Mammalian Biology

Zeitschrift für Säugetierkunde

Original investigation

The daily activity period of the brown hare (*Lepus europaeus*)

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Abstract

The times of 241 entries into and 573 exits by brown hares from their forms on a 65 ha area of the Somerset Levels, South West England, were recorded over a ten year period to reveal the variation during the year of the duration of the daily activity period. In December when nightlength was 16 h, activity was exclusively nocturnal; intervals between entry and sunrise were longer and less consistent than those between sunset and exit. In June with nightlength down to 7.4 h, activity was part diurnal, post-sunrise and pre-sunset, for a total of 6 h. From a peak duration of 14.5 h in December, the activity period declined to 12 h in the third week of March, mirroring night time duration. It then increased to 13.5 h in late midsummer before again reducing in the autumn. It is suggested that the proximate cause of this circannual cyclicity is an aversion to daylight activity.

Key words: *Lepus europaeus*, brown hare, activity period

Introduction

Research on the circadian and circannual activity of the brown hare (*Lepus europaeus* Pallas, 1778) has hitherto been effected either by direct observation of hares on their foraging grounds (HOMOLKA 1986) and travelling to and from them (MATUSZWESKI 1981) or by radiotelemetrical monitoring of their movements (PEPIN and CARGNELUTTI 1994), the one exception being HOLLEY and GREENWOOD (1984) where, for part of the year, hares were timed exiting their forms in the evening. Such studies all suggest an annual cycle in the circadian activity period.

The brown hare's day and that of some other leporids is divided into two distinct periods. One, comprising all or a large part of the daylight hours, is spent crouched in its form

or resting place. During much of the other, comprising mostly the night 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 rhythm. The objects of this study were, by monitoring the times of entry into and exit from forms throughout the year, to define any annual cycle in the duration of the daily activity period and to consider the reason or reasons for it.

Material and methods

The observations reported here were part of a larger study of behaviour of the brown hare (HOLLEY 1992) on approx. 65 ha, divided between 17 fields in the north western sector of the Somerset Levels, close to Brent Knoll, Somerset, U.K. (51°16′ N, 2°58′ W). Fields were predominantly permanent pastures with a minority being ploughed in rotation for cereal growing. There were few hedges, fields being divided by drainage channels. Observations were made from September 1977 to September 1987 from windows 9 m above ground level in the roof space of my house within the study area. Optical equipment employed consisted of 7×50 and 15×80 binoculars, a Zeiss Jena 20/40×80 binocular telescope and a Celestron 11 catadioptic astronomical telescope, giving magnifications in excess of 100×. The latter could be coupled to a Canon F1 camera as a telephoto lens with a focal length of 2 800 mm. With the equipment it was possible to identify and sex individual animals. Occupied forms were under observation over distances up to 400 m.

I recorded the times (Greenwich Mean Time throughout the year) of entry into or departure from forms. All entries and departures, except temporary departures, were included whenever observed although most were obtained during observation periods conducted for the purpose, commencing at least an hour before the earliest or closing at least an hour after the latest expected entry or departure, as the case might be. Usually, hares were noted either entering or departing their forms but not both on the same day. These will be referred to as once-a-day (OD) observations. In some cases, which will be referred to as twice-a-day (TD) observations, I recorded both the time a hare entered its form and the time it departed. Preliminary observation having confirmed the popular notion that hares become more noticeable in March, TD data were collected particularly intensively in March of each year. The OD data were collected throughout the study, the TD data being collected during the second five-year period. The population of the study area was thought to be between 5 and 15 adult hares each year. No individual hare was seen in more than four successive years.

At some times of the year it was possible to record six or more entries or departures in one observation period. In cases of doubt, when a hare appeared to be entering a new form but might merely be taking a rest before moving on, I only counted an entry if the hare was still in occupation after all other visible hares were also in their forms. For departures, where in doubt, I only included hares previously observed in occupation of the same form before noon on the day. Temporary departures caused, for example, by disturbance from humans, cattle or other hares were disregarded. Apart from such temporary exits, hares remained in their forms until the normal departure time, the only exception being when a doe was very close to, or in, oestrus; bucks could then be active throughout daylight. The interval between departing and entering forms is defined as the activity period although it may include within it periods of rest. Likewise, the interval between entering and departing forms is defined as the inactive period.

