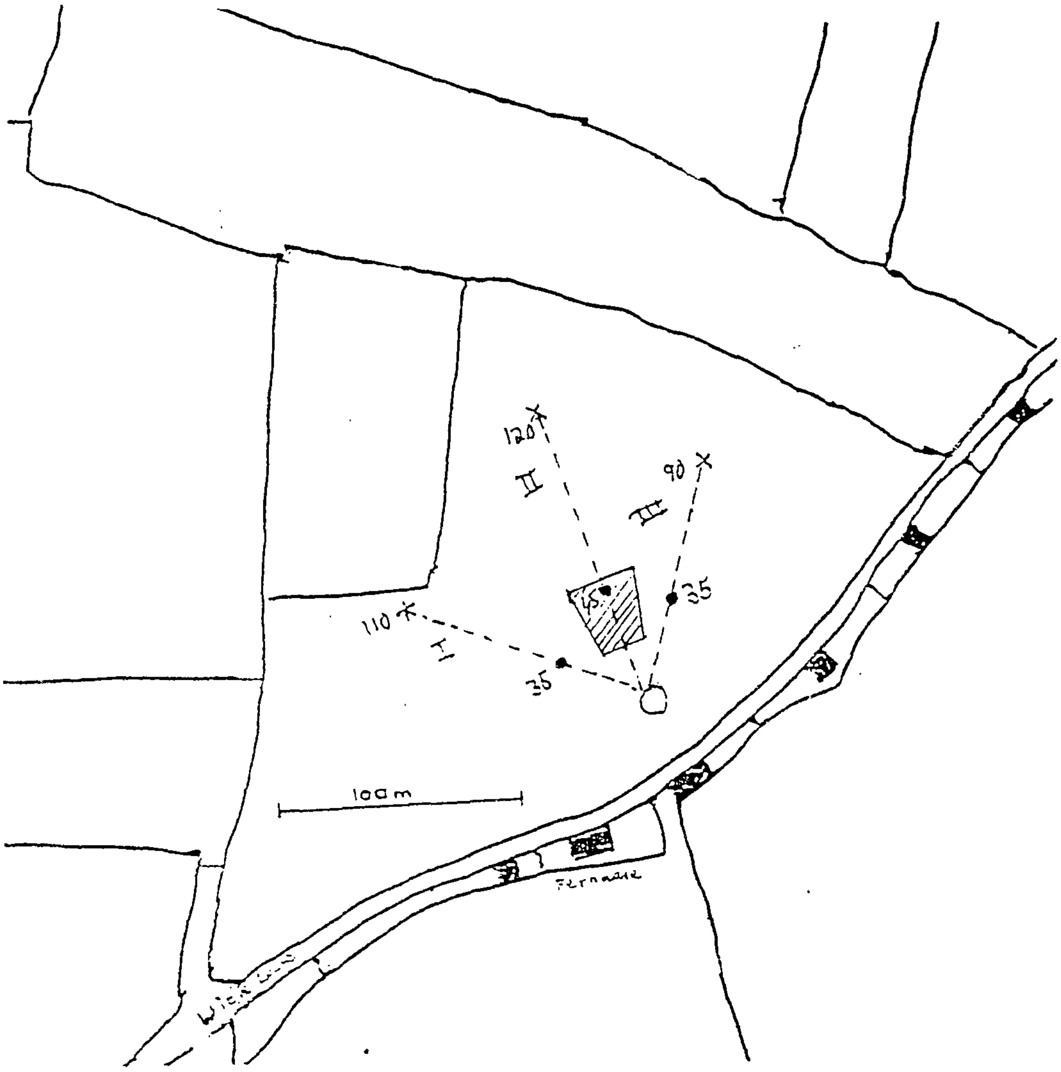


Figure 1. Dispersal of litter of three leverets, August 1985. Showing O-nursing point, ● and X-furthermost limits (m) of leverets' range at 9 and 16 days of age respectively and, hatched, the meeting area of the leverets prior to nursing.

Table IV. Observed approaches by unweaned leverets to adults other than their doe.

Date	Estimated age (days)	Time of approach before (- mins) or after (+ mins) sunset
22 Oct 1981	35	+ 29
20 Oct 1982	44	+ 15
25 July 1988	23	+ 40
26 July 1988	24	+ 26
26 July 1988	24	+ 76

area was within approximately 40m of the nursing point. Seven days later the leverets were at distances in the region of 100m from the nursing point. During exploration, each leveret kept within its own sector with the result, mentioned earlier in the Chapter, that they did not meet until shortly before the doe arrived to nurse.

Locomotor play

Bekoff & Byers (1981) suggest as a definition of play "all motor activity performed postnatally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing". Play can take the form, amongst others, of locomotor play, sexual play, play fighting and object play. The only form of play observed from leverets during the course of this study was locomotor play. The various components of this behaviour, all of which were not infrequently displayed in the absence of conspecifics, are described in Table V. All of the components were performed by leverets but some of them, indicated on the Table, by adults also.

Both young and mature adults and leverets stott, but the frequency of episodes and the number of stotts in an episode are greater in the case of leverets. I have not seen an adult perform more than three consecutive stotts, whereas multiple stotts from leverets are frequent. One seven week old leveret endeavouring to suckle from a doe (possibly its own mother, which had its next litter) was seen on being rejected to stott 14 times and in the process to jump right over the doe. Neither adults nor leverets were observed to display the white underside of the tail while stotting. During the course of the study encounters between foxes and hares were recorded (see Chapter 9). Hares did not stott in the presence of foxes and the behaviour does not carry the signalling-to-predators function of similar behaviour by Thomson's gazelles (Caro 1986).

Streaking is the most spectacular component of all locomotor play, particularly when it incorporates some of the other components. During the last seven years of the study, a note was taken whenever possible of all streaks (in which expression unless the context otherwise indicates I include single, return and multiple return streaks). Details of 38 streaks were obtained. Thirty-two (84%) were by leverets (from at least 13 litters) ranging from seven days of age upwards. Thirty-one of the 32 streaks by leverets, of which 16 (50%) were weaned, were seen in the evening and 29 (94%) of the 31 were during the first 40 mins after sunset, none being seen after that. In five

Table V. The components of locomotor play.

Component	Description	Observed from leverets/adults
Stott	An upward leap from all four legs either from a stationary position or whilst in motion, during which the direction faced by the animal can be changed so as to land reversed or at right angles to the original direction	Leverets and adults
Skater's leap	Upward leap, from a bipedal, stationary or running posture, spinning whilst in the air	Leverets
Extended leap	Long forward leap whilst in fast motion, with fore and hind legs stretched out straight in front and behind	Leverets
Victory roll	Long forward leap whilst in fast motion during which the animal turns over on its back and completes the turn to land on its feet	Leverets and adults
Upstanding run	A bipedal posture whilst in fast motion	Leverets
Streak	A burst of top speed motion, usually in a straight line ahead and then reversed so as to return to the point of departure but sometimes taking a circular route. Streaks are often repeated a number of times and may include any, or a combination of the preceding components	Leverets and young adults
Skipping	Self explanatory, but very occasional	Leverets and adults

(56%) out of nine meetings between litter mates prior to nursing one of them streaked. Of the six streaks by adults, three were in the evening and three in the morning. Ten (31%) of the streaks by leverets and one of those by adults incorporated other components. In at least six (19%) of the streaks by a leveret, but in none of those by adults, the white undertail was lifted onto the back. Three (8%) of the 38 streaks followed a circular route, the remainder were linear. Of the 35 linear streaks, 34 (97%) were return streaks and 17 (49%) were multiple return streaks. The distance covered in one direction of the linear streaks varied from a minimum of four metres by a seven day old leveret to more than 250m by an adult. Twenty-four (69%) were more than 50m, 10 (29%) more than 100m and four (three of them by adults) more than 200m. The indications were that all streaks were by young animals. Streaks by leverets were seen from the beginning of April until the end of October. Streaks by adults were only seen between January and March when some of the previous year's leverets would just be maturing. During seven years, I had under observation 26 identified adults. Some of them were seen in three successive years. None of those 26 individuals was ever seen to streak and I conclude that mature adults seldom if ever do so.

Young leverets confine their streaks to the area with which they have already become familiar. That area, as described earlier in this Chapter, becomes larger each day, giving longer stretches over which to career. Many streaks commenced from the point at which individual leverets and in one case two adults met. A streak by an individual on a subsequent day would be unlikely to be over precisely the same course as on a preceding day. Nevertheless I observed some older leverets making their way to a particular sector of their home range and from it streaking back and forth over the same stretch on separate evenings (Figure 2).

The distress scream

Leverets and adults have a distress call or scream. This appears to be emitted only when the animal is in extremis, being physically attacked by predators or being shot or captured by humans (personal observation). The call is loud and can carry for a considerable distance. Table VI sets out all instances of distress screams heard from leverets where the location and thus the distance from observer of the litter was known. In the one case where the cause of the screams was unknown, the part of the field in which the event was occurring was obscured from view. That litter was not seen afterwards. In three of the remaining four cases (two of which involved predation by foxes) there were no adult hares at the scene and none approached. In the other instance of predation by foxes, the fox struck just after the doe, Fuchsia, had finished suckling her three 16 day old leverets and while she was still in the immediate area. I missed the exact events of the attack and do not know whether Fuchsia attempted to intervene. Although I saw the fox searching the field for the others, only one leveret was taken that night. The instance involving magpies and carrion crows has been described in Chapter 6. A pair of magpies was seen harassing a very small leveret which was running away from their aerial attacks, emitting the loud distress scream. An adult hare, sex unknown, which had been about 30m away, moved over and

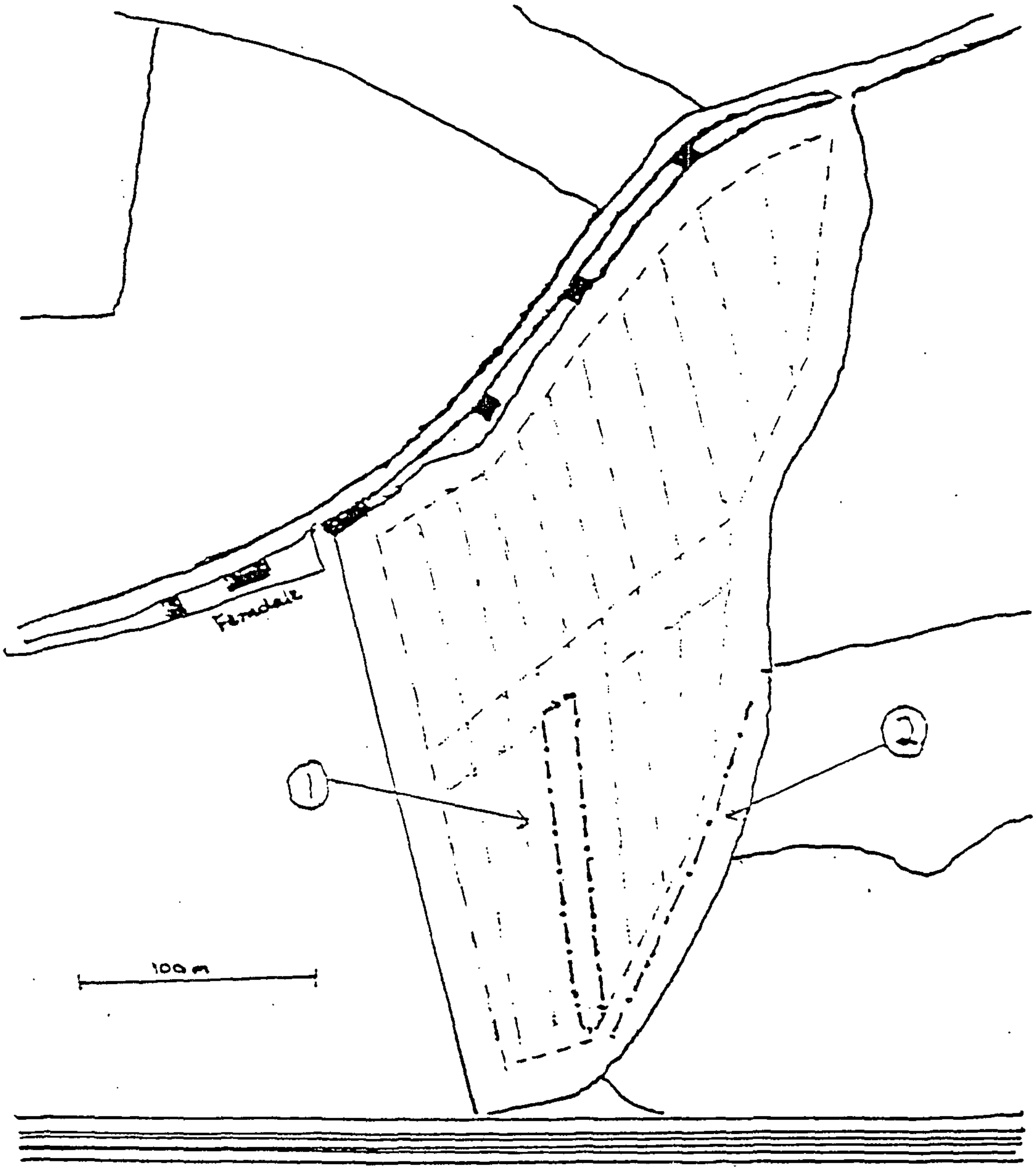


Figure 2. Showing –·–·–·– the routes taken on several evenings each by two older leverets when streaking and also, by faint lines, the run of the field drains.

Table VI. Distress screams of leverets.

Date	Time before (- mins) or after (+ mins) sunset	Cause of screams	Distance of litter from observer (m, estimated)
7 May 1981	-13	Predation by magpies/crows	100
20 April 1985	+15	Predation by fox	550
26 April 1985	+45	Predation by fox	350
8 May 1985	- 4	Unknown	250
18 Aug 1985	+57	Predation by fox	60

interacting with the magpies, appeared briefly to disperse them. A pair of crows then descended scattering both magpies and the hare. Within three minutes the crows had killed the leveret and were beginning to consume it. The hare did not intervene again.

Discussion

The basic antipredator strategy for leverets comprises hiding and dispersal (Broekhuizen & Maaskamp 1980). Dispersal causes them to move away from their birth place, their siblings and even their doe. Once every 24 hours the whole process is reversed. During reversal leverets are attracted towards the nursing point (their birth place), other leverets and of course the doe. When, during the daily cycle do these reversals commence? In summer, leverets can be active long before sunset and this situation can help to answer the question.

behaviour of leverets

Leverets do not meet up until after sunset, twenty minutes or so before the arrival of the doe. This applies even when they have been active for several hours before sunset. They meet when their paths towards the nursing place converge sufficiently closely for them to detect each other. The earliest commencement of movement towards the nursing point I noted was seven minutes before sunset, when a 17 day old leveret had a distance of about 110m to cover. In general, observation showed that the onset of movement towards the nursing place arises shortly after sunset. The resulting convergence brings leverets near each other and they eagerly join company. Data in this Chapter show, however, that some leverets joined company up to an hour before sunset. This appeared to be because they were in a situation where they could see each other at a distance and suggests therefore that attraction can commence well before sunset.

Broekhuizen & Maaskamp (1976) found that leverets only approached adults during the first one and a half hours after sunset, and results from this study accord. It is not clear whether at this time leverets have a predisposition to keep company with any adult or whether the approach is a misdirected response to the doe, who cannot be identified from a distance. Leverets do seem to break off from strangers even in the absence of physical rejection and circumstances point towards the latter interpretation. Some strangers are themselves attracted towards and play with the leverets.

Prior to nursing, leverets are together in company on average for just over 20 mins. Behaviourally, that period is divided into two distinct phases of approximately equal duration. The first is a time of apparently high excitement. Almost invariably, at first meeting leverets approach to within touching distance of each other and sniff noses. This behaviour upon meeting does not persist into adulthood. Sniffing the nose of another hare puts the owner's nose into danger of being bitten or claw raked by the other party. The only occasion when nose sniffing is seen between adults is in a sexual context (see Chapter 8). During the remainder of the first phase there is frequent high intensity and high profile locomotor play among the leverets, including streaking and stotting, in the course of which they sometimes jump over each other. Broekhuizen & Maaskamp (1976) say that only young hares of nursing age accepted the approach of other young but in this study some weaned leverets of up to twelve weeks of age were observed to meet up and keep company, with very similiar behaviour to that of nursing leverets. The commencement of the second phase of the gathering period marks a change in the leverets behaviour. They move together, but in a subdued rather than boisterous way, direct to the nursing place and there they assemble in a close, often physically touching group, waiting for the doe. There is no movement except for some grooming and allo-grooming. Although the litters studied met a short distance from the nursing point, it may well be that some meet at the nursing point. If so, it is anticipated that there would still be the two distinct phases of behaviour, as there are in the case of singleton leverets prior to nursing (personal observation).

A variety of aspects of nursing behaviour, such as the synchronous gathering of young, the shortness of nursing bouts and the occurrence only once every 24h and the short time duration of nursing, the licking of leverets urine by the doe and the dispersion of the young are interpreted as adaptations towards reduction of the risk of leverets being found by predators (Broekhuizen & Maaskamp 1980). It is a paradox, therefore, that the meeting together of leverets only shortly prior to nursing is accompanied by locomotor play, one of the most striking characteristics of which is precisely its conspicuousness. That paradox and the role of locomotor play will be discussed below. The function of the subdued phase of the pre-nursing gathering is probably intimately connected with the imminent approach of the doe. As shown in Chapter 6, the doe when travelling from her daytime lying up area to the litter is constantly monitoring for potential predators. If, when she arrived in the vicinity of the nursing point the leverets were mobile and behaving in the exhuberant fashion of the excited phase, it would be difficult for the doe to discriminate between her own litter and possible predators. If, however, her litter are gathered quietly together at a known point, any movement elsewhere in the vicinity could warn of possible danger.

There is as yet no quantitative data from any source as to the extent to which leverets disperse from the nursing point progressively with age. Data obtained in this study from one litter between nine and 17 days of age broadly agreed with that reported by Broekhuizen & Maaskamp (1980) for a litter in the Netherlands. What was particularly interesting in the study litter was that although the three leverets were active for long periods before sunset, during part of which they explored, they were never seen to meet until the usual time after sunset for pre-nursing gathering. From observation it appeared that exploration was conducted primarily along a straight line away from the nursing point, rather than in all directions, resulting in a familiar corridor within which the leveret was likely to be found. These corridors, like the spread fingers of a hand, only joined up and became contiguous with other corridors in the vicinity of the nursing point. If that was the case it would provide a mechanism impeding leverets from joining company until they moved towards the nursing point. Some evidence in support of the corridor concept comes from events on the evening of the study litter's seventeenth day. Just after nursing the previous night, leveret II had been predated by a fox. As will be seen from Figure 1, the range of that leveret was central, lying between those of the other two. On the seventeenth evening, unlike the seven previous occasions, the two remaining leverets did not join up at the usual meeting area but at the nursing point itself. This seemed to result from the presence of an empty corridor between them. That corridor even appeared to persist at the nursing point. Normally the leverets awaited the doe squatting in line abreast touching or almost touching each other. On this evening, the two squatted for ten minutes or so with a gap between them wide enough to take their absent sibling and only moved closer to each other shortly before the doe arrived. Unfortunately they also disappeared that night.

