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Ranging behaviour and time budgets of male wood mice *Apodemus sylvaticus* in different habitats and seasons

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Abstract Radiotelemetry was used to measure the range areas, activity patterns and time budgets of 21 adult male wood mice (*Apodemus sylvaticus*) between May 1991 and August 1992. The study investigated variation in range, total distance travelled, speed of movement and time budgets between wood mice in the nonbreeding and breeding seasons in a deciduous woodland (n = 8 and 6 respectively). We also examined habitat differences by estimating these same parameters for wood mice inhabiting maritime sand-dunes in the breeding season (n = 7). Insufficient males of an appropriate mass for radiotracking were captured to study the sand-dune mice in the nonbreeding season. Significant variation was found across both season and site. In the breeding season, in woodland, range areas were 5 times larger than during the nonbreeding season. Wood mice on the sand-dunes exploited ranges 28 times greater than their woodland counterparts. The pattern of variation in range area was parallelled by significant differences in total distances and average speeds travelled per night. Diurnal activity, *c*. 60 min day^{-1}, was frequently recorded, at both sites, but only, in the breeding season, which was attributed to the need to forage in order to maintain energy balance. The comparatively lower availability of food on the sand-dunes was considered the main factor explaining the greater range area, total distance moved, speed travelled and level of activity of animals at this site.

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Introduction

Movement and activity patterns of free-living wood mice have been the focus of numerous studies. These have involved a wide range of techniques, including the use of radio-isotopes (Karulin et al. 1976; Nikitina et al. 1977), tracking boards (Brown 1969), passage-counters (Halle 1988), direct observations at baited sites (Greenwood 1978) in conjunction with the use of red light (Garson 1975) and video-equipment (Lambin 1988), regular trap inspections (Kikkawa 1964; Crawley 1969; Canova et al. 1994) and chemiluminescent collars for visual observation (Benhamou 1990). Over the last decade the miniaturization of radio-transmitters has led to the extensive use of radio-telemetry (Wolton 1983; Tew 1992; Wilson et al. 1992; Rogers and Gorman in press). The majority of these studies have considered either activity patterns or aspects of the home range i.e. the area over which an animal normally moves (Burt 1943), particularly its size, shape, the spatial/temporal utilization of the area, and its spatial relationship to that of other individuals in the population.

An animal's home range must be large enough to provide the key resources for its survival, amongst the most important of which is food. Many factors may, therefore, be expected to influence the area required by individuals of a species, for example, site productivity, diet, body mass, sex, reproductive status and season. Indeed, intra-specific variation in home range area may be extensive, both temporally (Bubela et al. 1991) and spatially, within (Mares and Lacher 1987) and between (Fridell and Litvaitis 1991; Gompper and Gittleman 1991) populations.

Home range, however, is a concept and not a finite measurement. To understand the ecology and behaviour of an animal, it is consequently limiting to use range area alone but rather to include assessment of movement and activity patterns. The allocation and availability of time and energy to various physiological processes and daily activities e.g. foraging, mating and social interaction, is potentially important to an animal's survival and reproductive success (Masman et al. 1988; Ricklefs 1991; Boggs 1992). Wood mice have little reserve energy i.e. adipose tissue (Grodziński 1985), and consequently it may be important for them to maintain energy balance, i.e. for energy expenditure to equal energy intake, on a daily basis. Only after energy deficits have been replenished may time and energy be allocated to other demands, thus the time devoted to foraging is critical. The net energy intake is influenced by the time available for foraging, food availability and metabolic costs, which may vary with season, sex and habitat. For example, in winter colder ambient temperatures may increase metabolic demands.

At high latitudes midsummer nights are very short, and it is during these shorter summer nights that wood mice typically reach peak breeding intensity (Saint Giron 1967; Corbet and Harris 1991). Potentially, these short nights may act as an important constraint restricting the nocturnal activities of breeding male wood mice. In habitats where food availability is low we might expect, all else being equal, that a longer time will be required for foraging. Furthermore reproductively active females establish territories which are usually larger in habitats of lower productivity (Corbet and Harris 1991). Thus, a greater time may also be required in the search for females on less productive sites. These effects may result in interesting site differences in the activity patterns of male animals.