Employing standard optical equipment, it was possible by sweeping the study area to observe departures throughout the year but in December and early January, when the nights were longest, it was not normally possible to detect entries more than 40 mins before sunrise. Because of this problem, I mounted special watch, between 15 December 1985 and 6 January 1986, on one form occupied regularly by the same hare with the principal object of recording entry times.

The observed times of entries and exits were differenced from the day's sunrise/sunset values, averaged for each day and then averaged over the pertinent week. These weekly differentials indicate the time in relation to sunrise/sunset at which activity usually started or stopped. Those results having indicated a cyclic behaviour, harmonic functions were fitted to the a. m. and p. m. weekly mean differentials.

The fitted seasonal curves have the form

$$y = A.\cos(wx - \varnothing) + C$$

Where $w = 2\pi/T$, $T = 52$, the period in weeks of the function, y, and $x = 1,2,3, \ldots 52$, the weekly independent variable. A, C, $\varnothing$, are constants determined by an Ordinary Least Squares fit to the weekly averages, A being the amplitude, C the long run average of the variable y, and $\varnothing$ the phase of the cosine function. The phase can be expressed in terms of the week, P. marking the peak of the cosine function

$$P = \varnothing.T/2\pi$$

A test of statistical significance of the computed function, y, can be carried out on the constant A by an approximate F test with 2 and N-3 degrees of freedom, (N = number of weekly observations, somewhat less than 52). Likewise, the significance of the displacement of one cyclic seasonal from the other can be determined by an approximate z test of the difference between the two values of

P. The choice of positive and negative for the differentials was arbitrary.

Results

Altogether 241 entries into forms and 573 exits from forms were observed; 178 were from TD observations, leaving 152 entries and 484 exits from OD observations. The number and relative frequency of these records spread over the year is shown in table 1, which also shows in relation to sunrise and sunset the average weekly differentials of entries and exits of OD and TD observations, with the pattern of records appearing in figure 1. Seasonal variation in the number of observations primarily reflects detectability of the forms, except for the peak of TD data in March which reflects application of additional observer time. The statistics and tests of significance for the fitted harmonic curves are given in table 2.

The divergence between entry and exit curves, which is significant (Tab. 2), justifies

Fig. 1. Night duration differentials. The constants are respectively sunrise (a) and sunset (b) with the curves of the harmonic functions of entries into and exits from forms throughout the year. Observations of OD hares from which the curves have been constructed (●) and the excluded TD hares (○) are averages for each week.

their separate treatment. As nights shorten in the early part of the year, hares begin to leave their forms before sunset on average about two weeks earlier than they begin to enter them after sunrise (Fig 1). There are insufficient data from which to make the same analysis for the equivalent period in the second half of the year. The fit between both sets of data (OD and TD observations) and the curves is clear but there are indications in mid-summer that activity at both ends of the day extends for longer than the curves predict and also that from week 31, the first in August, onwards and until the end of October it is shorter than predicted.

In December and early January, when the nights are longest, hares are almost totally nocturnal, entering and leaving their forms in darkness. The time of exit is very consistent, being generally no more than 30 mins after sunset. For the reasons given in methods, quantitative data on the timing of entry were not obtained at this time of year. In figure 2 are the results of intensive daily observation of one form occupied by the same hare during December 1985 and January 1986. Exit times averaged 26.8 mins post-sunset (range = 19–36, n = 11 days). Entry time was only observed directly (by moonlight) twice (83 and 56 mins pre-sunrise), while on 6 occasions the hare was already in the form when first observed that day (range of 46-96 mins pre-sunrise). Intervals between entry and sunrise were therefore longer and less consistent than those between sunset and exit.