In the brown hare, play appears to be limited to locomotor play. No unequivocal examples of other categories of play were observed during the course of the study. The major part of locomotor play comprises streaking. This embraces behaviour first described, of adults, by Flux (1981), and called by "the racetrack", in which individuals in an enclosure raced up and down a familiar path to gain distance from pursuing conspecifics before darting off and evading them. Streaking is a wider category because although some, particularly the older, leverets make use of the same stretch of ground for the performance on successive occasions, others take a different course the next time. Furthermore, some performances involve a lot more than just running at full speed. Any streak is a very conspicuous movement which immediately catches the eye, but is even more conspicuous when the animal combines the run with a variety of acrobatic manoeuvres and also, possibly, displays its white tail flag. The fact that this would undoubtedly attract the attention of predators and therefore greatly increase the costs of play seems to contradict the commonly accepted interpretation of the hiding phase as a strategy for avoiding predators in closed habitats (Lent 1974; Estes 1976; Ralls et al. 1986). Locomotor play has generally been interpreted in the light of the functional "motor training hypothesis", which states that play improves physical condition, as well as enhances the ability to perform species-specific motor skills correctly later in adulthood (see Bekoff & Byers 1981). Gomendio (1988) argued that if predation has been a strong selection pressure for the evolution of hiding strategies and if the benefits of locomotor play are delayed until the adult stage, it is difficult to understand why these same selective pressures would not also have acted upon locomotor play, delaying it in ontogeny until a more advanced stage had been reached, when the young would be physically stronger and more developed and therefore not as vulnerable to predators. The apparent contradiction could be explained if the possibility of play having immediate benefit was considered. This possibility appears to be realised in the locomotor play of brown hare leverets. The defence strategy of adults against terrestrial predators was highlighted when observed being hunted by lurcher dogs. The first reaction was to freeze motionless, reducing their crouched silhouette to a minimum. If the dogs came too close the hare would burst into high speed flight, jinking as it went, making full use of its intimate knowledge of its large home range. It made for small gaps in hedges through which it could pass quickly, but which impeded the larger dogs and it would jump ditches at familiar points. In that way more often than not the hare would give the dogs the slip (personal observation). The most successful predators of leverets in the study area appeared to be foxes. Of the four instances of predation observed, three were by foxes. The maximum speed of an adult hare is almost half as fast again as that of a fox (Macdonald 1984) which can only catch them by stealth. The precocious leveret, although born full coated and sighted and capable of movement, has more limited speed. Initially, it has to depend exclusively upon hiding for its defence. I have seen a seven day old leveret hide itself in a clump of grass in a field drain and stay there hidden as a herd of cows passed back and forth through the immediate area and a hidden two and a half week old leveret stay immobile as a cow urinated right beside it. Increasingly from 12 days of age onward, leverets are taking vegetation and when feeding cannot remain totally hidden. As they increase in size they cannot hide so effectively. Selection pressures for the early development of the second line of defence, speed, would be anticipated. As has been discussed supra, the familiar range of a young leveret is very limited in extent and more cigar shaped than circular. Outside that area the terrain will be totally unknown to the leveret. Normally the home range will only cover part of a field and thus will not include the hedges, ditches and walls which are likely to be within the much larger range of an adult. As the leveret develops, its maximum speed will increase to a point where, in the best circumstances, it can outpace a fox. The best circumstances would include running over a course the topography of which the animal knew intimately, so that nothing need slow it down. If the course was not long enough to lose the fox, then the leveret would have no choice but to turn around and race back in the opposite direction, if necessary jumping right over the pursuing fox in the process, until a sufficient lead was obtained to dart off the course and again hide. I suggest that streaking is the means whereby leverets prepare themselves for such situations, both specifically by way of practice and also by way of exercising and developing their general locomotor ability and that results from this study and from that of Flux (1981) support the hypothesis. Over 84% of all streaks were by leverets. Leverets commenced streaking as early as seven days old and continued throughout their development into early maturity. Initially, the length of the streak was only a few metres and neither the length nor the speed of it could be any defence against the attack of a fox. The distances covered increased as the leverets aged and at least some of the older leverets, which were perhaps approaching or at the stage where their speed matched that of a fox, performed over a regular racetrack, sensu Flux (1981). Streaking persisted until early maturity, long before which time the individual would be able to outpace the fox. However, its familiar range would still be limited. It seems likely that in maturity the benefit of distance gained from a pursuer over a specific racetrack will be outweighed by the constraints of remaining close to the track. Increasing knowledge and experience of all features of an expanding range will enable use to be made of some features, such as gaps under hedges, for effective escapes. This would explain why none of the 26 study adults were seen to streak. It would also be supported by the events reported by Flux (1981). He was studying adult hares in a 3 ha enclosure. On release into the enclosure hares would at first explore increasing lengths of fenceline, circling back to the starting place. Within an hour they, three individuals on separate occasions, chose a racetrack about 50m long and established it by running at full speed from one end to the other two or three times. Flux comments

> "whenever a hare wanted to escape determined pursuit by another it had only to run to one end of the racetrack and sprint along it to leave any pursuer far behind, allowing time to confuse its tracks or hide".

The particularly interesting aspect of this report is the effect of the artificial restriction of adults by an escape proof barrier to a limited area of 3 ha, probably about one tenth of their normal home range (Tapper 1991). Only leverets would be expected to have as small a range in the wild. Confined to a leveret-equivalent range, the adults immediately adopted a leveret-equivalent defence strategy.

behaviour of leverets

Of observed streaks by leverets, of which 48% were weaned, 94% were during the first 40 mins after sunset. Although, out of the total observation hours there was a heavy bias in favour of the evening period, nevertheless there were many hours of observation before sunset, during the night by moonlight and before and after dawn and this apparent concentration of the behaviour during the short period after sunset is believed to be real. This is the only period during the 24h day, apart from at nursing itself, when leverets associate. For the remainder of the 24h all nursing leverets and probably weaned leverets also are dispersed. In the case of nursing leverets, the period precedes by only ten minutes or so the arrival of the doe to suckle. As mentioned earlier, it seems paradoxical that nursing, when doe and leverets are in the closest and most vulnerable proximity, should follow only by a few minutes episodes of highly conspicuous locomotor play by the leverets. Is there a credible explanation for this paradox? I suggest there is. It depends upon the assumption that the paramount defence strategy for leverets is dispersal, with the shortest period of association at the safest phase of the 24h cycle (Broekhuizen & Maaskamp 1980). If to that equation is added strong selective pressure for a period of locomotor play in association, then the solution has to be either two discrete periods of association or one period combining both locomotor play and suckling. If pressure favouring dispersal is strong enough the outcome will be a combined period. In that event a short, quiet phase between the two activities as revealed by this study might help to reduce the cost of the first, conspicuous, activity. The remaining question is why there should be a need for locomotor play in association, particularly when the behaviour is very similar whether performed in association or in isolation? At times of association, I have not seen leverets chase each other for more than a short distance nor have I seen two streaking simultaneously. I have, however, seen one leveret jump over another, both when streaking and when stotting and the judgement to perform that potentially life saving manoeuvre, which could not be practiced in isolation, might well be improved by such play. I have not been able to trace any references, specific or general, to locomotor play in leverets of the brown hare or any other species in the genus. The absence of any reference to it in Aniskowicz et al. (1990), who studied the nursing behaviour of three families of arctic hares in the Canadian arctic islands is particularly interesting. Their detailed report included descriptions of behaviour of leverets congregating before nursing as to which they said

> "whether the young met at the waiting spot or near it, they frequently ran to each other on first noticing a sibling and "greeted" each other by nuzzling. If several young were involved, the greeting was often followed by the whole group leisurely hopping single file in a partial circle. This would last only a few seconds but could be repeated with the arrival of each sibling".

There is no mention of behaviour involving any of the components of locomotor play reported of brown hare leverets in this study.

Fear or distress screams, a distinct category from alarm calls, are emitted by animals in utmost danger, sometimes not until seized by a predator. The screams are far-reaching, long lasting and consist of irregular bouts including high and low frequencies, which make them easy to locate (Hogstedt 1983). They are found mainly among birds and mammals, including man. Many species, however, remain silent when captured and this differential has generated a body of research and hypotheses (eg. Driver & Humphries 1969; Stefanski & Falls 1972; Rohwer et al. 1976; Perrone 1980). The hypothesis that screams are calls for help directed at kin or reciprocating animals (Rohwer et al. 1976) has been supported only in the context of parents defending their dependant young (Stefanski & Falls 1972). Perrone (1980) found that fear screams did not attract conspecifics in the non-breeding season. Hogstedt (1983) combined that hypothesis with another - that screams are directed at other predators which approach the scene in the hope of an easy meal, the screamer or the primary predator, and in the ensuing dispute between predators the prey may get a chance to escape - the secondary predator hypothesis. He showed that predators of a number of species hurried towards the broadcast distress screams of a starling and suggested that such screaming is a selfish trait, a cry directed at any animal capable of interfering with the threatening predator, be it an altruistic parent, a reciprocating individual or a selfish secondary predator. Hogstedt's hypothesis would explain the existence of distress screams in adults as well as dependant young.

As shown in this study, leverets of the brown hare scream. Adults do also (personal observation). The scream of the leverets is loud, far-reaching and has a bleat-like quality to it. What is the function of the scream? To a leveret, totally dependant upon hiding for defence and with very limited ability to escape, the secondary predator hypothesis is unlikely to confer any benefit. This was directly demonstrated by the incident described earlier in this Chapter when the screaming of a young leveret, being harassed by a pair of magpies, brought onto the scene a pair of carrion crows which supplanted the magpies and killed it. Might the screams trigger any form of parental defence? In still air I was able without difficulty to hear the distress screams of leverets from distances of up to 550m. It is to be expected that the hearing of an adult doe would certainly be no less acute than that of a 54 year old human. As reported in Chapter 6, I was able in five cases to record the daytime locations of both nursing does and their litters. All the does were lying up between 200 and 300m from their litters, distances which they would be capable of covering at maximum speed within 20 secs. It has been demonstrated on television (Christopher Knights on the Tony Soper Animals Programme) that hares, of unknown sex, will respond and approach extremely close to the source of human imitation of the leveret distress scream. Unfortunately, as yet there has been no attempt to test this scientifically. Schneider (1981), however, reports:-

> "I myself have observed adult female reaction to leveret cries. They sat up and tried to orientate themselves optically and acoustically to the sound. If crying continued some fled, others moved towards the origin of the vocalisation. On one occasion, a marked female was drawn very close to a tape recorder playing back the sound of a young hare, whereas a buck disappeared".

If there is a response by does, it is likely to be a general one to screams from the vicinity of their litter and not limited to those from their own offspring because, in the nature of things, they will be unlikely to have had any previous experience of the individual screams of that litter. The distress screams of leverets are, like those of other animals, very easy to locate. I found that in all cases I immediately spotted the fox or other predator if I looked in the direction from which I heard the screams, although there was a tendancy to underestimate the distance of the source. Could there be a selective benefit from does responding to such screams? Probably there would be little they could do if the predator was a fox, but the range of potential predators is larger whilst the leverets are in their vulnerable first two or three weeks of life and a doe might well be able to assist the leverets to escape from, for instance, a magpie, stoat or rat.

CHAPTER 8

INTRASPECIFIC COMMUNICATION

Introduction

In this Chapter I adopt Slater's (1983) definition of communication as

> "the transmission of a signal from one animal
> to another such that the sender benefits on
> average from the response of the recipient"

Signals can be visual, acoustic or olfactory, or a combination of those elements. They must have evolved specially, so distinguishing them from the many situations where the behaviour of one animal influences that of another without a signal as such being involved.

Some signals consist of an element of behaviour which has become ritualised or stereotyped so that, in the relevant context, it is capable of conveying an unambiguous message. In Chapter 9, I suggest that the adoption of a bipedal stance by hares upon approach by foxes is an example of such a signal. Other signals are given or made by means of physical aspects or structures of the animal which have evolved partly or wholly for the purpose. The brown hare is, with two exceptions, of generally uniform coloration so blending with the steppe environment in which it probably evolved. Exceptions are the coloration of the ears and the tail. The backs of the ears are greyish white for the most part but with black tips. The tail is white with a broad black band running the length of the upper surface (Fig. 1). Lifting the tail and pressing it back against the rump exposes the white flash or flag of the undertail (Fig. 2). It must be suspected that both the ears and the tail have some signalling function. The hare has a loud distress scream, almost certainly operating as an acoustic signal. Also reported by Flux (1981) are tooth grinding and quiet grunts, chucks or snorts. Scent producers are the harderian gland situated deep within the orbit of the eye, chin glands, anal glands, inguinal glands on either side of the penis/vulva and urine (Bell 1985). In comparison with the territorial and more social rabbit, the chin glands are about one quarter and the anal glands about one tenth the size but the inguinal glands are larger than those of the rabbit. Within the sexes, the harderian and chin glands of bucks are larger, but the inguinal glands of does are much larger than those of bucks (Mykytowycz 1965, 1966, 1968).

Schneider (1976, 1977a, 1977b, 1981, 1990) attempted to analyse visual communication. He reported that hares communicate with their ears, their bodies and their tails (Schneider 1990). Erected ears were a signal of a "friendly attitude" on the part of one hare approaching another (Schneider 1981). They also showed a buck's intention to mate (Schneider 1990) and "seemed to play some part as signal transmitters" when one rival buck confronted another (Schneider 1976). Ears flattened along the back demonstrated threatening behaviour (Schneider 1981, 1990) and were manifested also by the pursuer when one buck was chasing another (Schneider 1976). The

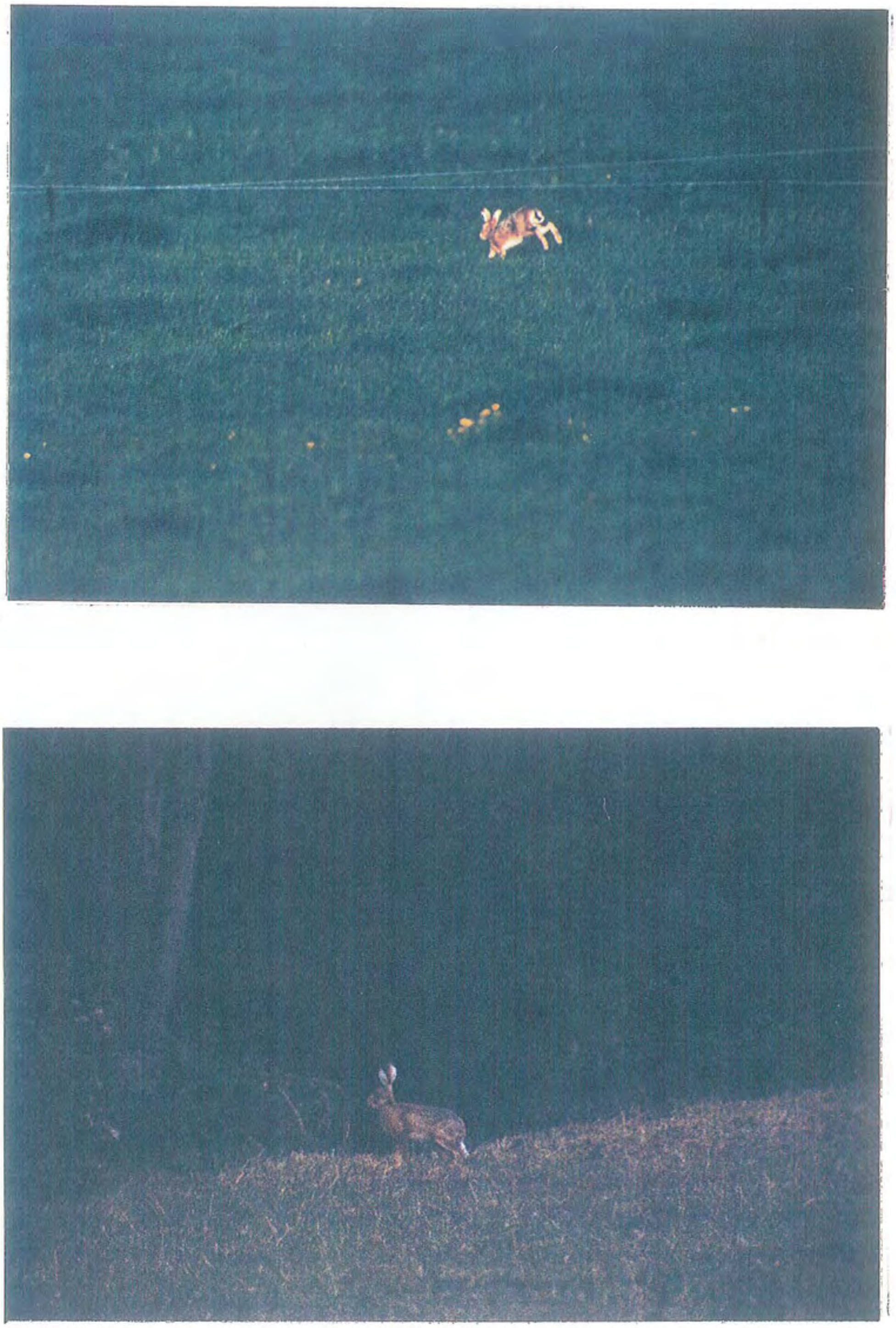


Figure 1. In low light conditions the light coloured backs of the ears and the white margins of the lowered tail stand out.

body signals were given by a buck standing bipedal and also by a buck arching his back and standing stiff legged like a cat. Schneider (1976, 1990) interpreted them as displays to impress either the doe or rival bucks and also as conveying the intention to mate. Tail shaking or waving by the doe was an invitation by the buck to follow (Schneider 1990). Schneider's only comment on the white flash of the upraised undertail is to suggest that it operates as a visual signal to conspecifics when a hare is scent marking by urine or fecal pellets (Schneider 1990).

The possession of a rump patch of contrasting coloration and size, ranging from those that cover the entire posterior and up along the back to those that are concealed on the undersurface of the tail, is a feature of a number of different phylogenetic lines of mammals. They are to be found in representatives of the bovids, antelope, cervids, lagomorphs and primates. In his review, Guthrie (1971) referred to the two theories to explain the wide occurrence of rump patches. The first saw the rump patch as a visual warning apparatus and individuals flashed their white rumps at other members of their group to warn them of approaching danger. He pointed out that there were really two different forms of the second theory, both viewing it as a "follow me" signal. One emphasized its use to maintain cohesiveness of the entire group in flight, while the other stressed its importance to offspring in keeping parents in sight. Guthrie (1971) challenged those views and presented a new theory that rump patches were organs of submission, used to communicate subordination. More recently, it has been suggested that tail-flagging by white-tailed deer, in which the undertail is lifted onto the rump displaying a brilliant white flash, operates interspecifically as some form of pursuit deterrent signal (Smythe 1970, 1977; Hirth & McCullough 1977; Coblentz 1980; Bildstein 1983).

The literature contains few specific references to behaviour associated with olfactory communication. Koenen (1956) reported that when hares squat upright glands in the anal area release their yellowish strong smelling secretions to the ground below, that hares often rub their noses (sic) against twigs or small branches marking them with their odour and that in the process of grooming hares anoint their bodies with secretions from their scent glands, the last confirmed by Schneider (1977a). Schneider (1976) appreciated that the tail-shaking of does, also mentioned by Koenen (1956), could involve a process of scent scattering. The release of urine by lagomorphs may often be target directed. In the rabbit, Bell (1980) distinguished three forms of urine depositing behaviour on the basis of the volume evacuated and the target at which it was directed; namely normal squat urination, urine-spraying and urine-squirting. The last two were regarded as forms of scent marking behaviour where small volumes of urine were ejected at conspecifics and prominent inanimate environmental features respectively. There are few references to urinary scent marking by brown hares but Boback (1954) and Schneider (1976) gave clear instances of urine squirting of conspecifics and Schneider (1976) also gave one instance of what may have been environmental target spraying.

In this Chapter I describe behaviour apparently involved in visual and olfactory intraspecific communication and also look at behaviour which has been suggested by others to have a signalling function. Acoustic communication is excluded because the distress scream is included in Chapter 7 and no other behaviour which might fall within that category has been noted in this study. Also, I have no evidence that fecal pellets are involved in olfactory communication. The anal glands of the hare are only one tenth the size of the more social and territorial rabbit and this also suggests that fecal pellets do not play an important role.

Results

It is not possible to make a sharp distinction between visual and olfactory communication because in some instances the behaviour observed probably combines both forms of communication. This account will take in order those parts of the body of the hare which are, or which have been suggested to be, involved in signalling commencing with the tail area followed by the main trunk, the ears and the muzzle and then concluding with enurination.

Tail up. Hares normally carry their tails in the tails down, relaxed position (Fig. 3.) In the tail up position the tail is lifted and flattened against the rump displaying the full extent of the totally white undertail (Fig. 2.) In this study, more than 90% of all tail-ups were by bucks, so it is a good initial indicator to the sex of an animal. Table I sets out the various behavioural situations in which bucks and does have been observed demonstrating the tail up position, distinguishing between those in which the behaviour is of regular and occasional occurrence. In the following comments on those various

Figure 2. Buck, Cavalier, escorting doe Celandine, his tail raised showing the white flash.

Figure 3. Buck, Bolingbroke, running with tail down in the normal relaxed position.

Table I. The behavioural situations when hares upturn their tails, showing the white flash. R - regular, estimated frequency > 70% of occasions. O - occasional, estimated frequency < 30% of occasions. In parenthesis, reference number of passage in the text.

By bucks when	R	O	By does when	R	O
(1) defecating	X		(1) defecating	X	
(1) urinating	X		(1) urinating	X	
(2) consorting with does	X		(6) consorting with bucks		X
(3) chasing other bucks	X		(7) consorting with litter	X	
(4) squatting upright	X				
(5) prospecting for does		X			

situations, numbered as in the Table, I will be looking particularly for possible recipients of any visual signal given by the white tail flash.

(1) Bucks and does lift their tails when urinating and defecating (Fig. 4). This suggests that the tail itself does not play any part in urinary scent marking. The brief white tail flash would be visible to any following hare.

(2) Bucks consorting with does regularly showed the white tail flash (Fig. 2). Consorting sometimes commenced weeks before the doe came to oestrus but tended to become more consistent as oestrus approached - to the point where, during the last two or three days, the doe might be permanently guarded by the consort with one or more satellite bucks in immediate attendance (see Chapter 4). Consorting bucks regularly showed the white tail flash whether or not other bucks

Figure 4. Buck, Cavalier, defecating with tail upturned. Tail sizes varied: his was particularly long.