In this study we used radiotelemetry to track and monitor the activity of adult male wood mice from two populations living in different habitats, at 57°N where midsummer nights are as short as 3.5 h. One population lived in deciduous woodland where food availability was markedly greater than on the maritime sand-dunes inhabited by the other population. Range areas, distances and speeds travelled were estimated, and time budgets were constructed. Our main aim was to investigate what factors influenced the activity of male wood mice. In particular we were interested in examining the effects of the short nights associated with the breeding season by comparing measurements between seasons i.e. breeding (summer) versus non-breeding (winter). Also, the effect of food availability was assessed by comparing the activity of wood mice across the two habitats (woodland and sand-dune).

Materials and methods

Male wood mice (*Apodemus sylvaticus*) living in deciduous woodland (National Grid Reference: NK090340) and maritime sand-dunes (NK012265), approximately 10 km apart, in north-east Scotland were radio-tracked between May 1991 and August 1992.

Radio-tracking

Equipment

Radio-collars consisted of a SS-1 transmitter (Biotrack UK Ltd., Wareham, Dorset, UK). Ideally the mass of a radio-collar should not exceed 10% of a small mammal's body mass (Wolton and Trowbridge 1985). For 15 of the 21 mice tracked, the mean mass of the collars was 1.90 g (SE = 0.045, range: 1.80–2.23 g), representing 10% (SE = 0.411) of body mass. Later, a shorter-life battery reduced collar mass to 1.65 g (SE = 0.046, range = 1.48–1.80 g), 7.8% (SE = 0.621) of the body mass. The transmitters operated at frequencies between 173.206 and 173.300 MHz, and were detected using a hand-held three-element Yagi aerial (Biotrack) and a RX-81 receiver (Televilt). The distance at which a signal could be detected was variable, depending on the habitat characteristics. The topography of the sand-dunes was such that by standing on a dune ridge it was possible to detect transmitters at distances exceeding 200 m. In the woodland, signals were often distorted by trees and undergrowth which limited the range of detection to less than 80 m.

A LA12 receiver (AVM Instrument Co., Livermore, Calif., USA), linked to a strip-chart recorder (Grant Instruments Ltd., Cambridge, UK), was used to monitor the presence or absence of mice from their nests. A dipole non-directional antenna was positioned as close as possible to the nest under study (< 1 m) resulting in maximum signal strength. Care was taken not to obstruct the entrance to the nest. The receiver and strip-recorder were housed in a portable, weatherproof wooden box, this was positioned approximately 5 m from the nest to reduce disturbance.

Tracking procedure

Wood mice caught in Longworth traps, were taken to Culterty Field Station, Newburgh (distances: woodland *c.* 8 km and sand-dune *c.* 2 km) and a radio-collar attached. To allow the mouse time to become accustomed to the collar before measurements began, it was placed overnight in a holding cage measuring 50 × 20 × 15 cm, supplied with nesting material, food and water ad libitum. Next morning the mouse was returned to the point of capture and the time of its release noted.

All individuals were radio-tracked over a minimum of 2 complete nights (maximum = 5). Tracking commenced at dusk, when the wood mouse normally emerged from the nest and ended when it finally settled in a nest around dawn. For most animals radio-fixes were taken at 10-min intervals. In the woodland, it was sometimes possible to track a second individual at the same time, because the ranges were smaller. However, for logistic reasons fixes for this second animal were taken every 30 min. The 10-min interval between fixes was chosen to maximise the information for estimating range area and the construction of time budgets. Errors for parameters calculated using the distances between consecutive fixes will be reduced as the interval is shortened.

By following the radio signal's increasing strength the wood mouse could be located to an accuracy of 2–3 m when the animal was underground or hidden by vegetation. If the animal was in the open, on a bright night or with the use of a head-torch, the position could be pin-pointed exactly (≤1 m). There was no evidence that the use of torchlight adversely affected the behaviour of mice, they remained relatively undisturbed. On the brief exposure to light mice did not flee, although, on occasion activities were momentarily halted.

The co-ordinates of the animal's position, to the nearest meter, were determined with reference to established trapping grids. If the animal ranged outside the grid, after it had left its position was marked with a stick, and the location mapped the following day. At the end of the night's activity when the mouse's nest position was known, the nest monitoring equipment was set up and recording commenced. Ambient temperature was recorded using a temperature data-logger (SQ8-4U, Grants Instruments Ltd.).