For the majority of entries and exits the identity and sex of the individual was not known. However, in a minority of cases individuals were recognised thereby providing additional information. Over a two year period, I obtained 17 exit times of a known buck, Bolingbroke, who at the time was the alpha male in the dominance hierarchy within the study area (HOLLEY 1986). In 13 (76%) instances his exit from the form was before the mean time of exit by the study population. The exceptionally late entry and early exit TD data appearing in figure 1 and table 1 for week 24 refer to a study doe,
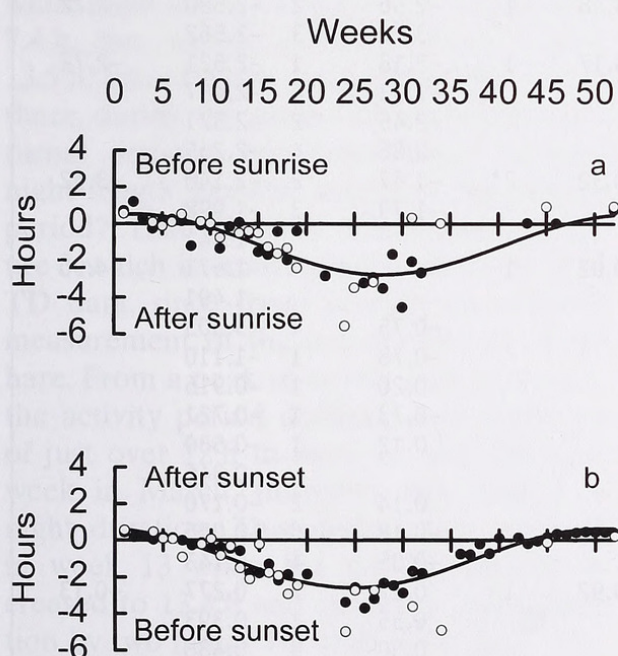
Table 1. The weekly means in hours for OD and TD hares of the differences between entries and sunrise (positive values before, negative values after) and exits and sunset (positive values after, negative values before). Also, nightime duration, sunrise to sunset, and the values of the fitted harmonic functions

Week	Nightlength	Entries am					Exits pm			
		OD hares	(n)	Fitted Function	TD hares	(n)	OD hares	(n)	Fitted Function	TD hares
1	15.983	0.70	6	0.517	0.56	4	0.43	21	0.591	0.57
2	15.817	1.19	2	0.526			0.18	19	0.528	
3	15.533	0.29	6	0.511			0.22	19	0.442	
4	15.233	−0.26	4	0.472	0.08	1	0.04	16	0.336	0.47
5	14.867	0.15	13	0.409	−0.12	4	0.18	36	0.211	0.09
6	14.483	0.24	16	0.325	0.10	5	0.14	23	0.069	0.22
7	14.050	0.15	2	0.219	0.51	2	−0.01	24	−0.088	−0.92
8	13.633	−1.22	1	0.093			−0.27	16	−0.258	
9	13.167	−0.07	1	−0.050	0.12	4	−0.14	40	−0.439	−0.22
10	12.717	−0.15	8	−0.209	0.02	1	−0.42	26	−0.627	0.08
11	12.267	−1.36	3	−0.382	−0.77	3	−0.39	17	−0.819	−0.83
12	11.800	−0.16	9	−0.565	0.12	17	−0.45	12	−1.014	−0.37
13	11.350	0.07	12	−0.756	−0.43	17	−0.58	20	−1.209	−1.62
14	10.883	−0.55	4	−0.953	−0.28	3	−1.78	20	−1.399	−2.22
15	10.450	−1.55	10	−1.153	−0.05	3	−1.77	13	−1.584	−0.22
16	10.000	−1.70	4	−1.352	−1.28	1	−1.30	4	−1.759	−1.75
17	9.550	−0.43	1	−1.548	−1.64	2	−2.17	7	−1.923	−1.92
18	9.150	−1.99	15	−1.738	−1.34	5	−1.86	8	−2.073	−2.92
19	8.767	−0.40	5	−1.919	−2.42	3			−2.206	−2.44
20	8.400			−2.088			−1.84	4	−2.322	
21	8.067			−2.243					−2.418	
22	7.817	−2.84	3	−2.382					−2.492	
23	7.617			−2.503					−2.545	
24	7.467			−2.604	−5.75	1	−3.38	1	−2.574	−4.97
25	7.417			−2.683	−3.48	1	−2.56	2	−2.580	−2.72
26	7.433	−3.22	1	−2.740			−3.70	3	−2.562	
27	7.533	−2.93	8	−2.773	−3.17	1	−3.18	1	−2.521	−2.72
28	7.733	−3.51	3	−2.782			−2.33	4	−2.457	
29	7.950	−1.68	5	−2.767			−2.45	2	−2.371	
30	8.267	−4.55	1	−2.728			−2.86	4	−2.265	
31	8.600	−2.08	4	−2.666	0.32	2*	−1.67	2	−2.140	−3.62
32	8.697	−2.68	1	−2.581			−1.79	3	−1.998	
33	9.367			−2.475					−1.841	
34	9.783			−2.349	0.02	1			−1.671	−4.90
35	10.217			−2.206					−1.491	
36	10.667			−2.047			−0.75	1	−3.303	
37	11.100			−1.875			−0.78	1	−1.110	
38	11.550			−1.691			−0.20	1	−0.915	
39	12.000			−1.500			−0.73	1	−0.721	
40	12.467			−1.303			0.12	1	−0.530	
41	12.917			−1.103					−0.346	
42	13.367			−0.904			0.14	2	−0.170	
43	13.850	0.040	2	−0.708			−0.18	6	−0.006	
44	14.217			−0.518			−0.05	4	0.143	
45	14.633			−0.338	0.92	1	0.17	7	0.277	−0.13
46	15.000	0.020	1	−0.168			0.35	1	0.393	
47	15.350			−0.013			0.30	9	0.488	
48	15.650			0.126			0.41	5	0.563	
49	15.867			0.247			0.47	5	0.615	
50	16.033			0.348			0.44	15	0.644	
51	16.117			0.427			0.44	15	0.650	
52	16.117	0.77	1	0.483	0.94	7	0.38	43	0.632	0.21
			152			89		484		