Figure 5. Cicero, tail raised, circles Celandine about four hours before her oestrus 11 July 1982. Also present, Bolingbroke with ears raised. Photographs, Figures 6 & 7, are part of the same sequence.

were present. Individuals varied as to the extent to which they did so, some carrying the tail up almost continually and others for only part of the time. During consortship, the buck follows the doe and his white tail flash would not therefore be visible to her, but it might be seen by any satellite bucks also in attendance. Occasionally, consorting bucks circled or cut across the front of the doe (Fig. 5) very much in the manner of the buck rabbit which regularly behaves in that way. On eight separate occasions when buck hares circled or cut across the front of the doe, on some occasions repeating the manoeuvre several times, I was able to note the position of the buck's tail. In every case it was up, showing the white flash. Only in those cases would the doe see the tail flash of her consort.

(3) When consorting couples were accompanied by satellites the consort buck from time to time charged at and chased away the satellites as described in Chapter 4. On eight separate occasions when such chases took place, six of them repeated, I noted the position of the consort buck's tail. On every occasion it was up. On five separate occasions, three of them repeated, I noted the tail position of the pursued buck. On all five occasions the tail was held down (Figs. 6 & 7). Additionally, I observed one instance of a buck repeatedly chasing rooks which were feeding in the area of its form and another of a buck repeatedly chasing a pair of magpies which were pestering it. During every chase the tail was held up. During chases between hares the tail flash of the pursuer would not be seen by the pursued but would usually be visible to the doe and, possibly, to other satellites.

(4) When squatting upright (Fig. 2a. Chapter 9), bucks regularly held

Figure 6. Celandine grazes in foreground. Behind her Bolingbroke, the alpha buck, faces towards Cicero who faces camera. See Figure 7 below for next event.

Figure 7. A second later Bolingbroke charges at Cicero who flees. Note Bolingbroke's tail fully up and Cicero's tail fully down. Note also, Bolingbroke lowers his ears to charge.

the tail up. They did this whether or not in the company of a doe and whether or not other bucks were present. Satellite bucks which had held their tails down while being pursued by the consort buck, would, when the pursuer broke off the chase, turn and face the couple from the upright squatting position with their tails up. Higher ranking bucks travelled for up to two kilometres to check on the does within their range. During journeys they stopped at intervals squatting upright monitoring the terrain. Whenever they did so the tail was held up. On the majority of such occasions there was no other hare in the immediate area. Bucks squatting upright faced towards any other hare, doe or buck, which might be nearby so that, in general, the white flash would not be visible to the other animal.

(5) Bucks occasionally carried their tails up when on the move searching, with their noses close to the ground, for the scent of an oestrous or near-oestrous doe in the area. They were usually solitary and the tail flash would be unlikely to be seen by any other hare.

(6) Occasionally, does carried tails up in the presence of bucks. In three of the four cases observed the doe put her tail up when meeting a buck during the first hour after sunset. The tail flash of the doe would of course be clearly visible to the following buck.

(7) Does regularly showed the tail flash when travelling to and visiting their unweaned leverets. Set out below are extracts from my diary notes illustrating this behaviour:-

> 14 June 1981. Field 17. Sunset 1928h.
> 2012h. Bluebell (then about 40m from the day old leveret) starts to move South in short stages appearing nervous and watchful. Whenever she stops her tail is cocked right up showing the

> white undertail for its maximum length up the back....
>
> 15 June 1981 (leveret has disappeared)
> 2040h. Cattle having moved on, Bluebell visits the exact spot where she suckled last night and remains within the immediate area for at least the next 35 mins. Behaviourally, again the tail is cocked up the back showing the white flash....
>
> 16 August 1985. Field 5. Sunset 1833h.
> 2025h. (a cow is lying at the nursing point). Fuchsia arrives in the field drain behind the cow and starts to suckle. The cow gets up and goes over to investigate whereupon Fuchsia jumps away and lopes North showing alot of white tail flash and followed by the leverets. Shortly, she stops and resumes suckling them.

The white tail flash would be clearly visible to the leverets following the doe.

Summarizing, the only situations in which the white tail flash of a buck was more likely to be seen than not by conspecifics were both relatively infrequent. The first was when a consorting buck circled or cut in front of his doe. The second was when a consorting buck chased away a satellite buck. For most of the time the white flash was unlikely to be seen. Does rarely showed their tail flash, Very occasionally the tail was lifted when greeting a buck and would have been visible to the following buck. The tail was, however, regularly lifted in the presence of the doe's litter.

Of the four rump patch theories mentioned in the Introduction, three involve the prediction that any flash will be shown when the animal possessing it is being pursued by a predator. The fourth predicts that it will be shown when the female of the species is being followed by its offspring. I have reported above that bucks pursued by bucks keep their tail down. During the course of the study I also observed that hares either startled from their form or chased by humans, dogs including lurchers and greyhounds or cats all raced off with their tails down. To follow the question further I approached a sporting press photographer and without giving any reason or explanation asked him to select at random and send me ten photographs showing the rear view of hares being coursed by greyhounds. Upon examination of the photographs in every one of them the tail was held down (Fig. 8).

Tail-shake. In this behaviour, which is within the repertoire of the doe only, she rapidly shook from side to side her horizontally held tail. Tail-shaking was only performed when the animal was standing or moving with the rear part of the body off the ground. Does crouched feeding or resting did not tail-shake. Each bout was brief, lasting no more than one or two seconds. In appearance the behaviour was identical to the tail-shaking of a young lamb taking suck from its mother. I have never observed bucks tail-shaking. Does only shook their tails in the close proximity of bucks. Solitary does were never observed to do so. Typically, a doe shook her tail when the escorting buck, normally to be found behind and following the doe, moved or ran up to rejoin the doe. As the buck approached and came within a maximum of 3m of her rear the doe started to move forward shaking her tail as she did so. The buck stopped at the point where she had shaken her tail and sniffed the ground (Fig. 9). This series of events could be repeated many times while the couple kept company. Between 1981 and 1989 I observed escorted does tail-shaking, usually

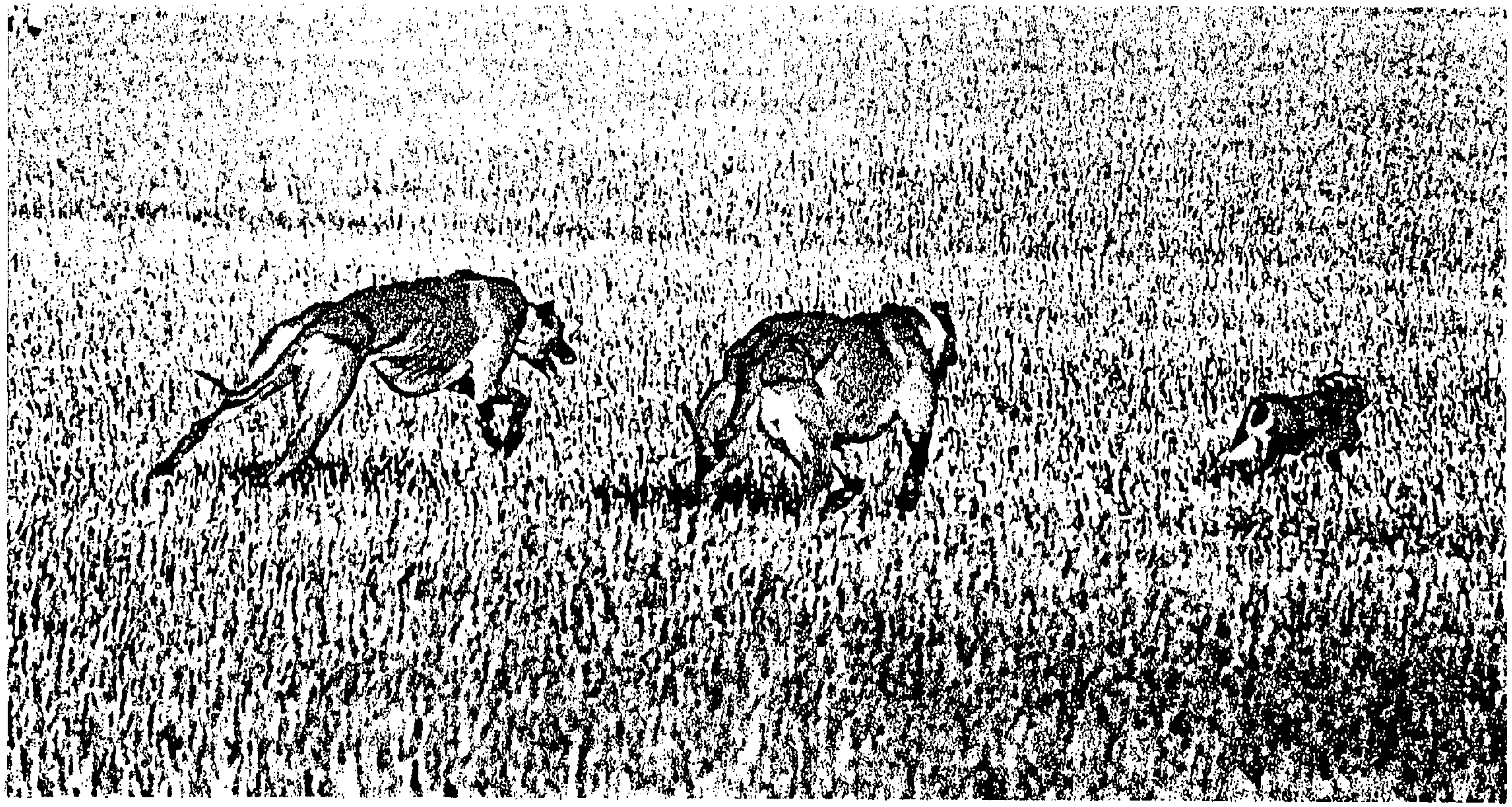


Figure 8. Hare being coursed by greyhounds. One of ten photographs, all selected at random. In all ten the tail was down.

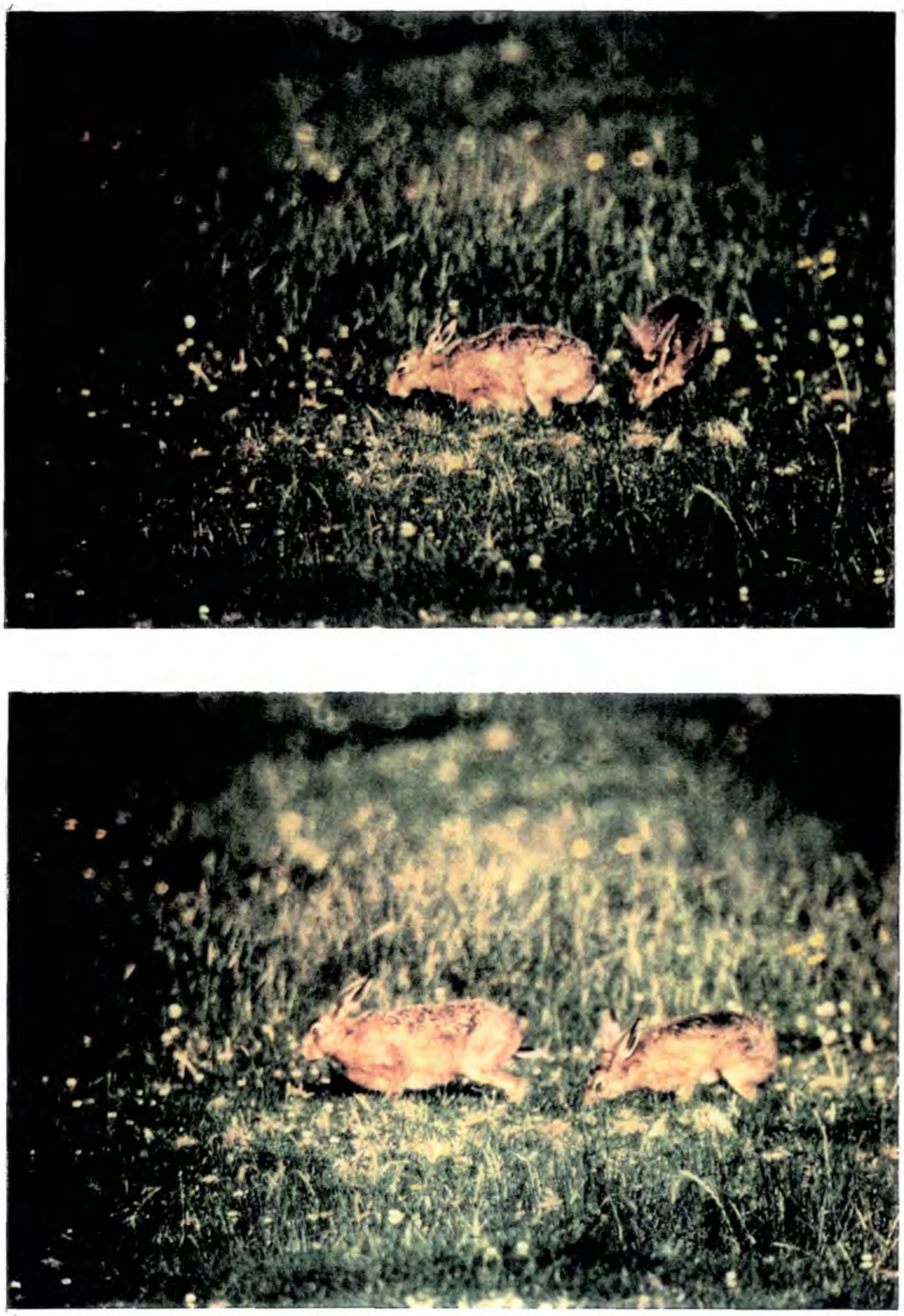


Figure 9. Celandine escorted by Bolingbroke about five hours before her oestrus 11 July 1982. Top, he is sniffing the ground where she has tail-wagged. Lower, she has moved forward and with tail held horizontal is about to tail-wag again.

involving repeated bouts, on a total of 55 separate occasions. The does included eight named individuals. None of the does were seen to tail-shake when the buck was more than 3m from them and in most cases the buck was within one metre when she did so. Does shook their tails when escorted at all stages of the oestrous cycle but were more likely to be escorted in the latter states (see Chapter 4). Set out below are extracts from my diary notes illustrating this behaviour:-

> 13 July 1982. Field 17.
> 1830h. Cavalier goes over to and joins up with Clover (then 12 days from oestrus) she moves in stages 80 to 100m in a northerly direction he follows. At intervals they stop she wagging her tail in front of him before doing so. He sniffs the ground at the spot. Also on a number of occasions Clover runs in the direction of Cavalier and in those cases when she reaches a point just ahead of him she wags her tail but in general he follows her.
>
> 19 March 1983. Field 17.
> 1710h. Bolingbroke in close company with Clover. On all 10 occasions when the buck ran at the doe and when I could see her tail she wagged it rapidly from side to side. Generally he would have come to within a metre when she started to do so. When the buck moved up the doe usually moved ahead tail-wagging as she did so. On at least two occasions when she moved ahead without the buck coming up to her she did not wag her tail. On some of the occasions when the doe wagged her tail as the male came up to her he did not stop but ran on ahead cutting across the front of her.

The only other situation in which tail-shaking by does was observed was during the course of sexual chases. Such chases, which are not restricted to oestrus or near-oestrus, most frequently followed after a couple met for the first time on any particular evening. During a chase the buck closely followed the doe, his chin at times touching or resting on her rump, while the doe pursued an irregular course involving many jinks or abrupt departures from a straight line of passage. Chases were mediated by does in that the majority of them were at less than full speed, some at no more than a lope and were terminated by the doe, the couple remaining together afterwards. During chases does frequently shook their tails.

Tail down. When hares were on their legs, the tail was normally held downwards. In that position the white margin to the broad black centre stripe on the upper surface was clearly visible over considerable distances, particularly in low light conditions (Fig. 1).

Whole body signalling. According to Schneider (1976, 1977a, 1990) agonistic interactions both intra- and inter- sexual are often decided by what he calls "impressive behaviour" involving hares either standing bipedal or arching their backs with stiff straight legs "like a cat". He also says that a buck "conveys his intentions to mate by raising his ears or arching his back" (Fig. 10). I have never observed either the bipedal or the arched back stance employed for obvious intra-specific communication. During agonistic inter-sexual interactions when bucks were harassing near-oestrous does, it was not uncommon for the doe in the last resort to stand bipedal, preparatory to striking down at the buck. In many cases the buck then withdrew. Likewise during interactions between rival bucks, one or other sometimes stood bipedal but only preparatory to imminent offensive or defensive action. No question of display appeared to be involved. As to the arched back stiff legged posture, I have been unable to distinguish the behaviour described by Schneider from the upward stretch of a hare. Upon rising at the end of a rest period hares commonly stretched first lengthwise (Fig. 12) and then upwards (Fig. 11). Cats

Abb. 1. Imponieren des Männchens vor dem Weibchen mit „Katzenbuckel". Zeichnung nach Orig.-Foto von E. SCHNEIDER.

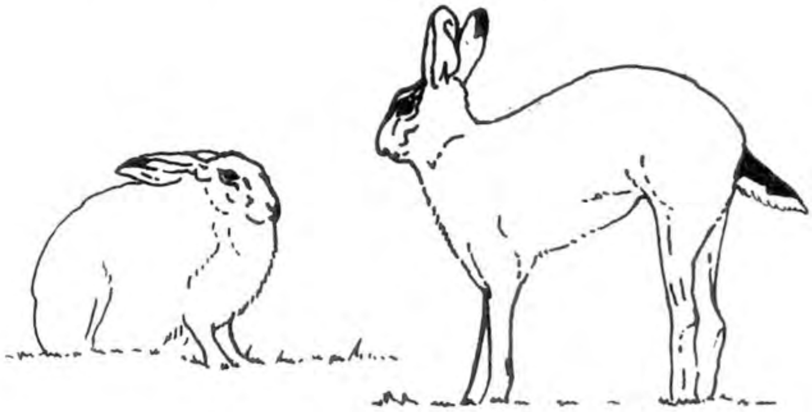


Abb. 1. Imponieren des Männchens vor dem Weibchen mit "Katzenbuckel". Zeichnung nach Orig. - Foto von E. SCHNEIDER.
Translation - The male impressing the female with his 'arched back'. Drawing from the original photograph by E.Schneider.
Figure 10. Figure 1 from Schneider (1976)

Figure 11. Buck, Cavalier. stretching upward on rising from a resting period. Also, see lower photograph at Figure 2, Chapter 3.

Figure 12. Upper, doe Celandine stretching upward. Lower, buck Bolingbroke stretching lengthwise.

are doing exactly the same thing when they arch their backs.

Ears up. Schneider (1976, 1981, 1990) suggested that one of the ways whereby hares communicate with each other is by the position of their ears. He said that bucks convey their intention to mate by raising their ears (Schneider 1990), that when rival bucks face each other their erected ears directed forward have some part as signal transmitters (Schneider 1976) and that the erected ears of one individual approaching another were a signal of a "friendly attitude" of the approaching animal (Schneider 1981). I have been unable to detect any indication of raised ears being used for anything other than acoustic purposes. Ears, which are highly mobile sound detectors, were normally carried raised at least to some extent and were moved together or singly to locate the source of a sound (Fig. 13). Fully erected ears pointing directly forward indicated alertness and interest, with all senses focusing together (Fig. 14). Consort bucks often approached oestrous or near-oestrous does from the front (see nose-sniffing post) and when so doing their ears were held up directed forwards, just as they were when facing a rival or when danger threatened. I saw no cases of ears being moved either together or singly in ways or in directions which did not accord with primary acoustic use.

The back surfaces of the hare's ears are distinctively coloured having a black tip with the area below grey/white. From the back the light coloured area stood out particularly brightly when the ears were fully extended facing forward, especially in low light conditions (Fig. 1). This pattern is not visible from in front of the animal.

Ears down. Both Schneider (1976, 1977b, 1981) and Lindlof

Figure 13. Bolingbroke resting but listening with one ear up.

Figure 14. Doe, Camelia, listening to sound ahead - I have whistled in her direction.

(1978) suggest that hares communicate a threat by laying their ears flat on the back and lifting the angle of their muzzle. I have seen such behaviour on many occasions but in all cases directed by does towards bucks. Most of them were when a buck approached a doe frontally to sniff its nose (see nose-sniffing post) and the doe reacted in that way. The behaviour takes the form of an intention movement, the ears dropping preparatory to a charge and the muzzle lifting preparatory to a bite from the underslung jaw. If bucks did not withdraw when so confronted, does charged at them. Nevertheless, the intention movement did appear to have undergone sufficient ritualisation to rank as a communication. I have not seen similar behaviour from bucks, which initiated charges apparently without notice (see Figs. 6 & 7). Dropping the ears alone did not constitute a threat. Ears were dropped when circumstances required inconspicuousness, for example when in their forms (Figs. 1, 2 & 4 Chapter 3) or when danger threatened, when travelling at maximum speed either pursuing (Fig. 7) or being pursued (Fig. 8) and when damage to the ears might be sustained in combat. The photographs in Figure 4 in Chapter 9 and Figure 15 in this Chapter, which were taken within seconds of each other as part of one sequence, show in the one frame the buck with ears dropped as the doe strikes and in the other frame the reverse situation.