Analysis

A total of 21 wood mice were radio-tracked, and were grouped according to site and season, giving three groups of animals: wood mice during the breeding season (March through early October) on the sand-dunes and in the woodland, and mice during the nonbreeding season (late October through February) in the woodland. In the nonbreeding season, the low numbers of animals trapped on the sand-dunes (Corp 1994) together with their light body mass, which precluded the use of radio-collars (see above), meant this group of wood mice was not represented in the study.

Daily time budgets

In constructing time budgets, only those days where a full 24 h of data had been successfully collected were used, i.e. both radio-tracking and nest monitoring data were obtained. Daily traces from the nest monitor were divided into 10-min blocks, to correspond to the inter-fix interval, the number of blocks when the animal was active i.e. out of the nest, and at rest, i.e. in the nest, were then tallied. Activity was assigned to either night or day, defined by the times of Civil Twilight i.e. when the sun is less than 6° below the horizon (Brown 1985). Thus the time budget consisted of four components: Night activity ($t_{\mathrm{N.active}}$), night rest ($t_{\mathrm{N.rest}}$), day activity ($t_{\mathrm{D.active}}$) and day rest ($t_{\mathrm{D.rest}}$).

Principal activity period

The time between emergence from the nest, around dusk, until the animal finally returning, about dawn, was defined as the "principal activity period". This may comprise one or more "active sessions" i.e. a period of activity between two rest phases. Measurements of movement were calculated using fixes from "nights" when the whole activity period had been successfully monitored. This allowed the inclusion of data that had to be omitted from the time budget analysis, either due to equipment failures (3 of 54 nest monitored days), or in one instance because the animal moved from the monitored nest during the day and did not return to it. Total distance travelled during the activity period was calculated by summing the straight-line distances between consecutive fixes, although this value is likely to be an underestimate as animals rarely move in a straight line between fixes. The apparent speed travelled was calculated by dividing the average distance by time interval between fixes, omitting consecutive fixes when the animal had returned to a nest or a rest site. For the purpose of this study a rest site refers to a location where the animal spent at least 30 min, below ground and stationary. Fixes from both complete and incomplete "nights" were used to determine the range of the individual. Range areas were determined by the minimum convex polygon (MCP) method (Mohr 1947), calculated using the computer program Home Range (Department of Fish and Wildlife Resources, Idaho), and by the restricted convex polygon (RCP) method (Wolton 1985), calculated using Geographic Information System (GIS) computer software (ArcInfo, Environmental Systems Research Institute, Calif., USA).

Table 1 Seasonal and habitat variation in average range area (m^2) of wood mice (*MCP* minimum convex polygon, *RCP* restricted convex polygon, SE standard error, *n* number of mice)

		MCP	RCP
Breeding season:			
Sand-dune	Median	50396	30699
	Mean ± SE	55822 ± 10776	33854 ± 7347
	n	7	
Woodland	Median	2686	1111
	Mean ± SE	3457 ± 862	2002 ± 864
	n	6	
Nonbreeding season:			
Woodland	Median	865	211
	Mean ± SE	974 ± 116	379 ± 92.1
	n	8	