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Table 2. Statistics of the harmonic function (a) and tests of statistical significance (b).

(a) Differentials	A(Amplitude) hours	C hours	P Peak-week
Entries	1.65	−1.1281	1.875 (Jan.)
Exits	1.62	−0.9647	−1.255 (Dec.)
(b) Amplitude, A	F-statistic	Degrees/freedom	p-value
Entry differentials	45.77	2 & 27	<.001
Exit differentials	340.49	2 & 41	<.001
Seasonal Displacement Difference of Peaks, P (am) – P (pm)		Approximate z-statistic	p-value
3.13 (weeks)		4.0	<.001

Bluebell, on the day of her parturition when she occupied her form for only six hours.

In mid-December, when night length in the study area exceeded 16 h, the activity period, all of it within those hours, occupied about 14.5 h (Tab. 1; Fig. 2). In mid-June when night length reduced to a minimum of 7.4 h, the activity period occupied about 13.5 h, six of them in daylight (Tab. 1). Is there, during the period of exclusively nocturnal activity, any relationship between night length and the length of the activity period? That question is addressed in figure 3 which is constructed exclusively from TD data, since these provide an accurate measurement of the activity period of the hare. From a peak of nearly 15 h in week 1, the activity period declined to a minimum of just over 12 h in week 12, the third full week in March, mirroring the decline in night duration. That decline was reversed in week 13 when the activity period increased to 13.4 h and exceeded night duration by two hours. By week 18 it was exceeding night duration by > 4 h. The results from this figure, supported by data in table 1, demonstrate a close correlation between respectively the lengths of the night hours and of the activity period between the start of the year and the latter part of March.

Discussion

The results of this study suggest that the brown hare is essentially a nocturnal animal. Given sufficient hours of darkness, all activity takes place within them. During the few weeks when there was a marked excess of the dark hours over the activity hours, hares consistently emerged from their forms and commenced activity within 30 mins after sunset, and the excess was reflected in the time they entered their forms and ceased activity, which was as early as one and a half hours before sunrise. However, it appears that when the night hours are insufficient, the activity period overlaps into daylight at either end of the day.