Nose-sniffing. This behaviour, which Schneider (1981) refers to as nose caressing, involved consorting couples. Typically, the buck approached the doe, which was in a crouched position either feeding or resting in its form, sticking out his muzzle so that his nose was only a few centimetres from hers. She pushed her muzzle forward to

Figure 15. Buck, Cadet, ears raised in boxing posture to doe, Camelia, ears down. For the reverse, see photograph at Figure 4, Chapter 9, taken within seconds of the above.

the point where the noses almost touched (Fig. 16). In a minority of cases they might actually touch. After sniffing for a few seconds the buck might withdraw. If, however, he failed to do so and persisted the doe then threatened by dropping her ears, if not already on her back, pushing her muzzle even further forward and lifting it at the same time. In most cases the buck then jumped back a metre or more, apparently in some alarm. In the small minority of cases where it failed to do so the doe either charged or struck at the buck. Sometimes this could lead to boxing but always the buck withdrew. This series of events could be repeated many times while the couple kept company. Nose-sniffing was frequently observed between leverets (see Chapter 7) but never between adults except inter-sexually as just described. Set out below are extracts from my diary notes illustrating the behaviour:-

> 10 January 1985. 0715-0900h. A group of four hares including a couple in close company within three metres and usually much less of each other. Throughout the period they remained in close company for the most part lying facing each other noses about 50cm apart. Periodically the buck approached the doe until their noses were touching - very gingerly. Sometimes the doe appeared to co-operate allowing her nose to be sniffed. Sometimes she would then turn her nose/muzzle further up towards the sky at which the buck would jump back 150cm in apparent alarm. During the period the doe threatened the buck on his approaching 22 times, the majority when they were lying facing each other but some when they were moving around with him following her.
>
> 16 May 1985. A group of three hares including consorting couple. In the next 10 mins. I see at least six approaches by the buck to the doe nose to nose and on each occasion the doe threatens and he withdraws.

Between 1981 and 1988 I observed inter-sexual adult nose-sniffing,

Figure 16. Upper, buck mateguarding doe, Celandine, in her form. Lower, buck has approached doe and both are in typical nose-sniffing attitudes.

frequently involving repeated episodes, on a total of 44 occasions. In 38 (86%) the initial approach was by the buck. In those the doe was always in a crouched position with her body on the ground, in contrast with tail-shaking behaviour when her body was always off the ground. On more than 50% of occasions the doe was in her form when the buck approached. In only six (14%) of the 44 instances were noses seen actually to touch. To obtain a measure of the extent to which threat by does, or apprehension of them by bucks, was involved I recorded all cases where the buck visibly jumped back, as compared with a relaxed withdrawal, while nose-sniffing. In many cases it was not possible to distinguish whether it was as a result of threat or sheer apprehension that it did so. Bucks jumped back on 29 (66%) of the 44 occasions although the doe only actually struck out or charged on five (11%) of them. In one unusual case the roles were reversed and it was the buck which charged. A doe was feeding and nearby a buck, which regularly consorted with her, was crouched resting. The doe went over to the buck and sticking her muzzle out appeared to threaten him. The buck jumped up and charged straight at the doe which jumped out of the way. The buck then returned and resumed its rest. In none of the remaining 43 instances did the doe withdraw or show any sign of being intimidated by the buck. There were indications that nose-sniffing behaviour predominated as a doe drew near to oestrus. I recorded all cases where the behaviour took place either when the doe was being mate guarded (the buck remaining within 5m of the doe whilst in her daytime form) or when there were one or more satellite bucks in attendance additional to the consort. Both of these situations are generally restricted to a period within, at its maximum, five days of oestrus (personal observation). In 14 cases there was mateguarding and in 12 further cases satellite bucks were in attendance making a total of 26 (59%) of the 44 instances.

Chin-marking. Between 1982 and 1987 I noted a total of 15 instances of chin-marking. Most of these involved several, sometimes many, examples from the individual concerned as the behaviour was repeated. The sex of the individual was known in 11 (77%) cases and these were all bucks. On 13 (80%) of occasions the individual was solitary. On the other two occasions the behaviour was demonstrated by the buck of a consorting couple. Nine (69%) of the 13 cases from solitary hares were when the animal was travelling (having already crossed at least one field margin) and in some instances (see example below) considerable distances were involved. Chin-marking was not restricted to high ranking bucks. On one occasion I observed several examples of the behaviour from one buck which had recently been chased by another in the adjoining field. All of the 15 instances were during the breeding season, January to August, with one exception on 4 October 1982. Generally, objects chin-marked were at or around eye level to a squatting hare. Where the objects marked were identified, grass clumps featured once, rush clumps three times and dead rushes and thistles nine times. Set out below are extracts from my diary notes illustrating the behaviour:-

> 20 March 1986. 0620-0655h. Prospecting buck covered 1-1½km during the period. Much rubbing of the chin on dead stems and other protrusions throughout the distance of its travels.
>
> 23 March 1987. Consorting couple. On a number of occasions the buck approaches the doe. When doing so he shows tail flash as also he does when moving round chin-marking upstanding objects.

Enurination. Urinary scent marking was under-recorded in the study, partly because observer/animal distances made it difficult to establish with certainty that, for example, spray had been observed. No targeting of conspecifics was observed. The only scent marking behaviour noted was urine spraying by bucks whilst on the move. Extracts from my diary notes illustrating the behaviour are presented below:-

> 23 April 1982. 1845h. Buck having been routed by another in the adjoining field crosses into field 17 and runs North in stages occasionally stopping to rub its chin on upstanding objects. I also see it urinate on its feet as it runs and kick back the urine spray.
>
> 11 March 1989. Group of three. Under observation 1030-1230h and 1515-1715h. During the period I saw the dominant buck do the kick back urine spray 15 times, particularly when near the doe and the subordinate buck did so three times. The doe did not do so.

Discussion

The white flash of the fully upturned undertail of the brown hare is its most striking visual signal. Its function is, however, not so obvious. Both sexes show it when defecating and urinating. Otherwise it is shown predominantly by bucks. The only situations when does were observed to upturn their tails were when meeting a buck after dark in just three cases and when approaching and consorting with their unweaned litter, where it was a regular feature. Bucks upturn their tails regularly when consorting with does and when chasing satellite bucks away from the doe. They also do so regularly when squatting upright whether in company or not and, occasionally, when on the move prospecting for does. If the upturned tail flash is a visual signal on those occasions it is a puzzle to what the signal is directed.

communication between hares

When consorting with a doe the buck for the most part follows her from which position she cannot see his tail flash. Perhaps the flash is a warning to other bucks which might be following but, if so, that does not seem to deter them. When consorting couples are accompanied by satellites there are frequent chases by the consort buck of the satellites. Always the pursuer has its tail up and the pursued has its tail down. The same applies to snowshoe hares according to Graf (1985) who says -

> "if the chase involved other males, the aggressive male doing the chasing had its tail up high, while the hare being chased kept its tail tucked down tightly against its rump".

As mentioned, I have even observed bucks showing the tail flash when they have been chasing birds. Obviously, in chases between hares the pursued hare cannot see the tail flag of the pursuer. Again, there is no obvious source towards which the signal is directed. Bucks squatting upright regularly, if not always, show the tail flash whether or not they are solitary at the time. If they are in company with other hares they squat facing towards not away from them, so the tail flash will not be visible. The tail flash of the doe can be interpreted as a "follow me" signal but there are no obvious interpretations of that of the buck in the various behavioural situations where it is displayed (Table II). A clue may lie in the passage from Koenen (1956) below -

> "Hares also have anal scent glands. They empty into three sacs that have ducts that can be protruded outside the anus. When the hare sits on its hind legs these glands release their yellowish, strong-smelling secretions to the ground below. The hare leaves a "calling card" in order to delineate familiar terrain and to announce its presence to other hares".

Table II. Apparent function, as a visual signal, of the upturned white tail flag. Behavioural situations from Table I.

Behavioural situations	Shown by	Apparent function
defecating and urinating	bucks and does	
consorting with does	bucks	unknown
chasing other bucks	bucks	unknown
squatting upright	bucks	unknown
prospecting for does	bucks	unknown
consorting with bucks	does	invitation to follow
consorting with litter	does	invitation to follow

The glands to which Koenen refers are clearly the anal gland and the paired inguinal glands lying on either side of the penis/vulva. The mixture of sebum and sweat produced by the inguinal glands empties into pouches of hairless skin at the base of the genital opening. Secretions from these glands are thought to function as a sexual attractant and also, probably in common with other scent producing glands, to convey individual identity (Mykytowycz & Goodrich 1974; Bell 1985). When squatting, bucks could not mark the ground with those secretions without lifting their tails. Presumably also, they could not release the odour from those glands to the air to full effect without lifting their tails. If lifting the tail and the release of sexual odour were interconnected, light might be cast upon those items in Table II where the function as a visual signal of the buck's tail flash is not apparent. In all of those the release of sexual odour would be appropriate. It would make sense that in a chase between bucks the one pursued would turn off its odour so as not to provoke the pursuer. I suggest that the white tail flash of bucks may be neutral or of no relevance as a visual signal but not so deleterious as to have been removed from one sex by selection and that the importance of the tail flash to the species is as a "follow me" signal between does and leverets. That signal would be enhanced and reinforced if accompanied at the same time by release of the doe's odour. This accords with one of the four rump patch theories, namely that the signal will be shown when the female of the species is being followed by its offspring. Clearly Guthrie's (1971) theory that rump patches are organs of submission, used to communicate subordination, does not apply to the brown hare. Possession of a white tail flag is common to many other species in the genus, perhaps with a common function.

Tail-shaking is exclusively a behaviour of does performed exclusively in the very close proximity of bucks. When shaked the tail is held horizontal showing neither the pattern of the upper tail nor the white flash of the undertail. It is unlikely that any visual signal is involved. The area of ground immediately below where the doe has shaked its tail is of extreme interest to bucks which often spend some time sniffing it. The impression given is that some secretion on the undersurface of the tail has been deposited onto the ground by the vibratory action of the tail. Does typically tail-shake when they are moving, with their bodies off the ground. They do so upon the very close approach of a buck, the doe moving forward and shaking her tail as she does so. If, having sniffed at the ground, the buck approaches the doe again she will repeat the process. Schneider (1976, 1990) refers to tail-shaking as an invitation to bucks to follow. It is both that and also an invitation to then continue to follow but first and foremost it is the provision of a concentrated source of information. Except when tail-shaking, does keep their tails down. It is to be assumed that the secretion producing glands are the inguinals which are larger in the brown hare than in the rabbit and far larger in the doe than in the buck (Mykytowycz 1966). Unlike many mammals, hares spend most of their lives in a crouched position with their bodies resting on the ground. In that position they both feed and rest. A buck can obtain no olfactory information on the reproductive condition of a doe by sniffing at her crouched posterior and it is only inexperienced young bucks that try to do so (personal observation). Information can, however, be obtained by a frontal approach, sniffing the facial area of a crouched doe, but bucks doing so place themselves in a vulnerable position to a charge or bite by the larger and heavier doe. They are extremely wary of doing so.

Is there any control by does of the amount of olfactory information they disseminate to bucks? In an attempt to answer the question, it is useful to look at the results of some research on the breeding behaviour of captive brown hares. They showed that there was a very high incidence, 180 out of 372 observations, of oestrus and mating of pregnant does several days before parturition resulting in superfoetation, where two ages of embryo are present in the uterus (Table III, taken from Caillol & Martinet 1981). Litters thus conceived were larger than those conceived post-partum. In the wild, on the other hand, examples of superfoetation are rare. Flux (1967)

Table III. Relation between the period when oestrous behaviour and mating takes place (calculated from the intervals between 2 successive parturitions) and the resulting mean litter size (from Caillol & Martinet 1981).

Interval between 2 successive parturitions	Period of oestrous behaviour	Number of observations	Litter size $\bar{x} \pm SE$
≤ 40 days	Prepartum oestrus, fertilization and superfoetation	180	2.30±0.065
41 to 43 days	Postpartum oestrus	19	1.68±0.17
45 to 55 days	Pregnancy + pseudopregnancy, oestrus at the end of pseudopregnancy	62	2.02±0.12
≥ 55 days	Oestrus in a non-pregnant, non-pseudo-pregnant female	111	1.67±0.07

found three cases in a total of 428 does at all stages of pregnancy. All three were within the group of 24 does with embryos over 100g representing 13% and the proportion rose to two of 11 (18%) in does with embryos of over 120g. Neither Lincoln (1974) nor Broekhuizen & Maaskamp (1981), examining respectively 83 and 107 pregnant does, found any cases of superfoetation. Why should there by such a difference in the behaviour of captive and wild hares? In this study I was able to observe the behaviour of three does, which could expect to have another oestrus that season, during the last two or three weeks pre-partum (Chapter 5). There was a marked difference between two of the does Bluebell and Fuchsia and the third, Clover, as to their own behaviour and also as to the extent they were escorted by bucks. During the period Bluebell and Fuchsia, which I referred to as the monitoring does, remained within the field and within 150m of the spot where they were to drop their litter. Both of them kept a low profile, only moving sufficiently to continue to graze. They were only occasionally accompanied by bucks. During the last seven days pre-partum Bluebell and Fuchsia were solitary for respectively 96% and 100% of observation hours (Fig. 4 Chapter 5). Both of them left the field after parturition, only returning to suckle. Clover, which I referred to as non-monitoring, occupied during the period a field separate from that in which she dropped her litter. She did not keep a low profile frequently moving about the field and was regularly escorted by bucks. During the last three weeks pre-partum she was escorted by bucks for 68% of observation hours and for the last seven days the percentage rose to 92% (Table III and Fig. 4, Chapter 5). She had her oestrus in the field she had been occupying and remained in it post-partum. I suggested in Chapter 5 that a proportion of pregnant does adopt a strategy of closely monitoring the prospective birthsite. Whilst so doing they are secretive and appear to avoid drawing attention to themselves. It seems that they succeed in this even at a time, the last few days pre-partum, when they would be expected to be a magnet for bucks. I suggest that this is achieved because they have the means of controlling the amount of information they disseminate as to their reproductive condition. Those means are their ability to limit communication from the posterior scent producing glands to such times as they shake their tails together with their ability by intimidation to deter bucks from frontal approach for information from their facial glands. Apparently, the limitation of scent production affects also the ability of hounds to track does during the reproductive season. Lovell Hewit (1975) writes -

> "the doe in kindle or in milk is a different matter as she leaves little scent. This failing of her scent glands seems to start with courtship. Once hares have started to congregate and run together when hunted the difference between the scent left by jacks and does becomes apparent. Hounds may run really well on the jack and then change to the doe. Immediately scent becomes sketchy and catchy in the extreme, although there can be no question of her being heavy in young at that time".

Just as does can avoid the attention of bucks, so it seems can they invite it. To do so they need to tail-shake in the presence of a buck and then to move on and tail-shake each time he catches up. Clover behaved in this way when regularly escorted during the three weeks pre-partum. It is difficult to see what benefit there is to the bucks in escorting a doe weeks before oestrus; on the face of it they are wasting time. The two which primarily accompanied Clover were Cavalier, of middle rank, and Chestnut, a subordinate. The alpha buck, Bolingbroke, was more discriminating, paying short visits only until near oestrus (see Table III and Fig. 1, Chapter 4). However, there may well be benefit to the doe in being escorted long before oestrus. Pregnant does feed voraciously and they will be able to spend more time feeding if they can reduce the proportion of time devoted to vigilance. Broekhuizen & Maaskamp (1982) and Monaghan & Metcalfe (1985) showed that with increasing group size individual hares spent less time in vigilance, making more time available for feeding. Non-monitoring does may, therefore, manipulate less experienced bucks to keep them company and thereby free more time for feeding.

Almost certainly a communication function is involved in the pattern of black central stripe and white margins of the upper surface of the tail. Hares on the move normally carry their tails down, thereby showing the upper surface. Observation demonstrated that the pattern stood out particularly in low light conditions. The signal which it constitutes would be a visual aid to one hare following another at night. Bucks frequently escort does and when so doing generally follow the doe. A permanent visual signal at the rear of the leader could be of benefit both to leader and follower in maintaining contact and also in reducing the need for potentially attention catching (to predators) search forays by the follower.

During the course of the study I obtained no data to support the suggestions by Schneider (1976, 1977a, 1977b, 1981, 1990) that hares signal to other hares with the whole body in the form of bipedal and stiff legged arched back postures and also that they signal with their ears. As to the ears, however, there are two exceptions. Flattening down of their ears in conjunction with tilting upwards the angle of the muzzle by does presages a charge at over attentive bucks. The movement itself has the effect of a threat which is generally heeded. Secondly, like the upper surface of the tail, the backs of the ears carry a pattern of dark and light areas which are particularly conspicuous when the ears are directed forward in low light condition. The signal from the ears would be visible to a hare following behind. Taken together, the message from the pattern of the downturned tail would be "here I am" and from the ears "and I am alert to something ahead of me". The benefit of the signal would be, for the follower, the warning which it conveyed and, for the leader, the effect which the communication for caution and discretion would have on the follower.

For bucks, nose-sniffing provides a secondary source of information on the reproductive condition of does. In the last few days before oestrus, does are likely to be guarded by a consort and the couple are often attended by satellite bucks. The inactive portion of each day is spent by the doe in her form in the usual way but her mateguarding consort also lies up within a metre or two. In many cases does undergo their oestrus during daylight hours. It is important therefore to the guarding buck to check from time to time upon the doe's state of readiness. Information cannot be obtained from the rear end of a doe crouched deep in her form but there is information to be had from her facial glands by a close frontal approach. The results demonstrate that such approaches are not always well received. In two thirds of all observed instances the bucks jumped back after closely approaching the doe as a result either of her threat or of sheer apprehension or, in a minority of cases, of attack from her. The reason for the aggressive behaviour of the does and apprehension of it by bucks would appear to be connected with the function of the form as a safe place of resort. Occupation of forms is primarily during daylight hours (Chapter 3) when the risk is from diurnal predators and the defence strategy is inconspicuousness, coupled with immobility. The close proximity of the guarding buck would reduce to a degree the inconspicuousness of the doe but the reduction would be marked if he was not immobile. Indeed, movement by the buck towards the doe would serve to draw attention to the couple. Does discourage such approaches and, although not measured, I formed the impression that older, more experienced, guarding bucks harassed does less in that way than the younger ones did.

CHAPTER 9

DO HARES SIGNAL TO FOXES?

Introduction

Amongst the mechanisms whereby prey seek to protect themselves are various forms of signalling to predators (Harvey & Greenwood 1978; Dawkins & Krebs 1979). Signals between individuals, whether of the same species or not, can evolve when both the sender and the receiver benefit from the response of the receiver and the message is not susceptible to cheating on the part of the sender. There is growing evidence that one function of anti-predator behaviour by potential victims is to signal to predators that they have been detected. Studies of klipspringer alarm duetting to black-backed jackals (Tilson & Norton 1981) and Thomson's gazelles stotting at cheetahs (Caro 1986) have shown as common features signals that were made from safe positions and directed at the predator. Signals, such as skylarks singing while under attack from merlins, can also be given by potential victims when they are within a range of distance from the predator in which, because of variations in individual condition or escape potential, some members of their population would be vulnerable to the predator but the signaller may be safe (ap Rhisiart 1989). This Pursuit Deterrence hypothesis has been clarified in a recent review by ap Rhisiart (1989) who split it into two sub-categories, "Perception Advertisement" and "Quality Advertisement", which he defined in terms of message-meaning analysis (Smith 1968);

> " (i) Perception Advertisement is a signal given by a prey animal, and directed at a potential predator, which has the message that it is aware of the predator's presence and the meaning that the profitability of the prey has thereby been reduced.
>
> (ii) Quality Advertisement is a signal given by a prey animal, and directed at a potential predator, which has the message both that the predator has been noted and information about the escape potential of the prey, and the meaning that the profitability of the prey has thereby been reduced."

Perception Advertisement occurs at distances at which the predator would find all prey of that type unprofitable to chase. Quality Advertisement occurs at a range of distances at which the predator would find it profitable to chase some members of the population, but not others. There is an important distinction between the two signals. Perception Advertisement is basically an honest cheat-proof statement that the predator has been spotted and is too distant to have any chance of success, whereas Quality Advertisement combines with it a statement, which could be cheated upon, as to the quality or escape potential of the signaller. The constraint against cheating is an associated cost, in the case of the skylark the possible oxygen debt caused by singing. Cost to the signaller is not, however, a requirement of Perception Advertisement.