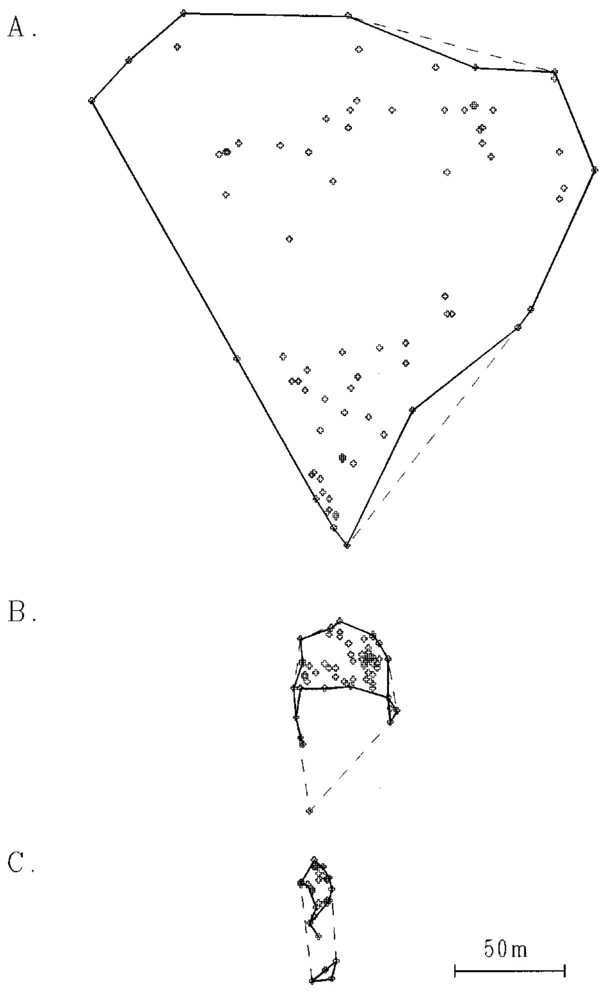


Fig. 1 Representative home ranges, minimum convex polygon (*dashed line*) and restricted convex polygon (*solid line*), of male wood mice during the breeding season **A** on the sand-dunes and **B** in woodland, and **C** during the nonbreeding season in the woodland. *Diamonds* represent radio-fixes

Results

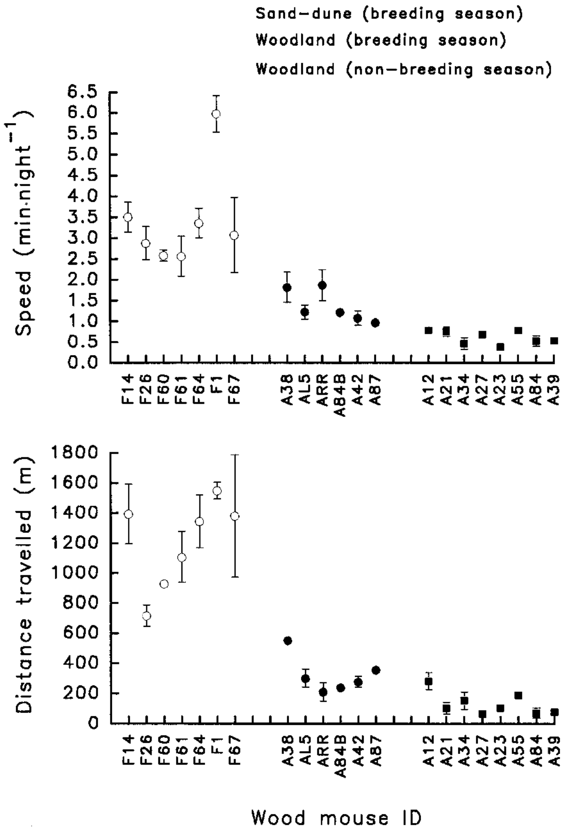
Home range area

The home range areas of mice living in the two habitats are shown in Table 1 and Fig. 1. In both habitats, home ranges estimated using minimum convex polygons were significantly larger than those areas from restricted convex polygons (Wilcoxon paired-sample test $T_{21} = 0.0$, $P < 0.001$). Minimum convex polygons are well known to over-estimate range areas by inclusion of large areas never visited by the individual (Harris et al. 1990), but are included here for comparison of ranges from other studies. The average range areas for the three groups of wood mice i.e. both sand-dune and woodland mice during the breeding season, but only woodland mice in the nonbreeding season, were significantly different between the three groups (Kruskal-Wallis, MCP: $H_2 = 17.73$, $P < 0.001$ and RCP: $H_2 = 16.70$, $P < 0.001$). To find the source of this effect, pairwise comparisons were made using Mann-Whitney's *U*-test, which showed significant effects due to both season (MCP: $U_{6,8} = 48$, $P = 0.0024$ and RCP: $U_{6,8} = 45$, $P = 0.0081$) and site (MCP: $U_{6,7} = 45$, $P = 0.0034$ and RCP: $U_{6,7} = 42$, $P = 0.0034$).

Total distance and speed travelled

Individual variation in total distance travelled and the speed of movement were investigated by analysis of variance (ANOVA) with animal identity as a factor (Fig. 2). On the sand-dunes, during the breeding season, there was significant inter-individual variation in the speed (ANOVA, $F_{6,9} = 5.45$, $P = 0.012$) but not in distance travelled. The effect of speed however was strongly dependent on the results for a single individual (Fig. 2). In the woodland there was a significant difference between individuals in distance travelled (ANOVA, $F_{5,10} = 2.41$, $P = 0.001$) but not in the speed moved. However in the nonbreeding season woodland mice showed no significant variation for either parameter.