This annual activity pattern conforms closely to that appearing in the observational reports of hare activity on their foraging grounds by MATUSZWESKI (1981) and HOMOLKA (1986) and also the results of radiotracking analysis of individual activity by PEPIN and CARGNELUTTI (1994). Limited evidence suggested, however, that certain individuals, such as pregnant and nursing does and alpha bucks, could be active for periods of up to 16 h or more. Such individual variation is also reported by PEPIN and CARGNELUTTI (1994).

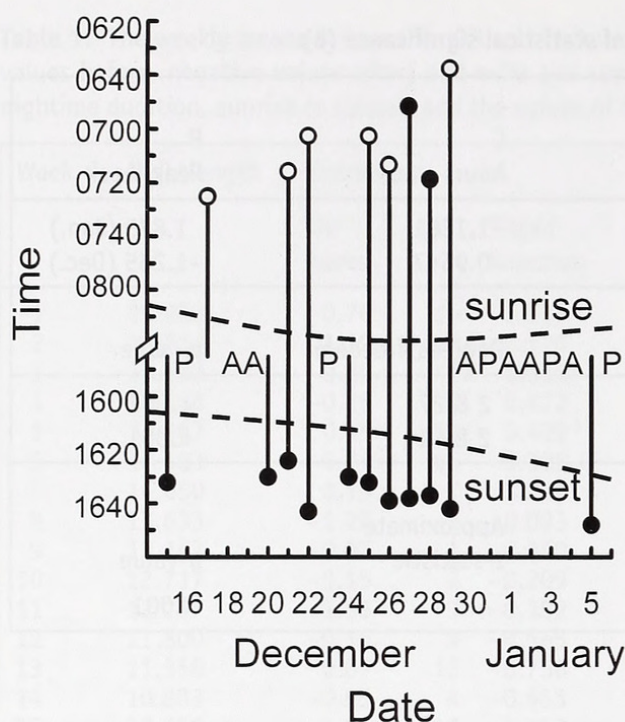The daily activity period follows a seasonal cycle, getting shorter as the hours of day-

Fig. 2. Observed occupation (vertical lines) of one form by the same hare between 15 December 1985 and 6 January 1986. Symbols indicate observed entry or exit (•), earliest sighting of hare already in form (○), hare present in form on the day but entry and exit not observed (P) and hare absent that day (A).
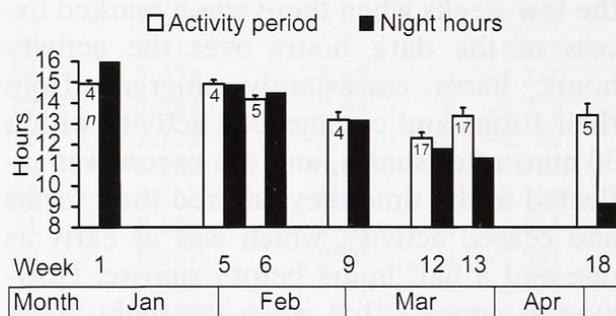

Fig. 3. The mean daily activity period (i. e. length of time out of forms (+SE) based on TD observations) compared with the average night length, sunset to sunrise, during the first 18 weeks of the year. Data only presented for weeks with four or more TD observations (sample size in histogram).

light increase. This produces the surprising outcome that it is substantially longer before the breeding season commences in late December (Tapper 1991) than it is in the peak reproductive months of February to June. Why should that be? Why does it cycle at all? The answer appears to lie in not just a nocturnal preference but an aversion to daylight activity on the part of the brown