In my study area foxes are often to be seen in the same field as one or more hares. The fox can either be travelling or foraging in the field. In the former case it is likely to trot through in a matter of a few minutes, but if it is foraging it may remain in the field for 20 mins or more. That particularly applies when the fox is feeding on earthworms. In some months earthworms can provide over 60% of the average fox's calorific intake (Macdonald 1980). Hares in the same field as a fox generally continue feeding, but if the fox approaches them to a distance of less than 50m their reaction is to stand bipedal, facing the fox until it passes. In a minority of cases when the fox approaches closer still, the hare will move away usually quadrapedally, but sometimes bipedally, to no great distance and still within the field.

Hares can form a substantial part of the diet of foxes particularly where, as in my study area, the rabbit population is low. In one part of Hampshire hares were the largest single component (30%) of fox diet in Summer and were a major feature (16%) in Winter. It is probable that leverets formed a high proportion of the total catch of hares (Barnes & Tapper 1982). In an area of Poland from which rabbits were absent, hares formed 38% by volume of the stomach contents of foxes (Pielowski 1976). That volume was divided equally between adults and leverets. Adults weighed on average 3kg and leverets 0.5kg. The contents of a full fox stomach average 520g, enabling a fox in theory to take five or six complete meals from one adult hare. Assuming that each fox took three meals from an adult hare and that half the adults were already dead when found, Pielowski calculated that foxes in his study area were taking annually an average of six live adult hares and 35 leverets. To test to what extent the foxes might be scavenging, the bodies of 15 adult hares which had

Figure 1. Hares crouched feeding.

recently died were left out. The majority were never touched by foxes and only one was completely consumed. In another case, the night after the food was left out, a fox ate part of the body but never approached the remains again. Pielowski concludes that foxes prefer live prey to carrion. Although there is no direct evidence, it seems clear that foxes do capture and kill adult hares, though not as frequently as they take leverets. To capture a hare, an extremely agile and athletic animal with a maximum speed almost half as fast again as its own (Macdonald 1984), the fox must depend either on stealth or ambush.

Why do hares stand bipedal before approaching foxes? Is it for purely functional reasons, the better to observe the fox, or might there be some form of intra- or inter- specific signalling involved? It is these questions which I will be looking at in this Chapter.

Methods

During the study I spent approximately 5000h observing hares, divided as to 60% of the time in daylight, 30% in twilight (defined as the first hours after sunset and before sunrise) and 10% at night. Records were kept of all cases when hares crouched feeding, resting or grooming reacted by a posture change (reacted) to foxes approaching them and of the estimated distances, believed to lie within a 10% margin of error, between animals at the time of the reaction. I distinguished between hares approached by foxes across open ground and those approached from cover, in the form of ditches or hedges, with the fox only making an appearance when close to the hare. Hares always rest in a crouched position and generally crouch to feed

(Fig. 1). Some grooming is also from a crouched position. Change of posture on the part of these animals, which will be referred to as sedentary hares, could be more accurately recorded than in the cases of hares already on their feet, or travelling or interacting in one way or another with conspecifics. The possible posture changes were to squat up on haunches (squat), to stand bipedal (stand) or to move away (move). Hares squat in many situations. When travelling any distance they stop at frequent intervals and from the squatting position check their surroundings. They sometimes squat to feed on taller vegetation and to groom. Characteristically, they adopt the posture, in which the animal is primed for action ready to propel itself whether in pursuit or flight, during high intensity inter- and intra- sexual interactions (Fig. 2a, b, c, and d). They also squat when nursing (Fig. 3). When squatting, hares can be multi-directionally alert, looking in one direction and with their ears cocked in other directions, or uni-directionally alert with all senses, including often a twitching nose, focusing directly ahead. Apart from standing before approaching foxes, hares stand in three other situations. The first, which can take place in any level of vegetation during intra- and very rarely inter-sexual interactions, involves boxing or the threat of boxing and is of infrequent occurrence (Fig. 4). The second, which is again of infrequent occurrence, happens when a buck is searching for a doe or for rival bucks in tall vegetation and stands to see over the top. The third, of regular occurrence in June and July, is when hares are consuming tall pre-flowering grassheads which they can only reach by standing (Fig. 5).

Figure 2a. Buck, Bolingbroke, squatting during a break whilst travelling.

Figure 2b. Doe, Celandine, squatting feeding on grass heads.

Figure 2c. Buck, Cadet, squatting grooming.

Figure 2d. Buck, Cadet, squatting during interaction with doe, Camelia.

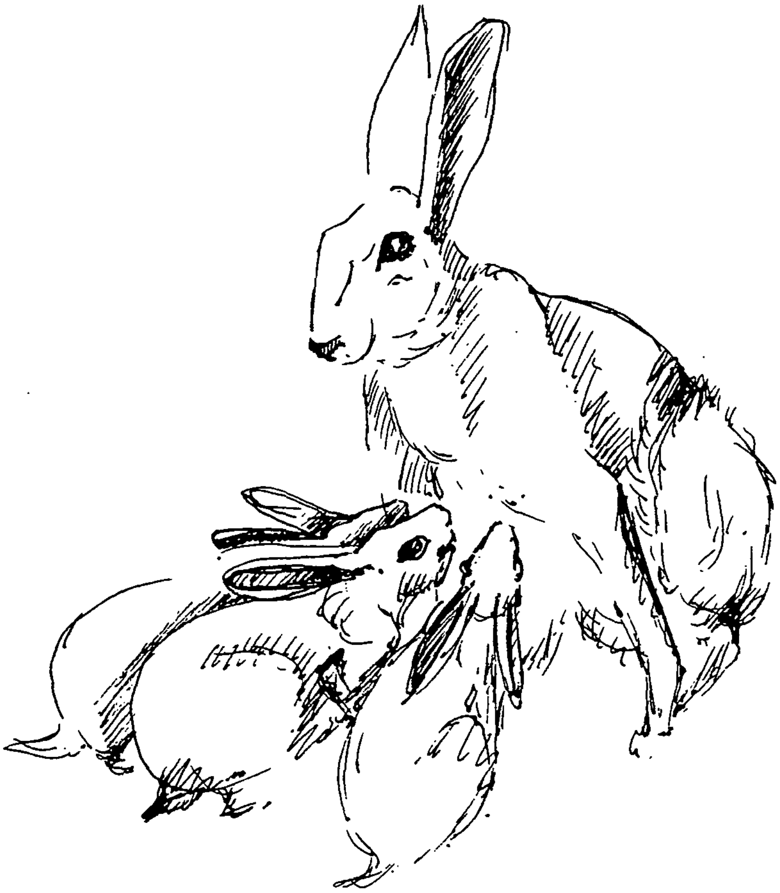


Figure 3. Doe squatting to suckle litter.

Figure 4. Doe, Camelia, standing bipedal to lunge at buck, Cadet.

Figure 5. Buck, Bolingbroke, standing bipedal to feed on tall grass heads.

hares and foxes

When hares stood before foxes I noted the height of the vegetation between them as low (less than 15cm), medium (between 15-30cm) and tall (more than 30cm). I classified hares as solitary only if at the time they stood there was no other hare in the vicinity, whether or not in the same field, which might have been able to see the posture change.

For comparison purposes I noted the reactions of hares approached by dogs mostly accompanied by, but not leashed to, humans but including lurchers and greyhounds actually coursing the hares and also their reactions to cats, which can take hares although probably almost exclusively leverets (von Schantz 1980; Liberg (1981).

Results

Sedentary hares did not react to approaching foxes at a greater distance than 50m, but no hare was approached closer than 20m without reacting (Fig. 6). On a total of 32 occasions foxes in the open approached sedentary hares sufficiently closely for the hares to react. On 31 of the 32 occasions the reaction of the hare was to rise from the crouched position and to stand, ears erect, directly facing the fox and to turn its body so as to remain facing the fox as it passed. (Fig. 7). Sometimes the hare bounced on its toes, possibly to keep balance. In the process of standing, hares display in the direction of the fox the white coloration, shared with many mammals, of the ventral area of their body stretching from thorax to tail. To illustrate the situations in which this behaviour occurs, I set out below three extracts from my diary notes:-

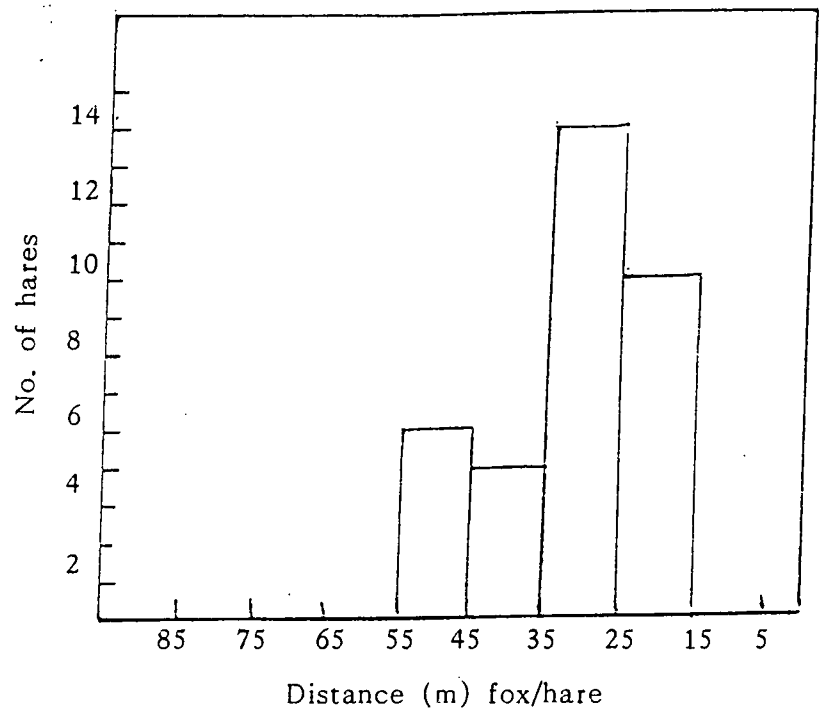


Figure 6. The distances at which sedentary hares reacted to a fox approaching in the open. All foxes were more that 70m distant at first appearance. 31 (97%) of the 32 reactions were to stand bipedal. No hares were approached closer than 20m without reacting.

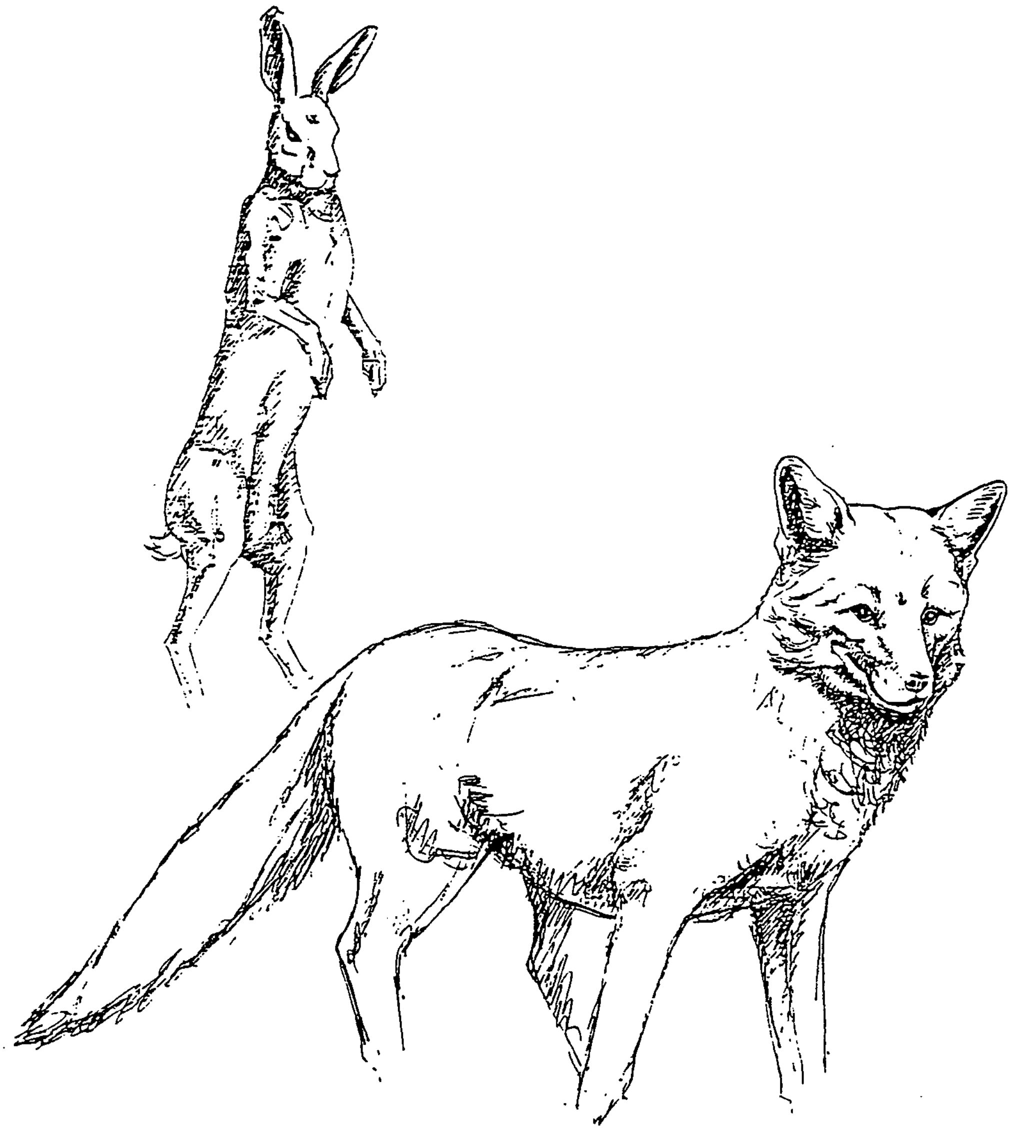


Figure 7. The hare continues to stand facing the fox as it passes.

> "6.9.88. Field 4. Grass ley stocked. Grass low. Sunset 1948.
> 2015. A hare is about 10m out into the field from the north boundary feeding. It rises and takes a bipedal stance. There is a fox coming along the east margin of the hedgerow about 30m away. Fox stops when the animals are about 8m apart. The hare has not moved but has dropped to the squatting position. Fox also adopts that position. So they stay for about 2 mins. then the fox trots on west in the lee of the hedgerow. I lose it but about a minute later it looks back at the hare from the hedgerow and I see the hare briefly adopt the bipedal posture again.
>
> 1.6.90. Field 4. Grass ley mown about three weeks ago. Sunset 2118.
> 2130. Within vision are a doe lying resting/feeding, a six week old leveret (regular) and three bucks which had been competing for the doe.
> 2135. Fox crossing the field towards the hedge of field 3. One buck stands bipedal at 40m but does not move away. Another buck stands at 25m but does not move away. Third buck stands at 20m and then lopes off for about 40m. The doe which at its nearest was 50m and the leveret at its nearest 70m from the fox did not stand or show any reaction.
>
> 4.6.90. Field 4. Sunset 2121.
> 2145. Doe followed by buck enters the field and settle within 2m of each other.
> 2150. Fox proceeding slowly in their direction being mobbed, mostly from the ground, by four crows and two magpies. Fox now only 25m from the hares which are still crouched apparently unconcerned. Then the fox charges at the tormenting birds bringing it within 20m of the hares both of which stand bipedal and then move away about 30m."

Set out in Table I are particulars of all 37 occasions when foxes approached close enough for hares to react. There is a clear difference in the reactions of hares approached in the open and those approached from nearby cover. Of the former, none of the 32 moved away whereas of the latter three of the five did so. Of the former, the reaction of 31 of the 32 was to stand whereas none of the latter

Table I. The reaction - standing bipedal (stand), squatting upright (squat) or moving away (move) of sedentary hares approached by foxes (a) in the open and (b) from cover and the distance between animals at the time of reaction: only those marked * reacted immediately upon the appearance of the fox.

Estimated distance (m) between fox and hare	First reaction of hare (numbers of hares)					
	(a)			(b)		
	Stand	Squat	Move	Stand	Squat	Move
50	5	1	-			
40	4	-	-			
30	11	-	-	-	-	3*
25	5	-	-			
20	6	-	-	-	2*	-
Totals	31	1	-	-	2	3

did so. Both comparisons show high statistical significance, $P < 0.005$ and $P < 0.001$ respectively (Fisher's exact test of independence in a four-fold table). The mean estimated distances between foxes and hares approached in the open at the time of reaction was 32m. Four of the 37 reactions by hares to foxes were observed in daylight, the remainder taking place during twilight and at night, the periods when the two species were mainly active. Twenty-one were in low vegetation, 12 in medium and four in tall vegetation. This proportion reflects the preference of hares to feed in the open in low levels of vegetation at night (personal observation), Reacting hares were of both sexes. On 13 (42%) of the 31 occasions when hares stood before foxes the hare was solitary; in the remaining cases there was at least one other hare to which it could have signalled. Flashing of the white undertail was not observed, but the tail area would only have been visible in a minority of cases. The tail flash is not shown by hares being chased by dogs or conspecifics, but is displayed in various contexts related to the reproductive behaviour of the species (personal observation). None of the 37 hares were chased. The gait of the approaching fox, which ranged between a fast trot and a slow walk, was not recorded, but I formed the subjective impression that the slower the approach the shorter was the distance at which the hare stood. The reactions of foxes to hares standing appeared to be negative. They carried on with whatever they were doing before the posture was adopted. In just one case a fox jumped back a pace when a hare stood at 20m distance.

Of the 31 reactors which stood (Table I) 21 (70%) returned direct to their former posture as the fox receded from them. The remaining 10 adopted a second posture change as the fox continued to approach. The mean estimated distance between fox and hare at second action was 19m (Table II). In nine (90%) of the cases the change was to move away from the fox. Movement, in seven cases quadrapedal and in two bipedal, was at half speed only and to a distance of less than 50m. The remaining hare did not move as the fox drew nearer, but dropped to the squatting position when the fox was about 10m distant. None of the hares were chased. None of them left the field in which they had been when first approached by the fox.

The data in Table II show that standing hares move away from

Table II. Ten hares showed a second posture reaction. The second reaction - squatting upright (squat) or moving away (move) - of the individuals and the distances between animals when they were initiated are shown

Estimated distance (m) of fox when hare first reacted	Estimated distance (m) of fox at second reaction	Second reaction
50	30	move
30	20	move
30	15	move
30	15	move
30	15	move
30	10	squat
25	20	move
25	15	move
20	15	move
20	15	move

foxes approaching them closer than about 20m. Was there any posture in which hares would tolerate foxes in closer proximity without moving? Table III shows the occasions when, apart from the two chases mentioned below, I have seen foxes and hares within 10m of each other. On all three occasions the hare was squatting and on none of them did it move away, although in one case the fox passed by only five metres away and in another the fox actually started to charge at it. Twice during the course of the study, I saw

Table III. Foxes within 20m of stationary hares.

Estimated distance (m) when fox nearest to hare	Hare posture	Circumstances
10	squat	fox and hare looking at each other at 20m distance. Fox starts to charge at hare, which does not move and fox turns away
8	squat	see diary note for 6.9.88 extracted at page 188 supra
5	squat	fox emerges from cover of a ditch, nearby crouched hare squats. Fox passes by within 5m without hare moving away

foxes chase adult hares. On each occasion the chase was already underway when first observed, was short and the hare escaped.

I obtained 28 observations of hares reacting to domestic dogs either by crouching lower or by taking flight or both, in that order. These were mostly accompanied by, but not leashed to, humans but included lurchers and greyhounds actually coursing the hares. On no occasion did any hare stand. In four cases I have observed hares reacting to unaccompanied domestic or feral cats. All were in high vegetation. On two occasions the hares departed from the immediate area and on the other two occasions the hares stood.

Discussion

The results show that standing is the uniform response of a hare to a fox approaching in the open, but not to a fox emerging from nearby cover. As to the function of the response, possible explanations fall into three categories - purely functional (Predator Surveillance), signal to conspecifics and signal to predator (Pursuit Deterrence in its subdivision of Perception Advertisement). In the succeeding paragraphs the results of this study are examined against the predictions which would flow from the competing hypotheses. In two interactions with cats hares moved away and in two cases they stood. All four interactions were in tall vegetation and the hares could have stood either to see the cats over the intervening vegetation or to signal to them. The results for cats, therefore, do not assist in testing the hypotheses and are excluded.

The Predator Surveillance Hypothesis.

This hypothesis states that by standing, the hare can better monitor the movements and behaviour of the predator. It predicts that from that posture, visual discrimination of the predator is enhanced in some way. Results show that hares only stand when the fox approaches to within about 50m, although it may have been visible for at least twice that distance. Provided the fox approaches close enough they stand on all occasions, whether in short or tall vegetation and whether in daylight, twilight, moonlight or darkness. Hares are primarily adapted for a quadrapedal rather than a bipedal stance. The approach of a fox, a potential predator albeit no match for speed, is obviously an occasion for alertness, but so also are many other events particularly those within the sexual cycle such as bucks searching for oestrous does or for competitors. On those other occasions, however, hares do not stand unless they are in very tall vegetation and need to see over the top. They adopt, instead, the squatting position. That position gives them some height but perhaps more importantly a stable platform from which to maintain vigilance and, if required, to launch into instant movement. I suggest it is not plausible that a hare, facing a fox walking towards it in broad daylight or full moonlight across a mown field, stands when the fox is about 30m away in order to see the fox better.