Fig. 2 The speed (*top*) and distance (*bottom*) travelled by individual male wood mice, determined during the principal activity period. Values represent means ± SE. *Alpha numeric codes* indicate individuals. Group means were significantly different from each other for both speed and distance travelled



The data on mean total distance and speed are summarized in Table 2. These parameters were compared for woodland and sand-dune wood mice, using ANOVA with group as a factor, after data had been

Table 2 Speed (m min^{-1}) and total distance travelled per night (d_{total} in m night^{-1}) of male wood mice during the principal activity period. Values are means ± SE, *n* number of animals, numbers in parentheses are total number of nights

	n	Speed	d_{total}
Breeding season:			
Sand-dune	7 (16)	3.43 ± 0.443	1201 ± 112.5
Woodland	6 (16)	1.36 ± 0.157	321 ± 50.4
Nonbreeding season:			
Woodland	8 (19)	0.61 ± 0.056	130 ± 26.1

Fig. 3 Daily activity patterns for male wood mice, in the breeding season **A** on sand-dunes and **B** in woodland, and **C** during the nonbreeding season in woodland, exemplified by individuals F14, A84b and A55 respectively. Dates refer to the day the 24-h period commenced

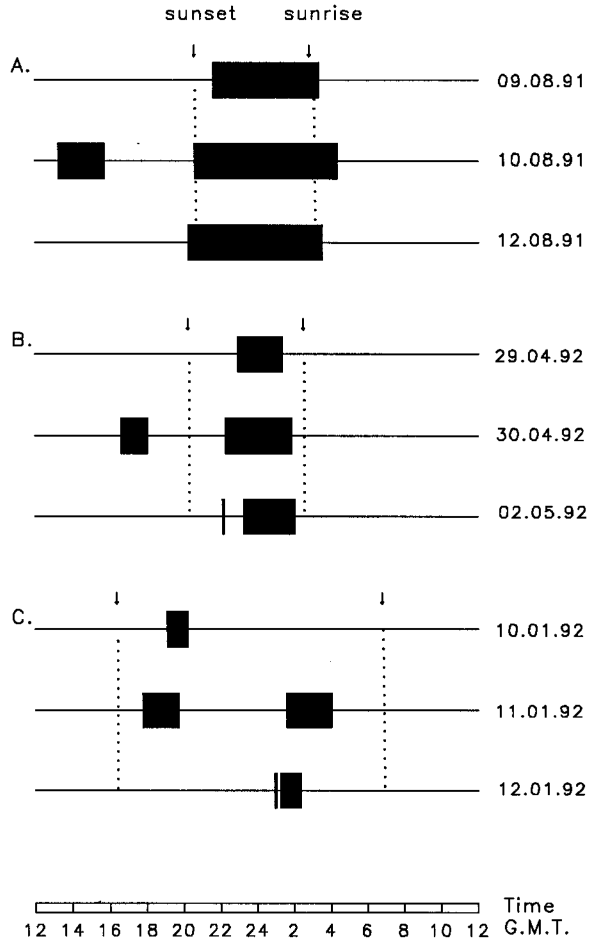


Table 3 Daily time budget (min day^{-1}) for male wood mice at the two sites. (Abbreviations: diurnal activity ($t_{D.active}$) and rest ($t_{D.rest}$); nocturnal activity ($t_{N.active}$) and rest ($t_{N.rest}$), and total time active ($t_{T.active}$); *n* number of animals.) Values are means ± SE

	$t_{D.active}$	$t_{D.rest}$	$t_{N.active}$	$t_{N.rest}$	$t_{T.active}$	*n*
Breeding season:						
Sand-dune	66 ± 21.0	963 ± 58.6	338 ± 28.9	74 ± 56.1	403 ± 39.0	6
	↕ns^a		↕*		↕*	
Woodland	56 ± 34.8	940 ± 39.2	217 ± 27.7	224 ± 55.6	278 ± 27.2	6
	↕*^{a}		↕ns		↕ns	
Nonbreeding season:						
Woodland	0 ± 0.4	616 ± 32.5	196 ± 24.9	628 ± 47.4	196 ± 24.9	8

Tukey's multiple comparison test, ns non significant, *$P < 0.05$
^{a}Mann-Whitney *U*-test, ns non significant, *$P < 0.05$

normalized by log-transformation. There were significant differences between groups for both speed (ANOVA, $F_{2,18}$ = 71.49, $P < 0.001$) and total distance travelled (ANOVA, $F_{2,18}$ = 62.42, $P < 0.001$). In the breeding season, wood mice on the sand-dunes travelled further and faster than did mice in the woodland (Tukey, $P < 0.001$, both parameters), and in the breeding season all mice travelled further and faster than they did in the nonbreeding season (Tukey, $P < 0.001$, both parameters).