hare. Preference is shown by choice, aversion by withdrawal. Assuming an optimal activity period of over 14 h, it would be expected that the transition from a totally nocturnal activity period to a partially diurnal one, as the night hours drop below 14, would not affect the length of the period. That, however, is not the case, the duration of the period in fact declining from nearly 15 h in the first week of January to a minimum of just over 12 h in the third full week of March, mirroring the duration of the night hours. Then, towards the end of March the activity period begins to increase and takes in some of the daylight hours. Why does the duration of the activity period not remain constant instead of reducing substantially January to March and then increasing to mid summer? Perhaps hares might need longer hours feeding in winter to meet the higher energetic demand of lower ambient temperature and to allow for the lower calorific value of food. That possibility seems unlikely because there is no sign of any extension of the activity period following the onset at the end of December of the reproductive season with its dependent energetic demands. The pattern of events does seem to indicate, first, that some inhibitory factor is preventing easy transition from a totally nocturnal to a partially diurnal regime and, secondly, that there is a point, at roughly 12 h of duration, beyond which the activity period cannot easily be contracted. This suggests that the inhibitory factor is daylight itself: hares are shy of daylight activity. Another manifestation of the inhibitory factor is in the difference between the harmonic curves for the times of form entry and departure. In spring, the departure curve crosses the sunset line into daylight two weeks before the entry curve crosses the sunrise line. Daylight activity extending before sunset precedes daylight activity lasting after sunrise. In the evening, after spending the day in its form, a hungry hare will be less shy of daylight activity than a well fed one returning to its form in the morning. The results from this study show the difference to apply as well before as after commencement of the

breeding season and thus cannot be entirely connected to reproductive and agonistic interactions which in both nocturnal and diurnal mammals and birds often peak at activity onset (for review see DAAN and ASCHOFF 1982). Although hares, once they are regularly active diurnally, rapidly extend the duration of daylight activity, none the less the inhibitory factor appears to be still operating to the extent that, in this study area, the duration of activity remains 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.

Of related species, studies using automatic activity recording of mountain hares (*Lepus timidus*) in Sweden by CEDERLUND and LEMNELL (1980) and LEMNELL and LINDLOF (1981) showed a close relationship between sunset and onset of activity and sunrise and cessation of activity in winter. Daylight activity gradually increased up to 50% in summer when the nights were very short. The study of MECH et al. (1966) on five radio-collared snowshoe hares (*Lepus americanus*) in Minnesota, USA, also showed that seasonal changes from January to May in both onset and cessation of activity followed the trend of changing sunrise-sunset times, but with the difference that

contraction of the activity period continued into May when it amounted to less than nine hours. I propose that the proximate cause of cyclicity in the activity period of brown hares is an aversion to daylight activity. It seems that this may be shared by a number of other leporid species.

The emergence of the brown hare from darkness on to the daylight arena in March, as demonstrated in this study, adds further clarification to the explanation of the "mad March hare" of literature (CARROL 1865) given by HOLLEY and GREENWOOD (1984).

Acknowledgements

Zusammenfassung

Die tägliche Aktivitätsperiode des Europäischen Feldhasen (*Lepus europaeus*)

Um die Veränderung der Länge der täglichen Aktivitätsperiode im Laufe eines Jahres für Feldhasen zu bestimmen, wurde die Nutzung der Sassen auf einem 65 ha großen Gebiet in Südwestengland aufgezeichnet. Dabei wurde das Aufsuchen (n = 241) und das Verlassen der Sasse (n = 573) protokolliert. Im Dezember (Nachtlänge: 16 h) waren die Hasen ausschließlich nachtaktiv. Die Intervalle zwischen dem Aufsuchen einer Sasse und dem Sonnenaufgang waren länger und inkonsistenter als jene zwischen dem Verlassen der Sasse und dem Sonnenuntergang. Im Juni (Nachtlänge: 7,4 h) reichte die Aktivitätsperiode für insgesamt 6 h in den Tag hinein: Sie endete erst nach Sonnenaufgang und begann bereits vor Sonnenuntergang. Die Länge der Aktivitätsperiode verkürzte sich entsprechend der Nachtlänge von 14,5 h im Dezember auf 12 h in der dritten Märzwoche. Darauffolgend stieg die Aktivitätslänge auf 13,5 h im Spätsommer, um im Herbst wiederum zu sinken. Diese Ergebnisse weisen daraufhin, dass eine proximate Ursache für den circannuellen Rhythmus bei Feldhasen eine Vermeidung von Aktivität bei Tageslicht ist.

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