The hypothesis predicts that in the process of predator surveillance the potential prey should not draw attention to itself. Yet that is exactly what the brown hare does. Not only would the movement of standing up catch the eye but when erect the hare, measuring perhaps 75cm from the ground to the tips of its ears, would present a much more striking profile than when it lay crouched. Additionally, it would be displaying the whole of its white ventral area in the direction of the predator. The hypothesis also predicts that hares should stand before approaching dogs, another potential predator, but they do not do so. Of the three predictions flowing from this hypothesis, support from the results is at best very questionable in the first and is absent from the other two.

Signals to conspecifics

In this category are explanations of the signals as warnings to conspecifics or as requisitions to other individuals to group or to stay grouped together (Hirth & McCullough 1977; Bildstein 1983). In this study results that on more than 42% of occasions the signaller was solitary, within the very narrow definition of that term adopted, that the signal was not given as soon as the predator was detected but only when it was within a certain distance of the signaller and that the signal was directed towards the predator cannot be reconciled with any of these explanations. That is not to say, however, that conspecifics may not use for their own benefit any information which the response may convey.

Perception Advertisement hypothesis.

This hypothesis states that by standing the hare informs the fox that it has been seen and consequently its chances of catching it are diminished. It predicts that the signal should be given at the most profitable moment to the hare and before it is in danger of being caught. Results from this study suggest that provided a healthy hare, which is in the open and in the right posture, has spotted a fox it is in no danger from that fox, no matter how close it may be. Hares remained in the squatting posture within 10m of foxes and in one case when being charged at by the fox, which gave up and turned away. That standing hares move away from foxes which come within 20m of them indicates, however, that in other postures there is a distance within which they could be vulnerable. Hares spend most of their time crouched. In that posture they rest and from it, with few exceptions, they feed. Crouched hares feeding 70m from an approaching fox do not react. That is not to say, however, that they ignore the fox. In fact they keep it under scrutiny by breaking off from grazing and looking over towards the fox from time to time. As the fox gets closer the breaks for scrutiny become more frequent until there is little profitability in continuing to feed. Whilst the hare is aware of the fox, that fact may not be clear to the fox which as it gets closer might initiate a charge. There is a cost to the hare in evading such a charge, both in energy consumed and also in the danger of running into the jaws of another predator, perhaps a second lurking fox. There could come a point, therefore, when it would be more profitable to the hare to demonstrate beyond doubt that it is watching the fox than to risk being charged. It seems plausible, although there is no direct evidence, that such point may coincide with the range of distance within which hares stand before foxes. Whilst the prediction is not confirmed, it receives support from the data.

The hypothesis predicts that hares should direct the signal towards the predator: confirmed. It predicts that they should signal on all occasions whether in tall or short vegetation: confirmed. It predicts also that the signal should only be given in the presence of stealth dependent predators.

It would be counter productive for a potential victim to give a signal drawing itself to the attention of a potential predator, which could pursue faster than it could escape. Predators can be divided into four main types: ambushers, stalkers, coursers relying on speed and coursers relying on stamina. The same predator can of course fall within one category in relation to one prey species and within a second category in relation to another. As predators of adult hares, foxes are not coursers but are likely to be ambushers and, possibly, stalkers. They are stealth dependent. Dogs are coursers, some breeds such as greyhounds relying on speed and others such as beagles relying upon stamina, and as such are not stealth dependent. The prediction is confirmed. Finally, the hypothesis predicts that foxes should not chase hares which signal as frequently as those which do not do so. None of the 31 hares which stood was chased. The prediction is not confirmed but is supported. Of the five predictions, three are confirmed and two are supported by the results.

Of the competing hypotheses, Pursuit Deterrence in the form of a Perception Advertisement signal is strongly indicated. It is a transparently honest signal, the constituents being such as to ensure its honesty. It is not given until the fox is well within the visual range of the hare and is made by the hare pointing itself directly towards the fox. This contrasts with other visual signals such as tail-flicking, tail-flashing and stotting, where the signaller is normally facing and often moving away from the receiver when giving the signal. The signal is constructed from an aspect of the hare's behaviour which has become ritualised and stereotyped, but without being exaggerated. Hares in tall vegetation stand in order to see over the top of it. When they are not in tall vegetation they do not need to stand and they do not do so except in the relatively close proximity of foxes. When standing for a fox the hare is behaving out of context and thereby an unambiguous signal can be transmitted. If one human mimes to another by standing on tiptoe, with neck craned and one hand clapped above the eyes facing a particular direction, the other immediately interprets that as the action of a person in a crowd closely observing some event in the distance. The standing hare is conveying a similar message so well that we tend to interpret it anthropomorphically and conclude that the hare needs to stand in order to observe the fox. But the human does not need to stand tiptoe when there is no intervening obstacle to vision, such as a crowd; nor does the hare. At night, hares generally resort to open areas with relatively low levels of vegetation, presumably to reduce the risk of ambush (personal observation). The signalling function of standing has evolved by the behaviour being shown out of context, but the same message would be conveyed in the few cases when hares do encounter foxes in tall vegetation and really need to stand in order to monitor the fox. The signal is not given when foxes emerge from nearby cover. That is because in such situations there is no time to give it. Hares already standing move away if a fox approaches closer than about 20m, suggesting that in that posture at shorter distances they could be vulnerable to a charge from the fox. Hares approached from nearby cover, therefore, do not stand but either move away or adopt the squatting, primed for action, posture. It could be asked why, if the squatting posture is the least vulnerable, any signal should not be given from it. The answer is that the posture is of such frequent and variable use that it is not capable of conveying an unambiguous signal.

The benefits to the fox of the hare's signal are obvious. It is saved the energetic expense and also the time of what would have been an abortive chase. As to the hare, by giving the signal it not only avoids being chased but also is able to remain in the area it was occupying when the fox appeared. Of all the hares which stood, 70% were still at exactly the same spot on the ground after the fox had departed. Of the remainder, none left the field in which they had been when the fox approached and only one moved more than 50m. Hares choose their feeding places with care and these can vary from one month to another, according to the variety and stage of growth of the crop, but whilst in favour the same field will be frequented night after night (Barnes & Tapper 1982). Not infrequently the two species will be in the same field. Foxes commonly forage in pastures for earthworms and in so doing can meander around a field for long periods. By spending a few minutes standing bipedal at any close approach of the fox, the hare can remain in the field with it and still be there when the fox has gone. At the frequency observed in this study such close encounters are likely to be experienced by a hare at least once every four or five nights.

Of other related species, only the arctic hare is known to stand in the presence of predators including the arctic fox and also, at times, humans. Parker (1977), studying arctic hares on Axel Heiberg Island, reported:

> "The behaviour of hares to human approach varied. Sudden approach, however, usually brought the hare to its hindlegs, standing erect on its toes. That position affords the hare a better view and is probably the reason for its use. If the hare is unable to distinguish the object of disturbance and a rapid approach is continued, it usually flees in "kangaroo fashion". If pursued, the hare quickly drops to a quadrupedal position and moves up slope to cover, often assuming an upright stance once high ground is reached, to look back at the object of danger."

Dr. David Gray who filmed an arctic fox approaching and chasing a group of arctic hares on Ellesmere Island writes in a personal communication:

hares and foxes

> "It was an interesting set of observations in that although hares usually respond to approaching or passing foxes by standing bipedally, the fox seldom chases the hares for more than the initial few seconds after the approach. In this case and one other observed later that day, the fox was unusually persistent and chased the group and individual hares for several minutes. The hares all moved together, stood on hindlegs, then ran bipedally away from the fox. As the fox persisted, the hares ran, hesitated, stood on hindlegs, scattered, ran again and the fox chased one hare away from the others. It ran up a hill and the fox departed. The interesting thing was that we think the fox had killed a hare which had broken a leg a day or so previously. So the fox had perhaps had a relatively easy kill and was "hoping" for another."

He also adds the following general information. Arctic foxes almost never make a direct approach - usually a zig-zag, seemingly uninterested indirect approach. Hares do not stand bipedal until the fox is close enough to see them. They may face or turn side to the fox while standing bipedal. Standing certainly seems to have a secondary element of alarm signal to conspecifics, although it is done by solitary individuals. Sometimes, but not regularly, the hares bounce up and down. This appears to be a matter of maintaining balance while stretching up on tiptoes. Bouncing while standing bipedal is seen before, during and after chases. Arctic hares only use bipedal locomotion in response to predators and in a long chase revert to quadrapedal locomotion to escape. Conspecific chases always progress quadrapedally. Arctic hares stand bipedal to avian predators also - snowy owl, gyr-falcon and raven - also to approaching humans at certain times and under some circumstances. It is interesting that the arctic hare sometimes stands sideways on to the fox. Might it be a case of the hare attempting to cheat by standing when seeing others doing so, without actually spotting the predator at the time? Interesting also that the arctic hare stands for a number of avian predators. If standing is a signal to the predator, then it can be concluded that the predator has a better chance of capturing a hare which has not spotted it, than one which has.

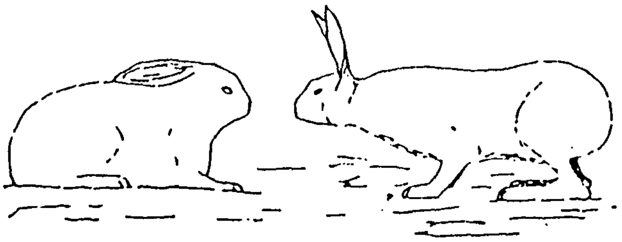
CHAPTER 10

GENERAL DISCUSSION

Until very recently there was uncertainty as to whether the brown hare was crepuscular or nocturnal in its activity. According to the first edition of The Handbook of British Mammals "active feeding times (are) dawn and dusk and probably through night" (Southern & Thompson 1964). That statement is only partially correct. During November, December and January hares are almost exclusively nocturnal and there is minimal activity at dawn or dusk. During the summer months, on the other hand, there is regular activity for two or three hours after sunrise and before sunset. According to the second edition of The Handbook "(hares) may feed in daylight, particularly in spring, but mostly nocturnal" (Hewson 1977): again, this is only partially correct. It is only in the third edition, referring to work carried out in this study (Holley & Greenwood 1984), that it is correctly stated "activity normally nocturnal but extends into mornings and evenings during summer" (Tapper 1991). From April to July inclusive, hares are active during daylight hours to a much greater extent than they are in March. Why, therefore, is it that in the popular mind they appear suddenly in March and equally suddenly disappear again? As this study has demonstrated, if there are sufficient nocturnal hours all activity will be confined to them. Hares prefer to be active by night. When, during the annual cycle, reduction of night length reaches a certain level hares become part diurnal. It can then be observed that there are contrasting preferences of habitat during nocturnal and diurnal activity, the latter including twilight. At night hares prefer to be on open ground in short vegetation (Fryelstam 1976; Hewson 1977; Tapper & Barnes 1986 and personal observation). A similar preference is reported from the mountain hare (Hewson 1976; Moss & Hewson 1985) and from the black-tailed jackrabbit (Lechleitner 1958). When active by day, brown hares prefer to be in or immediately close to tall vegetation or in the lee of hedgerows and they avoid open ground. They move out into the open after sunset and leave it before sunrise (personal observation). The pattern of habitat preference suggested by this analysis is modelled in Figure 1. It would account for the rapid decline in observed daylight activity after March which has contributed towards the March Hare myth. It may also have an effect upon the type of form occupied during the inactive period. As reported in Chapter 3, during the winter months November to April inclusive brown hares occupy forms on open ground, making it much easier to observe entry and exit times. During the long nights of winter, hares are entering their forms in darkness before daybreak. The model predicts an aversion to activity in tall vegetation or its equivalent, eg. hedgerows, in darkness. Activity would of course include the movement towards and the entry of the form. It would be expected, therefore, that forms entered in darkness would

	DARKNESS		DAYLIGHT	
	active	inactive	active	inactive
short	*	*	x	*
tall	x	x	*	*

Figure 1. Model of habitat (short or tall vegetation) occupied during active (out of form) and inactive (in form) periods of darkness and daylight. Habitat type accepted - * ; habitat type avoided - X.



Male snowshoe hare (right) in the "inquisitive" posture attempting to sniff a female (left) to determine her reproductive condition. Female is displaying the aggressive "ears down" posture.

Figure 2. Buck snowshoe hare nose-sniffing doe. Illustration and legend from Graf (1985), for comparison with similar behaviour by brown hare - see Fig. 16, Chapter 8.

be in the open and those entered into by daylight would be in taller vegetation. It would be expected also that hares in open forms would be loth to leave them during daylight unless there was cover close by. Why should there be the difference in preference of habitat types for daytime or night-time activity? The answer appears to be that the hare has an aversion to night-time activity in taller vegetation. That aversion could well be a response to the threat of ambush from foxes, probably its main predators. Flux (1970) and Thirgood & Hewson (1987) report that in the winter many mountain hares in Scotland use open peat scrapes in exposed positions as their forms instead of having forms in the heather, as they do for the remainder of the year. In the absence of snow this makes the animals in their white winter pelage very conspicuous, prompting the question whether similar pressures are affecting both species.

The reproductive season of the doe, to which references appear in Chapters 5, 6, 7 and 8, may run from the last week in December, when she has her first oestrus, to the end of October or early November in the following year when prolonged suckling of the final litter ceases. For much of that period she will be simultaneously pregnant and lactating. Commonly, she will have three litters in the period (Fryelstam 1980). During each lactation, she is likely to remain within a direct line distance of 300m from her litter. From there, she could respond to their distress screams. Each evening, she travels discreetly by a circuitous route to her litter, monitoring as she goes for potential predators and tracking them if they might present a threat. Suckling is for a brief period of a few minutes only during which the doe must remain vigilant and be ready to lead the leverets away, with her white tail flash, should the need arise. Suckling continues for about 30 days with the exception of the last litter of the season which is nursed for up to nine or ten weeks. When pregnant, some does take up residence close to where in due course they drop their litter. Their continuous presence shows them to be monitoring the spot. These does contrive to remain solitary, unattended by bucks for the majority of the time. Most strikingly, they are unattended during the last seven days pre-partum when they must either mask or suppress the pre-partum oestrus which captive brown hares undergo. It seems likely that in some cases the immediate post-partum oestrus is also masked or suppressed with the result that mating takes place about seven days after parturition, as in the case of Celandine in July 1982 (Chapter 6). Other pregnant does which take up residence away from the prospective birthsite and do not monitor it may contrive to be escorted by bucks before it would, on the face of it, be profitable for the bucks to spend time so doing. During the last few days before oestrus, does are likely to be escorted day and night by a consort buck and several satellites with considerable agonistic interaction between the consort and the satellites. Does are themselves harassed by the consort testing their scent. That this is particularly unwelcome when does are in daytime forms is demonstrated by the does threatening and sometimes boxing their escort.

The above summary of the does' long reproductive season serves to underline some of the pressures they undergo, to which must be added the stress of losing many of their leverets to predators before weaning. It also highlights three features of the does' behavioural ecology. First, that once mating has taken place all nurture and care of the leverets is the exclusive province of the doe, the bucks playing no part whatever. Secondly, that the breeding system appears to depend at a number of crucial points upon the effect of domination of bucks by the doe. Thirdly, that during the reproductive season the population as a whole will be as dispersed as the does are dispersed.

Bucks do not protect or provision their mates or their offspring in any way. Their contribution to the next and succeeding generations is exclusively genetic. In mating systems in which one sex is exempted from parental care polygamy is prevalent (Emlen & Oring 1977). It will be advantageous to that sex, in the case of the brown hare the males, to produce as many offspring as possible. That strategy is likely to require males to practice polygyny coupled with resource defence or female defence or male dominance (Emlen & Oring 1977). Bucks do not defend territories nor do they generally defend feeding sites. The strategy which they adopt is female defence polygyny in which dominant bucks consort with and guard does approaching oestrus (Chapter 4). Guarding is against subordinate bucks which persist in attending the consorting couple notwithstanding being repeatedly driven back by the master buck. The satellites are adopting an alternative low cost low benefit strategy. There is a chance that when the consort buck is pursuing another satellite or during the wild chase after the doe has commenced her mating run the satellite may be able to secure a sneak copulation. Satellites have no alternative but "to make the best of a bad job" (Dawkins 1980). Such alternative tactics are likely to be adopted by a proportion of males when the operational sex ratio, defined as "the ratio of reproductively active males to females in a breeding site during a specified interval of time" (Emlen 1976), is highly skewed towards males, as it is in the case of the brown hare. Strategies of this kind have been adopted by subordinate males of many species across a wide range of taxa including bees (Alcock et al. 1977), pupfish (Kodric-Brown 1986), tree frogs (Perril et al. 1978), ruffs (van Rhijn 1973) and topi (Gosling & Petrie 1990). Competition between males for females with male dominance hierarchies are reported, or suggested in reports, of the snowshoe hare (Severaid 1942; Graf 1985), black-tailed jackrabbit (Haskell & Reynolds 1947; Lechleitner 1958; Pontrelli 1968), mountain hare (Flux 1970; Hewson 1990) and white-tailed jackrabbit (Blackburn 1973). Just as it is in the interest of bucks to sire the maximum number of offspring, so it is in the interest of does to mate with bucks of quality whose male offspring are likely themselves to be successful in mating and thereby in the production of offspring (Fisher 1950). It is possible that an element of female mate preference, defined as "any trait (eg. behaviour, morphology) that leads a male (or female) to mate more frequently with certain males (or females) rather than others" (Halliday 1983) is involved in the system. This could arise, for example, through incitement of male competition by does travelling for their oestrus to areas where bucks are more concentrated. Results from this study have shown that does which, while pregnant, have been resident close to and monitoring the prospective birthsite, leave the area immediately after parturition and before their next oestrus, but have not revealed their destination. Do they, perhaps, seek out certain preferred bucks?

The reproductive system appears to depend at a number of crucial points upon the effect of domination of bucks by the does. The most obvious of these points is the period leading up to oestrus when does are likely to be mateguarded by bucks. Guarding includes the daytime period when does are in their forms. To avoid the attention of potential predators, occupation of forms requires immobility and inconspicuousness. That cannot be achieved if the doe is being harassed by frequent approaches from the guarding buck. Such behaviour in fact puts both of them in jeopardy. As reported in Chapter 8, guarding bucks approached does in their forms very warily and promptly withdrew if the doe threatened. In the few instances when bucks persisted and does struck at them, I have never seen the buck emerge the victor. Holley & Greenwood (1984) analysed film of an interaction between an oestrous doe, Camelia, and a young buck, Cadet, who was chasing after her. During the interaction there was a sequence of 35 short, rapid chases: each chase by the buck of the doe alternated, as the buck caught up with the doe, within 34 separate boxes. In 24 cases, the doe alone boxed, beating the head of the buck with her paws as he lunged forward beneath her. In eight cases the two hares started boxing simultaneously while in the remaining two cases the buck started to box after the doe had initiated. Again, it is anticipated, although I have no quantitative data to confirm, that at times when does contrive to be solitary during the monitoring of prospective birthsites when pregnant (Chapter 5) and during the nightly visit when lactating, perhaps, some manipulation of bucks is involved. Domination of bucks by does during the breeding season, with bucks dominating out of the season, has been reported of the snowshoe hare (Graf 1985).

Females of the brown hare are, on average, slightly larger and heavier than males (Tapper 1991) and this is the case with most lagomorphs including both the hares, which have precocial coated sighted young and the cottontails with altricial naked and blind young (Swihart 1984). In mammals generally, larger female size is the exception (Ralls 1977). This reversed sexual size dimorphism of the brown hare is the more unexpected in the light of the social system of female defence polygyny, with an operational sex ratio highly skewed in favour of males. Such systems promote intense competition between males. Darwin (1871) stressed that as a product of that competition the evolution of weapons and large body size should be favoured by the process he termed sexual selection. Bigger and stronger males should acquire more mates than their smaller and weaker competitors. A positive correlation between polygyny and sexual dimorphism has been demonstrated across species in various vertebrate taxa - frogs, toads and salamanders (Shine 1979), snakes (Shine 1978), turtles (Berry & Shine 1980), pinnipeds, ungulates, primates and humans (Alexander et al. 1979). There are exceptions in which, despite strong competition between males, females are larger such as the common toad (Davies & Halliday 1979). Why should the majority of lagomorphs, including the brown hare, be exceptions also. Some constraints must be operating so as to reduce reproductive fitness when males are as large as or larger than females, notwithstanding the advantage which size would be expected to give males in competition: in the mountain hare, females of which are again heavier than males, male dominance order was correlated with weight (Hewson 1990). Might one of those constraints be either increased mortality of the males or of litters in consequence of reduced female dominance? Events reported in Chapter 6 point to the possibility that the lactating pre-oestrus doe Celandine took positive action to deter consort bucks from keeping her company on nightly visits to suckle her litter. The loss of a litter, which the female was visiting to suckle, caused by the behaviour of a following male would of course reduce the fitness of that male if, but only if, he had sired the litter.