Table 4 Onset and end of activity relative to dusk and dawn (mins), negative values refer to before dusk and dawn. Values are means ± SE, *n* sample size

	Onset	End	*n*
Breeding season			
Sand-dune	−1 ± 21.0^a	17 ± 12.0	6
	↕ns	↕ns	
Woodland	38 ± 40.3	−23 ± 26.9	6
	↕*	↕**	
Nonbreeding season			
Woodland	146 ± 21.6	−255 ± 54.2	8

Tukey's comparison, ns non significant, *$P < 0.05$, **$P < 0.005$
^{a}$n = 5$

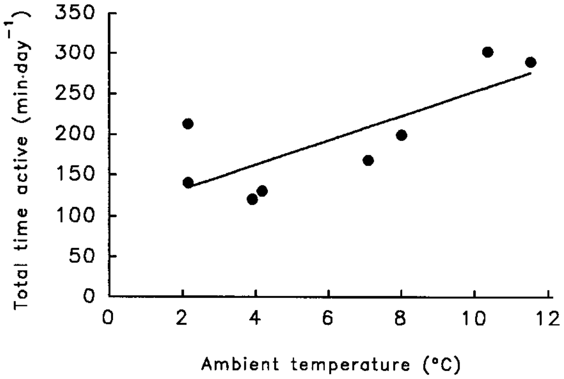


Fig. 4 The relationship between time spent active at night ($t_{N.active}$) and ambient temperature (T_a), for male wood mice in the woodland during the nonbreeding season. $t_{N.active} = 102 + 1.52 \cdot T_a$. (model I linear regression, $r^2 = 0.545$, $F_{1,6} = 9.40$, $P = 0.022$)

Daily time budget

Within the three groups of wood mice there was no significant inter-individual variation in total time active (ANOVA, woodland: breeding season $F_{5,9}$ = 2.47, P = 0.113 and nonbreeding season $F_{7,17}$ = 2.09, P = 0.101, sand-dune: breeding season $F_{5,8}$ = 2.76, P = 0.97). The daily time budgets for each group of animals are summarized in Table 3. There were significant differences in the amount of time active at night (ANOVA, $F_{2,17}$ = 7.77, P = 0.004) and in total, i.e. over 24 h (ANOVA, $F_{2,17}$ = 12.25, P = 0.001), between the three groups. In each case, Tukey's multiple comparison showed this was due to differences between sites ($P < 0.05$) and not between seasons. During the breeding season, mice on the sand-dunes spent more time active at night (56%) and in total (45%) than did mice in the woodland. There was a significant effect of group on diurnal activity (Kruskal-Wallis, H_2 = 8.39, P = 0.015) in that pairwise comparisons made using Mann-Whitney *U*-tests revealed that wood mice were active for significantly longer (*c.* 60 min) in the breeding, as compared to the nonbreeding season. However, no site difference was found during the breeding season (Table 3). In general diurnal activity was a result of the principal activity period beginning before dusk and ending after dawn, although, there were cases where individuals were absent from their nest during the middle of the day (Fig. 3).

Onset, duration and end of activity

The time of emergence relative to dusk and the end of activity relative to dawn (Table 4), were significantly different between the three groups (ANOVA, dusk: $F_{2,16}$ = 7.40, P = 0.005 and dawn: $F_{2,17}$ = 13.78, $P < 0.001$). This group effect was due to a significant difference between seasons in the woodland (Tukey, emergence: $P < 0.005$ and end: $P < 0.05$) and not inter-site variation. Further, in the breeding season these times did not differ significantly from dawn or dusk (paired *t*-tests, $P > 0.05$), while in the nonbreeding season activity began significantly after dusk (paired *t*-test, t_8 = 6.76, P = 0002) and ended significantly before dawn (paired *t*-test, t_8 = 4.70, P = 0.0024).

The number of active sessions did not differ significantly between the three groups (Kruskal-Wallis,

$P > 0.05$). Insufficient data on the interval between active sessions (sand-dunes: $n = 3$) precluded the comparison of all three groups for this variable.