During the reproductive season, the population as a whole will be as dispersed as the does are dispersed. Monaghan & Metcalfe (1985) demonstrated that hares can benefit when foraging in groups. They have an increased corporate vigilance as group size increases and are able to allocate more time to feeding and less to vigilance. Monaghan & Metcalfe concluded by asking why hares do not forage in groups more often. Results from this study point to a reason. Some pregnant does take up residence in the immediate vicinity of the prospective birthsite of their litter. They monitor the site remaining there both during active and inactive periods. None of the nursing litters studied were in the same field as another nursing litter, with the results that they were well spaced out. The population of the study area was about 10 hares/km^2, at the lower end of those reported in the U.K. (Tapper 1990). Broekhuizen & Maaskamp (1980) studying 47 litters did not give the density of their population but referred to two litters within 40m of each other. That this may be unusual is suggested by their report that the litters sometimes mixed and if they were still mixed when one of the does arrived all the leverets were accepted and nursed. Mechanisms of parent-offspring recognition should evolve in species where a parent invests heavily in its offspring and where the potential exists for a parent to confuse its own young with others.

General Discussion

Parent-offspring recognition has been documented for a number of vertebrates including sandmartins (Beecher et al. 1981), squirrel monkeys (Kaplan et al. 1978), reindeer (Epmark 1971) and Mexican free-tailed bats (Balcombe 1990). Where parents fail to discriminate between their own young and others the most parsimonious interpretation is that intermingling happens so infrequently that selection for a recognition mechanism has not had the opportunity to operate. Support for this explanation of dispersal of the population - that pregnant does space themselves out - is given in the case of the mountain hare by data from Hewson & Hinge (1990) that the size of groups increase out of the breeding season. Parker (1977) reports that at the end of the short breeding season on Axel Heiberg Island, Canadian Northwest Territories, young leverets of the arctic hare collected together in nursery bands and by early August most hares in the study area had formed into several large herds containing both young and adults.

The most surprising data which emerged from observing the behaviour of leverets (Chapter 7) were those relating to their locomotor play. So much of the behaviour, both of does and leverets, is geared specifically to avoiding the attention of potential predators that the eyecatching performance of a leveret streaking represents a challenge to explanation. One of the first questions to arise when considering the behaviour was as to why, when there were two or more leverets meeting together, all streaks were performed singly with no chasing one after the other. That turned out to be because each leveret streaked over a course within its own familiar dispersal corridor which was exclusive to it. Corridors met close to the meeting point but the meeting area was of small extent and only served as a starting and finishing point for a return streak. Formerly all play including such categories as sexual play, play fighting, object play and locomotor play was regarded as a single entity. The assumption that play is homogeneous as to its causation, function and evolution is no longer tenable (Bateson 1981). Only locomotor play was observed from the leverets. The widely accepted view that play has immediate costs but delayed benefits (Fagen 1981; Smith 1982) is being increasingly questioned. The costs of play can be high. Harcourt (1991) found that 84% of South American fur seal pups caught and killed by southern sea lions were predated whilst playing. Gomendio (1988), studying the play of calves of Cuvier's gazelle, argued in relation to locomotor play that predation pressures would have selected for young animals to develop ways of enhancing endurance and general physical strength as quickly as possible. She continued:

> "when confronted with alarming stimuli, hiders normally exhibit a prone or freezing response, which then wanes with age as it is substituted by a flight response. This strongly suggests that young calves of hider species are not physically strong enough, when very young, to be able to flee successfully from predators and that the flight response starts to develop only gradually with age as a more appropriate mechanism. Locomotor play could be a way of rapidly improving physical abilities crucial for an adequate flight response.... It must also be born in mind that this kind of play might also allow the young calves to become familiar with the characteristics of the terrain they live in, which might have crucial benefits for the calves when confronted with a predator."

Exactly the same applies to the streaking behaviour of leverets. I have suggested in Chapter 7 that its function is to develop motor skills and strength but more importantly to develop at the earliest moment a last resort defence strategy for employment up to adulthood.

To the human observer, intraspecific communication in the brown hare appears very simple and limited, far less extensive than that of, say, the herring gull. Most of the gull's signals are a combination of visual and acoustic such as the long call, the mew call, choking and head tossing but there are others which are purely visual such as the upright or the red spot at the base of the adult lower mandible. (Tinbergen 1959). In contrast, the brown hare has but one acoustic signal, the distress call and four visual signals, the black and white pattern of the down turned tail with the message to a nocturnal follower "I am here", the contrasting pattern on the back of the cocked ears with the message to a follower "I am listening to something ahead", the white flag of the upturned tail with the only known message - from the doe to her leverets - "follow me" and, lastly, the threat posture of the doe to bucks. Why should there be such a small repertoire of acoustic and visual signals? As to the former, probably because of predator pressures. Sounds reveal presence and selection would be expected to operate against providing such clues. In the context of visual communication, it must be remembered that the brown hare is preferentially a nocturnal animal and vision is limited at night. However, much of communication between hares is too subtle to observe. It takes the form of social odours received by highly developed olfactory senses, which are lacking in the herring gull. The social odours play a prominent part in mammalian communication. For example, the production of pheromones that signal oestrous condition is widespread among mammals (Brown 1979). The field observer cannot detect the pheromones. He or she can only look for the visible signs, the lifted or shaken tail, objects being chin-marked or ground being sniffed, which indicate that they are being employed.

The possession of a conspicuous white underside of the tail in many species of lagomorphs (reviewed in Cowan & Bell 1986) has caused speculation as to its function, in particular as a warning or as some form of pursuit deterrent signal. Although the rule is not absolute, those species with tail flags tend to exploit more open habitats while species spending much of their time in thick cover generally lack tail flags (Cowan & Bell ibid.). They point out that tail flags are present in the less social leporids, eg. Lepus spp. and absent in two of the more aggregated species (Sylvilagus aquaticus and S.idahoensis) and comment that this would appear to argue against a warning function. This study has demonstrated that brown hares being pursued by predators or by conspecifics keep their tails down. The tail flag does not have either a warning or a pursuit deterrent function. It does have a function as an invitation to follow during interactions between does and their leverets. It may well be that it possesses the same function for other lagomorph species which show the tail flag. In species such as the brown hare, in which the doe only visits her leverets briefly about 50 mins after sunset each day, it would be very easy to overlook the use of the tail flag during that short interaction.

As to interspecific communication, results from this study suggest that brown hares signal to foxes that they have been seen and accordingly the fox's prospects of a successful attack are reduced. In a recent review Hasson (1991) pointed out that pursuit deterrent signals are most expected when they are most apt to change the predators behaviour. The cheetah, for example, tends not to alter its choice of prey animal once a hunt is started and Thomson's gazelles stott less in response to cheetah than to other predators (FitzGibbon & Fanshawe 1988). The gazelles, nevertheless, increase their stotting rate towards the end of pursuits, when cheetahs are more likely to estimate a failure and discontinue (Caro 1986). In contrast to the low stotting rate towards cheetahs, Thomson's gazelles stott vigorously at hunting dogs, coursing predators that select their prey during the hunt, although the probability of escaping relentless pursuit by hunting dogs is much lower (FitzGibbon & Fanshawe 1988). A perception advertisement signal from hare to fox is precisely the sort which would be expected to change the predators behaviour. If a fox does not know whether it has been spotted by a hare crouched feeding by night, it might well be worth initiating a charge in the hope of catching the hare. If, however, the hare makes it clear beyond all doubt that it is aware of the predators presence, then the fox faces a very different situation. It has neither the speed nor the agility of the hare and pursuit is likely to be profitless. The result of the hare's signal is that the fox is unlikely to charge. Such a signal gives information only about alertness of the potential prey. From observations quoted in Chapter 9, it appears that in the presence of arctic foxes and other predators arctic hares not only stand bipedal but also, if approached closer, move off bipedally kangaroo-fashion. They maybe signalling information not only as to alertness but also as to relative escape ability, or quality advertisement. Whether other species of hare signal to predators by a bipedal posture is not known. It seems probable, however, that another form of signalling to predators is employed by three species of New World hare. The antelope, white-sided and Tehuantepec jackrabbits share, as a feature of their pelage, white or light coloured areas encompassing all except the dorsal part of the body, the neck, head and feet. While at rest the antelope jackrabbit is moderately well concealed, but it explodes in a blaze of white when alarmed. The flanks and vest portion are white and can be erected by pulling the skin dorsally. The first few leaps are accompanied by a flashing of this white hair in the direction of the observer. As the hare changes direction, the skin is pulled round so that the side facing the observer is whitest. The similarity of this behaviour to the ungulate rump patch display was probably responsible for it being named after the pronghorn antelope (Seaton 1929).

The general behaviour of other species within the genus has not been intensively studied but there is accumulating a body of description of various aspects of behaviour covering a number of species. These have been referred to in the preceding Chapters and show a high degree of uniformity across species. An example of such uniformity is given by comparing the illustration at Figure 2 (from Graf 1985) of nose-sniffing behaviour of the snowshoe hare with the same behaviour of the brown hare (see Fig. 16 Chapter 8). It is anticipated that when the ethology of one species has been fully explored the results will assist in interpreting much of the behaviour of the remainder.

SUMMARY

1. This study has been concerned with aspects of the behaviour of the brown hare (*Lepus europaeus*). The study area was approximately 65 ha of agricultural land on the Somerset levels. Observation was from a fixed elevated point by means of high power optical equipment, enabling identification of individuals. There was no disturbance of subject animals.

2. During the study, I recorded the times of 242 entries by hares into their forms and of 512 exits from forms. In 180 instances I obtained both the times of entry and of exit from form on the same day. The majority of the records were obtained during the months December to March inclusive when hares occupy forms on open ground. From April onwards, forms are in longer vegetation and less visible.

3. In the study area, night lengths (sunset to sunrise) ranged from a maximum of 16.1h in December to a minimum of 7.4h in June. In December, hares were nocturnal leaving and entering their forms by night. In June they were part-diurnal, being active in daylight several hours before sunset and after sunrise.

4. Harmonic functions were fitted to the entry and exit data. The resulting curves revealed a mean activity period of 13.8h compared with a mean night duration of 11.7h. At peak night duration of more than 15.5h the activity period occupied more than 14h. At lowest night duration of less than 8h it occupied some 13h of which more than five are in daylight.

5. In spring, the transition from exclusively nocturnal to part-diurnal activity is not as smooth as the curves predicted. They showed a crossing over into part-daylight activity in week 8. The data show that during the following four weeks hares continued to avoid activity in daylight notwithstanding a reduction in night length over the period of nearly one and a half hours.

6. There was a highly significant dominance hierarchy among bucks competing for oestrous does. In a total of 31 chases or contests between bucks there were no reversals and this applied even when the loser was supplanted as consort of a doe. There was no respect of ownership.

7. Subordinate bucks escorted does at earlier stages of their oestrus cycle than dominant bucks. The closer a doe was to oestrus, the higher the ranking of her consort was likely to be.

8. Three does were under observation for between two and three weeks before parturition. Two of them occupied the field in which they were to drop their litter and appeared to be monitoring the prospective birth site. The third occupied a field apart from that in which her litter was to be dropped. Bucks escorted each of the two monitoring does for 10% of the total observation time

against 68% in the case of the non-monitoring doe. During the last seven days before parturition, when a pre-partum oestrus might be anticipated, the monitoring does were escorted for respectively 4% and 0% of total observation time against 92% in the case of the non-monitoring doe.

9. During the study hares were observed chasing crows on five occasions, four of them involving repeated chases. All chases were by does and three of the five were by does known to be pregnant.

10. During the day, does lay up within a direct line distance of 250m from their litters but generally took a circuitous route when visiting them to suckle. They left for their litter about sunset and the mean time of arrival was 48mins after sunset. Does delayed or detoured if foxes were met on the journey. When circumstances permitted, does varied the direction of their arrival at the litter, thereby keeping the nursing point static.

11. A consort buck and satellite bucks which had been keeping her close company did not follow a doe when she journeyed to suckle her litter the day before her oestrus, although the consort had accompanied her on the two previous evenings.

12. Four autumn litters, probably the last of the does' breeding season, were suckled for at least 43, 51, 59 and 62 days. The duration of suckling of one leveret reduced from 2mins 30s at five weeks of age to 1min 30s at nine weeks.

13. Sucking leverets normally met up with their litter mates after sunset a short distance from the nursing point. Upon meeting, they often sniffed each others noses and followed that with a short period of exuberant play activity - see 15 below. On average, they remained in the meeting area for about 10mins and then moved quietly to the nursing point. There their behaviour was subdued as they squatted close together, often touching, waiting for the doe, their only activity apart from listening being some grooming of themselves and, on occasions, each other. When the doe arrived, they rushed to meet her.

14. Some weaned leverets were observed to meet up around sunset, to show similar greeting and play behaviour and to keep company for up to 35mins.

15. The play of leverets was limited to locomotor play which most frequently took place during the first 40mins after sunset. The main constituent was streaking - running at top speed along a straight course and then, very often, returning along the same track at the same speed. Streaks frequently included other gymnastic components involving a variety of leaps. Streaking was observed from all stages of immature animals.

16. On five occasions distress screams were heard from leverets when the location, and thus the distance, of the litter was known. The two furthest distances were estimated at 550m and 350m. As does lie up during the day within 250m of their litter, it is likely that they would hear their screams. The cause of the screams on four of the five occasions was the act of predation and on the other occasion was unknown.

17. What is the signal of the upturned white undertail? Bucks regularly showed the tail flag, does only occasionally. Bucks flagged their tails when in the presence of does and when squatting on their haunches, whether in company or solitary. They also showed the tail flag chasing conspecifics but not when being chased by conspecifics or potential predators. Does showed the tail flag occasionally when meeting up with bucks and regularly when attending their litter. A litter was observed following a doe with her tail up raised. No evidence was obtained of any visual signalling function of the buck's tail flag which probably has only an olfactory function. On the other hand, evidence suggested that the white tail flag is used by the doe as a visual signal, coupled probably with an olfactory one, to her litter to follow her.

18. Does, but not bucks, tail-shaked - a rapid side to side vibration of the horizontally held tail. They did so only when in the presence of bucks and when their hindquarters were within 3m of a buck's nose. Bucks sniffed the ground under which a doe has tail-shaked suggesting that droplets of social odour are scattered by the action. An olfactory, not visual, signal appeared to be involved. Does tail-shaked at all stages of the oestrus cycle. The signal can only be given when their bodies are off the ground, normally when they are moving.

19. I suggest that tail-shaking may enable does to control the amount of information, in the form of social odour, which they release as to their reproductive condition.

20. The hare's tail is normally held downwards, rendering visible the pattern on the upper surface of a broad black central stripe bordered by a white margin. That margin is visible over considerable distances in low light conditions and would help to pick out one hare to another following it.

21. Schneider (1976, 1977a, 1990) suggested that the bipedal stance and the 'arched back stiff-legged stance' are forms of 'impressive behaviour' employed in agonistic interactions and also that a buck conveys his intentions to mate by arching his back. I did not observe any instances of either stance being employed for intra-specific communication. The arched back stiff-legged stance is nothing more than a hare stretching upwards upon rising from a rest.

22. Schneider (1976, 1984, 1990) suggested that hares conveyed messages by their raised ears which in one situation could signal an intention to mate, in another signal a 'friendly attitude' and in another pass information to a rival buck. I have been unable to detect raised ears being used for anything other than acoustic purposes.

23. When ears are raised and directed forwards the light coloured area below the black tip at the back of each ear stands out particularly brightly, especially in low light conditions. I suggest that this helps to draw attention of a following hare that the leader is listening to something ahead of it.

24. I agree with Schneider (1976, 1977b, 1981) and Lindolf (1978) that hares communicate a threat by laying their ears flat on their back and lifting the angle of their muzzle, although I have only seen the signal given by does. Both flattening the ears and lifting the muzzle are movements preparatory to an aggressive charge.

25. In adults, nose-sniffing has only been observed intersexually,

on 86% of occasions the initial approach being from the buck. It appears to be an alternative means of obtaining olfactory information about a partner whose rear end is on the ground and thus inaccessible. It is frequently employed by bucks approaching a doe in her form. On at least 59% of the approaches by bucks the doe was close to oestrus at the time. On 66% of the approaches by bucks, the interaction terminated by the buck jumping back under threat from the doe or, apparently, from apprehension of it.

26. I recorded 15 instances of chin-marking upstanding objects the majority of which were dead vegetation. Most of the instances involved many examples as the behaviour was repeated. In all of the 11 cases where the sex of the individual was known it was a buck. On 80% of occasions, the individual was solitary and in most cases was travelling at the time.

27. Enurination was under-recorded in this study. The only urinary scent marking behaviour noted was urine spraying by bucks whilst on the move.

28. Sedentary hares, crouched grazing or resting, did not react by a posture change to foxes approaching them across open ground at greater distances than 50m. No sedentary hare was approached closer than 20m without reacting by a posture change.

29. On 32 occasions, foxes approached sedentary hares in the open sufficiently closely for the hares to react by a posture change. The mean estimated distance between animals at the time of the reaction was 32m. The reaction on 31 of the 32 occasions was to stand bipedal facing directly towards the fox. The reaction of the one exception was to adopt the upright squatting position. Reacting hares were of both sexes. Hares were solitary on 42% of the occasions when they stood. None of the hares were chased.

30. Of the 31 reactors which stood, 21 (70%) returned direct to their former posture as the fox receded from them. The remaining 10 adopted a second posture change at a mean estimated distance of 19m as the fox continued to approach. In nine cases the change was to move away. The remaining hare did not move but dropped to the upright squatting position when the fox was about 10m distant. None of the hares were chased. None of them left the field in which they were when first approached.

31. I also observed 5 occasions when foxes approached sedentary hares, having emerged from nearby cover. There was a clear difference in the reactions of the hares in the two situations. None of the hares approached from nearby cover stood. Three of the five moved away, the other two squatted upright. None of them were chased.

32. I conclude that in standing before approaching foxes hares are giving a pursuit deterrent signal. It takes the form of a perception advertisement, informing the fox unambiguously that it has been spotted and is under observation with no opportunity for a sneak attack.

33. I suggest a model of habitat preference for active hares, varying between daylight and night hours. By day, hares prefer to be active in cover in longer vegetation; by night, they choose open ground with good all round visibility.

34. Unusually in mammals and particularly those in which there is strong competition between males for females, does are larger and heavier than bucks and, during the reproductive season, dominant to them. I suggest that constraints must be operating so as to reduce reproductive fitness when males are larger than females and that one of those constraints might be increased mortality either of bucks or of litters with reduced female dominance.

35. Other research has shown that hares can benefit when foraging in groups, each individual being able to allocate more time to feeding and less to vigilance. I suggest that the reason the population is as dispersed as it is during the long breeding season is connected with the behaviour of pregnant does, some of which remain for several weeks close to and monitoring the prospective birthsite of their litter.

36. I suggest that the conspicuous and potentially costly locomotor play of leverets has immediate rather than delayed benefit, as preparation for a defence strategy against some predators whilst its home range is of limited extent.

REFERENCES

Alcock, J., Jones, C.E. & Buchmann S.L. 1977. Male mating strategies in the bee Centris Pallida. Am. Nat., 111, 145-155.

Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, M. & Sherman, P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. In: Evolutionary Biology and Human Social Behaviour (Ed. by N.A. Chagnon & W. Iron), pp. 402-435. North Scituate, Massachusetts: Duxbury Press.

Aniskowicz, B.T., Hamilton, H., Gray, D.R. & Downes, C. 1990. Nursing behaviour of arctic hares (Lepus arcticus). In: Canada's Missing Dimension: Science and History in the Canadian Arctic Islands Volume II (Ed. by C.R. Harington) pp. 643-664, Ottawa: Canadian Museum of Nature.

Balcombe, J.P. 1990. Vocal recognition of pups by mother Mexican free-tailed bats, Tadarida brasiliensis mexicana. Anim. Behav., 39, 960-966.

Barnes, R. & Tapper, S. 1982. Why we have fewer hares.

references

The Game Conservance Annual Review, 14, 51-61.

Bateson, P. 1981. Discontinuities in development and changes in the organization of play in cats. In: Behavioural Development. The Biefeld Interdisciplinary Project (Ed. by K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main), pp. 281-295. Cambridge: Cambridge University Press.

Bayfield, N.G. & Hewson, R. 1975. Automatic monitoring of trail use by mountain hares. J. Wildl. Manage., 32, 214-217.

Beecher, M.D., Beecher, I.M. & Hahn, S. 1981. Parent - offspring recognition in bank swallows (Riparia riparia): II development and acoustic basis. Anim. Behav., 29, 95-101.

Bekoff, M. & Byers, J.A. 1981. A critical reanalysis of the ontogeny and phylogeny of mammalian social and locomotor play: an ethological hornets nest. In: Behavioural Development. The Biefeld Interdisciplinary Project (Ed. by K. Immelmann, G.W. Barlow, L. Petrinovich & M. Main), pp. 296-337. Cambridge: Cambridge University Press.

Bell, D.J. 1980. Social olfaction in lagomorphs. Symposia of the Zoological Society of London, 45, 141-164.

Bell, D.J. 1985. The rabbits and hares: order Lagomorpha. In: Social Odours in Mammals. (Ed. by R.E. Brown & D.W. Macdonald), vol. 2, pp. 507-530. Oxford: Oxford University Press.

Bildstein, K.L. 1983. Why white-tailed deer flag their tails. Am. Nat., 121, 709-715.

Blackburn, D.F. 1973. Courtship behaviour among white-tailed and black-tailed jackrabbits. Great Basin Nat., 33, 203-204.

references

Boback, A. 1954. Zur Frage des 'Hamspritzens' beim Feldhasen Lepus europaeus. Saugetierk Mitt., 2, 78-79.

Broekhuizen, S., Bouman, E. & Went, W. 1986. Variation in timing of nursing in the brown hare (Lepus europaeus) and the European rabbit (Oryctolagus cuniculus). Mammal Rev., 16, 139-144.

Broekhuizen, S. & Maaskamp, F. (1980) Behaviour of does and leverets of the European hare (Lepus europaeus) whilst nursing. J. Zool. London, 191, 487-501.

Broekhuizen, S. & Maaskamp, F. (1981) Annual production of young in European hares (Lepus europaeus) in the Netherlands. J. Zool. London, 193, 499-516.

Broekhuizen, S. & Maaskamp, F. (1982) Movement, home range and clustering in the European hare (Lepus europaeus Pallas) in the Netherlands. Zeit. Sauget., 47, 22-32.

Brown, R.E. 1979. Mammalian Social Odours, a critical review. Advances in the Study of Behaviour, 10, 103-162.

Caillol, M. & Martinet, L. 1981. Estrus behaviour, follicular growth and pattern of circulating sex steroids during pregnancy and pseudopregnancy in the captive brown hare. In: Proceedings World Lagomorph Conference. (Ed. by K. Myers & C.D. McInness), pp. 142-154. Ontario: University of Guelph Press.

Caro, T.M. 1986. The functions of stotting in Thomson's gazelles: some tests of the predictions. Anim. Behav., 34, 663-684.

Coblentz, B.E. 1980. On the improbability of pursuit invitation signals in mammals. Am. Nat., 115, 438-442.

Cowan, D.P. & Bell, D.J. 1986. Leporid social behaviour and social organization. Mammal Rev., 16, 169-179.

Darwin, C. 1871. The descent of Man and Selection in Relation to Sex. London: Murray.

Davies, N.B. & Halliday, T.R. 1979. Competitive mate searching in malecommon toads, Bufo bufo. Anim. Behav., 27, 1253-1267.

Dawkins, R. 1980. Good strategy or evolutionary stable strategy? In: Sociobiology: Beyond Nature/Nurture? (Ed. by G.W. Barlow & J. Silverburg), pp. 331-370. Boulder, Colorado: Westview Press.

Dawkins, R. & Krebs, J.R. 1979. Arms races between and within species. Proc. R. Soc. Lond. B, 205, 489-511.

Driver, P.M. & Humphries, D.A. 1969. The significance of the high-intensity alarm call in captured passerines. Ibis, 111, 243-244.

Emlen, S.T. 1976. Lek organisation and mating strategies in the bullfrog. Behav. Ecol. Sociobiol., 1, 283-313.

Emlen, S.T. & Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating system. Science N.Y., 197, 215-223.

Epmark, Y. 1971. Individual recognition by voice in reindeer mother-young relationship. Field observation and playback experiments. Behaviour, 40, 295-301.

Erlinge, S., Fryelstam, B., Goransson, G., Hogstedt, G., Liberg, O., Loman, J., Nilsson, I.N., Schantz, T. Von & Sylven, M. 1984. Predation on brown hare and ring-necked pheasant populations in southern Sweden. Holarct. Ecol., 7, 300-304.

Estes, R.D. 1976. The significance of breeding synchrony in the wildebeest, E. Afr. Wildl. J., 14, 135-152.

references

Evans, G.E. & Thomson, D. 1972. The Leaping Hare. London: Faber.

Fagan, R. 1981. Animal Play Behaviour. New York: Oxford University Press.

Fisher, R.A. 1915. The evolution of sexual preference. Eug. Rev., 7, 184-192.

Fitzgibbon, C.D. & Fanshawe, J.H. 1988. Stotting in Thomson's gazelles: an honest signal of condition. Behav. Ecol. Sociobiol., 23, 69-74.

Flux, J.E.C. (1967) Reproduction and body weights of the hare Lepus europaeus Pallas, in New Zealand. N. Z. J. Sci., 10, 357-401.

Flux, J.E.C. 1970. Life history of the mountain hare (Lepus timidus scoticus) in north-east Scotland. J. Zool. Lond., 161, 75-123.

Flux, J. 1981. Field observations of behaviour in the genus Lepus. In: Proceedings World Lagomorph Conference. (Ed. by K. Myers & C.D. McInness), pp. 377-396. Ontario: University of Guelph Press.

Fryelstam, B. 1976. Effect of cattlegrazing and harvesting of hay on density and distribution of a European hare population. In: Ecology and Management of European Hare Populations (Ed. by Z. Pielowski & Z. Pucek), pp. 199-203. Warsaw: Polish Hunting Association.

Fryelstam, B. 1980. Reproduction in the European Hare in southern Sweden. Holarct. Ecol., 3, 74-80.

Geist, V. 1971. Mountain Sheep: a Study in Behaviour and Evolution. Chicago: University of Chicago Press.

Gomendio, M. 1988. The development of different types of play in gazelles: implications for the nature and functions of play. Anim. Behav., 36, 825-836.

Gosling, L.M. & Petrie, M. 1990. Lekking in topi: a consequence of satellite behaviour by small males at hotspots, Anim. Behav., 40, 272-287.

Graf, R.P. 1985. Social organization of snowshoe hares. Can. J. Zool., 63, 468-474.

Guthrie, R.P. 1971. A new theory of mammalian rump patch evolution. Behav., 38, 132-145.

Halliday, T. 1983. The study of mate choice. In: Mate choice. (Ed. by P.P.G. Bateson), pp. 3-32. Cambridge: Cambridge University Press.

Harcourt, R. 1991. Survivorship costs of play in the South American fur seal. Anim. Behav., 42, 509-511.

Harvey, P.H. & Greenwood, P.J. 1978. Anti-predator defence strategies: some evolutionary problems. In: Behavioural Ecology: An Evolutionary Approach (Ed. by J.R. Krebs & N.B. Davies), pp. 129-151. Oxford: Blackwell Scientific Publications.

Haskell, H.S. & H.G. Reynolds. 1947. Growth, developmental food requirements and breeding activity of the California jackrabbit. J. Mammal., 28, 129-136.

Hasson, O. 1991. Pursuit-deterrent signals: Communication between Prey and Predator. Trends Ecol. Evol., 325-329.

Hewson, R. 1976. Grazing by mountain hares Lepus timidus, red deer Cervus elaphus and red grouse Lagopus L. Scoticus on heather moorland in North-east Scotland. J. Appl. Ecol., 13, 657-666.

references

Hewson, R. 1977a. Brown hare. In: The handbook of British Mammals. (Ed. by G.B. Corbet & H.N. Southern), pp. 140-144. Oxford: Blackwell.

Hewson, R. 1977b. Food selection by brown hares (Lepus capensis) on cereal and turnip crops in North-east Scotland. J. Appl. Ecol., 14, 779-785.

Hewson, R. 1990. Behaviour population changes and dispersal of mountain hares (Lepus timidus) in Scotland. J. Zool. Lond., 220, 287-309.

Hewson, R. & Hinge, M.D.C. 1990. Characteristics of the home range of mountain hares Lepus timidus. J. Appl. Ecol., 27, 651-666.

Hewson, R. & Taylor, M. 1975. Embryo counts and length of the breeding season in European Hares in Scotland from 1960-1972. Acta theriol., 20, 247-254.

Hirth, D.H. & McCullough, D.R. 1977. Evolution of alarm signals in ungulates with special reference to white-tailed deer. Am. Nat., 111, 31-42.

Hogstedt, G. 1983. Adaptation unto death: function of fear screams. Am. Nat., 121, 562-570.

Holley, A.J.F. 1986. A hierarchy of hares: dominance status and access to oestrous does. Mammal Rev., 16, 181-186.

Holley, A.J.F. & Greenwood, P.J. 1984. The myth of the mad March hare. Nature, Lond., 30, 549-550.

Johnson, C.H. & Hastings, J.W. 1986. The elusive mechanism of the circadian clock. Am. Sci., 74, 29-36.

Kaplan, J.N., Winship-Bell, A. & Sim, L. 1978. Maternal discrimination of infant vocalisations in squirrel monkeys. Primates, 19, 187-193.

Kodric-Brown, A. 1986. Satellites and sneakers: opportunistic breeding tactics in pupfish (Cyprinodon). Behav. Ecol. Sociobiol., 19, 425-432.

Koenen, F. 1956. Der Feldhase. Neve Brehm Bucherie. Ziemsen: Wittenberg Lutherstodt. 80 pp.

Lechleitner, R.R. 1958. Certain aspects of behaviour of the black-tailed jackrabbit. Am. Midl. Nat., 60, 145-155.

Lemnell, P.A. & Lindlof, B. 1981. Diurnal and seasonal activity pattern in the mountain hare. In: Proceedings World Lagomorph Conference (Ed. by K. Myers & C.D. McInnes), pp. 349-356. Ontario: University of Guelph Press.

Lent, P.C. 1974. Mother infant relationships in ungulates. In: The Behaviour of Ungulates and its Relation to Management. (Ed. by V. Geist & F. Walther), pp. 14-55. Morges, Switzerland: International Union fot the Conservation of Nature and Natural Resources.

Liberg, O. 1981. Predation and social behaviour in a population of domestic cat. Unpublished Ph. D. thesis, University of Lund.

Lincoln, G.A. (1974) Reproduction and 'March madness' in the Brown hare, Lepus europaeus. J. Zool. Lond., 174, 1-14.

Lindlof, B. (1978) Aggressive dominance rank in relation to feeding by European hare. Viltrevy, 10. 146-156.

Lockley, R.M. 1961. Social structure and stress in the rabbit warren, J. Anim. Ecol., 30, 385-423.

Lovell Hewitt, W. 1975. Hare hunting. The Lonsdale Library.

London: Seeley Service.

Macdonald, D.W. 1980. The red fox, Vulpes vulpes, as a predator upon earthworms, Lumbricus Terestris. Zeit. Tierp., 51, 1-22.

Macdonald, D.W. 1984. The Encyclopaedia of Mammals. London: Unwin Hyman.

Martin, P. & Bateson, P. 1986. Measuring Behaviour. Cambridge: Cambridge University Press.

Matuszewski, G. 1981. Circadian activity of European hares in spring, on the Kampinos forest border. In: Proceedings World Lagomorph Conference (Ed. by K. Myers & C.D. McInnes), pp. 357-365. Ontario: University of Guelph Press.

Maynard-Smith, J. (1982) Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Mech, L.D., Heezen, K.L. & Siniff. 1966. Onset and cessation of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Anim. Behav., 14, 410-413.

Meddis, R. 1975. On the function of sleep. Anim. Behav., 23, 676-691.

Meddis, R. 1977. The Sleep Instinct. London: Routledge & Kegan Paul.

Meddis, R. 1983. The evolution of sleep. In: Sleep Mechanisms and Functions (Ed. by A. Mayes), pp. 57-106. London: Van Nostraud Reinhold.

Monaghan, P. & Metcalfe, N.B. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. Anim. Behav., 33, 993-999.

Moss, R. & Hewson, R. 1985. Effects on heather of heavy grazing by mountain hares. Holarct Ecol., 8, 280-284.

Mykytowycz, R. 1965. Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit. Anim. Behav., 13, 400-412.

Mykytowycz, R. 1966a. Observations on odiferous and other glands in the Australian wild rabbit and the hare. I. The anal gland. CSIRO Wildl. Res., 11, 11-29.

Mykytowycz, R. 1966b. Observations and odiferous and other glands in the Australian wild rabbit and the hare. II. The inguinal glands. CSIRO Wildl. Res., 11, 49-64.

Mykytowycz, R. 1968. Territorial marking by rabbits. Scient. Am., 218, 116-126.

Mykytowycz, R. & Goodrich, B.S. 1974. Skin glands as organs of communication in mammals. J. Invest. Derm., 62, 124-131.

Packer, C. (1979) Male dominance and reproductive activity in Papio anubis. Anim. Behav., 27, 37-45.

Packer, C. & Pusey, A.E. (1982) Co-operation and competition within coalitions of male lions: kin selection or game theory? Nature, Lond., 296, 740-742.

Packer, C. & Pusey, A.E. (1985) Asymmetric contests in social mammals: respect, manipulation and age-specific aspects. In: Evolution - essays in honour of John Maynard Smith. (Ed. by P.J. Greenwood, P.H. Harvey & M. Slatkin), pp. 173-186. Cambridge University Press, Cambridge.

Parker, G.A. (1974) Assessment strategy and the evolution of animal conflicts. J. theor. Biol., 47, 223-243.

Parker, G.R. 1977. Morphology, Reproduction, Diet and Behaviour of the Arctic Hare (Lepus articus monstrabilus) on Axel Heiberg Island, Northwest Territories. Can. Field-Nat., 91, 8-18.

Perril, S.A., Gerhardt, H.C. & Daniel, R. 1978. Sexual parasitism in the green tree frog, Hyla Cinerea. Science N.Y., 200, 1179-1180.

Perrone, M. 1980. Factors affecting the incidence of distress calls in passerine birds. Wilson Bull., 92, 404-408.

Pielowski, Z. 1976. The Role of Foxes in the Reduction of the European Hare Population. In: Ecology and Management of European Hare Populations. (Ed. by Z. Pielowski & Z. Pucek), pp. 135-148. Warsaw: Polish Hunting Association.

Pontrelli, M.J. 1968. Mating behaviour of the black-tailed jackrabbit. J. Mammal., 49, 785-786.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. Am. Nat., 111, 917-938.

Ralls, K.B., Kranz, K. & Lundrigan, B. 1986. Mother-young relationships in captive ungulates: variability and clustering. Anim. Behav., 34, 134-145.

van Rhijn, J.G. 1973. Behavioural dimorphism in male ruffs Philomachus pugnax. Behaviour, 47, 153-229.

ap Rhisiart, A. 1989. Communication and anti-predatory behaviour. Unpublished D. Phil thesis, University of Oxford.

Robinson, J.V., 1980. A necessary modification of Trivers' parent-offspring model. J. theor. Biol., 83, 533-535.

Rohwer, S., Fretwell, S.D. & Tucksfield, R.C. 1976. Distress screams as a measure of kinship in birds. Am. Midl. Nat., 96, 418-430.

Rongstad, O.J. & Tester, J.R. 1971. Behavior and maternal relations of young snowshoe hares. *J. Wildl. Manage.*, 35, 339-346.

Sohantz, T. von. 1980. Prey consumption of a red fox population in southern Sweden. In: *The Red Fox*. (Ed. by E. Zimen) Biographica: vol 18, pp. 53-64. The Hague: Junk.

Schneider, E. 1976. Derzeitige Kenntnisse nber das Paarungsverhalten des Feldhasen. In: *Ecology and Management of European hare populations.* (Ed. by Z. Pielowski & Z. Pucek), pp. 41-57. Warswa: Polish Hunting Association.

Schneider, E. 1977a. Beobachtungen zum Korperpflegeuerhalten des Feldhasen. *Beitr. Naturk. Niedersachs.*, 30, 7-19.

Schneider, E. 1977b. Verhaltensstudien am Feldhasen. *Beitr. z. Jagd-und Wildforschung*, 10, 277-288.

Schneider, E. 1981. Studies on the social behaviour of the brown hare. In: *Proceedings World Lagomorph Conference.* (Ed. by K. Myers & C.D. McInness), pp. 340-347. Ontario: University of Guelph Press.

Schneider, E. 1990, Hares and rabbits. In: *Grzimek's Encyclopedia Mammals.* vol. 4, pp. 254-297. New York: McGraw-Hill.

Seaton, E.T. 1929. *Lives of game mammals.* Vol. 4, part 2. New York: Doubleday Doran & Co.

Severaid, J.H. 1942. *The snowshoe hare; its life history and artificial propagation.* Maine Dept. Inland Fish and Game. 95 pp.

Smith, P.K. 1982. Does play matter? Functional and evolutionary aspects of animal and human play. *Behav. Brain Sci.,* 5, 139-184.

Smith, W.J. 1968. Message-meaning analysis. In: *Animal Communication: Techniques of study and results of research.* (Ed. by T.A. Sebeok), pp. 44-60. Bloomington: Indiana

University Press.

Smythe, N. 1970. On the existence of "pursuit invitation" signals in mammals. *Am. Nat.*, 104, 491-494.

Smythe, N. 1977. The function of mammalian alarm advertising: social signals or pursuit invitation. *Am. Nat.*, 111, 191-194.

Sorenson, M.F., Rogers, J.P. & Baskett, T.S. 1972. Parental behavior in swamp rabbits. *J. Mammal.*, 53, 840-849.

Southern, H.N. & Thompson, H.V. 1964. Brown Hare. In: *The handbook of British Mammals.* (Ed. by H.N. Southern), pp. 255-259. Oxford: Blackwell.

Stefanski, R.A. & Falls, J.B. 1972. A study of distress calls of song, swamp and white-throated sparrows. (*Aves: Fringillidae*). I. Intraspecifics responses and functions. *Can. J. Zool.*, 50, 1501-1512.

Stieve, H. 1952. Zur Fortpflanzungsbiologie des europaischen Feldhasen (*Lepus europaeus*). Zoologischer Anzeiger, 148, 101-114.

Swihart, R.K. 1984. Body size, breeding season length and life history tactics of lagomorphs, *Oikos*, 43, 282-290.

Tapper, S.C. 1991. Brown hare *Lepus europaeus*. In: *The handbook of British Mammals.* (Ed. by G.B. Corbet & S. Harris), pp. 154-161. Oxford: Blackwell.

Tapper, S.C. & Barnes, R.F.W. 1986. Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *J. Appl. Ecol.*, 23, 39-52.

Thirgood, S.J. & Hewson, R. 1987. Shelter characteristics of mountain hare resting sites. *Holarct. Ecol.*, 10, 294-298.

Tilson, R.L. & Norton, P.M. 1981. Alarm duetting and pursuit deterrence in an African antelope. Am. Nat., 118, 455-462.

Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae) : a progress report. Behaviour, 15, 1.70.

Trivers, R.L. 1974. Parent-offspring conflict. Am. Zool., 14, 249-264.

Webb, W.B. 1975. Sleep: the Gentle Tyrant. Englewood Cliffs, New Jersey: Prentice-Hall.

APPENDIX

Index of specific names of animals mentioned

bee	Centris pallida
Pecos River pupfish	Cyprinodon pecosensis
common toad	Bufo bufo
green tree frog	Hyla cinerea
merlin	Falco columbarius
gyr falcon	Falco rusticolus
ruff	Philomachus pugnax
herring gull	Larus argentatus
barn owl	Tyto alba
snowy owl	Nyctea scandiaca
skylark	Alauda arvensis
sand martin (bank swallow)	Riparia riparia
starling	Sturnus vulgaris
magpie	Pica pica
raven	Corvus corax
carrion crow	Corvus corone
hooded crow	Corvus corone cornix
rook	Corvus frugilegus
jackdaw	Corvus monedula
Mexican free-tailed bat	Tadarida brasiliensis mexicana
antelope jackrabbit	Lepus alleni

index of specific names of animals mentioned

snowshoe hare	Lepus americanus
artic hare	Lepus articus
black-tailed jackrabbit	Lepus californicus
white-sided jackrabbit	Lepus callotis
brown hare	Lepus europaeus
Tehuantepec jackrabbit	Lepus flavigularis
mountain hare	Lepus timidus
white-tailed jackrabbit	Lepus townsendii
European rabbit	Oryctolagus cuniculus
topi	Damaliscus lunatus
Cuvier's gazelle	Gazella cuvieri
Thomson's gazelle	Gazella thomsoni
pronghorn antelope	Antilocapra americana
reindeer	Rangifer tarandus
domestic dog	Canis familiaris
African wild dog	Lycaon pictus
artic fox	Alopex lagopus
fox	Vulpes vulpes
cheetah	Acinonyx jubatus
domestic cat	Felix catus
lion	Panthera leo
southern sea lion	Otaria byronia
South American fur seal	Arctocephalus australis
squirrel monkey	Saimiri sciureus
olive baboon	Papio anubis