There was no evidence that length of night affected the time an animal spent active during any part of the diel cycle for any group of wood mice (least square regression, $P > 0.150$ all cases). Ambient temperature, however, influenced the time active at night during the nonbreeding season (least square regression, $F_{1,6} = 9.40$, $P = 0.022$; Fig. 4), but this was not so in the breeding season at either site.

Discussion

Home range area

Range areas estimated in this study did not necessarily delimit the home range as defined by an asymptotic plot of cumulative area versus number of fixes (Morris 1988; Harris et al. 1990), although in many cases (primarily in the breeding season) asymptotes were reached. Consequently areas calculated here should be considered underestimates of home range. We intended, however, not to describe home range in detail, but rather to emphasize the seasonal and site differences in the movement parameters and time budgets of male wood mice.

Several methods have been devised for home range analysis (critically reviewed in Kenward 1987; Worton 1987; Harris et al. 1990; White and Garrot 1990; Andreassen et al. 1993). The minimum convex polygon (MCP) and restricted convex polygon (RCP) methods, both non-probabilistic, were considered the most appropriate to define the areas used by wood mice in this study. However, areas estimated using these two methods may depend on sample size, i.e. increase indefinitely as a function of the number of fixes. The MCP technique is also sensitive to peripheral fixes, which often results in the inclusion of large areas never used by the animal, especially when excursions are taken out with the area "normally" used. The range area defined by RCP is based on the MCP but sets a maximum length to the distance between peripheral points. This value is calculated from the mean distances between fixes and arithmetic centre of activity (Hayne 1949). The RCP method is, consequently, less sensitive to peripheral movement than MCP, although the maximum length assigned to delimit the area's periphery has no biological basis. The MCP estimate, widely used, provided comparisons with other studies of wood mice (Brown 1969; Cody 1982; Wolton 1985; Attuquayefio et al. 1986). In recent years, the RCP method has been widely accepted as a more realistic estimate of the species' home range (Tew 1992; Wilson et al. 1992; Rogers and Gorman in press).

Mean range areas for breeding male wood mice in woodland were 32% (MCP) and 39% (RCP) of the areas reported previously at a similar woodland site approximately 10 km away (Wolton 1985). In the nonbreeding season this difference was reduced: ranges in this study being 88% than in that of Wolton (1982). On the sand-dunes range areas (MCP) for wood mice exceeded values reported previously at the same site, at 1.68 times (Attuquayefio 1984) and 1.71 times (Akbar 1990) the size. Furthermore these ranges are the largest recorded, to date, for wood mice.

Range areas during the breeding season were approximately 5 times larger than in the nonbreeding season, a pattern consistent with previous studies of wood mice (Randolph 1977; Green 1979; Wolton 1985; Attuquayefio et al. 1986; Rogers and Gorman in press). Since, in the breeding season, females utilize smaller home ranges than do males (Wolton 1985) but daily energy demands are probably greater (e.g. ground squirrels *Spermophilus saturatus*, Kenagy et al. 1989), this seasonal increase may be largely attributed to males expanding their ranges to maximize the probability of encountering oestrus females (Wolton 1985; Tew 1992), rather than to meet the additional energetic costs associated with reproduction.

Inter-site variation in range was extensive. During the breeding season male wood mice on the sand-dunes utilized areas (RCP), on average, some 28 times larger than those of their woodland counterparts. This was associated with a markedly lower population density (Corp 1994) and productivity (Gorman and Akbar 1993) on the sand-dunes. It may be necessary for wood mice to cover a larger range on the sand-dunes in order to accrue sufficient food to meet their energy demands. Food supplementation experiments, conducted at the same sand-dune site, resulted in a localized increase in population density and a reduction in the mean home range area, suggesting an important role of food availability in influencing the spatial organization of wood mice at this site (Akbar and Gorman 1993a,b). Similar responses to the addition of extra food have been reported in other mammals (Boutin 1990), including rodents (Ims 1987; Jones 1990; Taitt 1981). These studies, together with geographic variation in home range within species, with longitude (Gompper and Gittleman 1991) and latitude (Harestad and Bunnell 1979), lend support to a strong negative correlation between range area and habitat productivity.

Activity pattern

Wood mice exploiting larger ranges may be expected to travel further distances each night. Although there was no significant relationship between total distance travelled and range area, the mean distance varied between sites and seasons in parallel with changes in range area. The distance travelled is a function of the time active and speed at which an animal travels. Given the range areas and distances in this study, all else being equal, we might predict that one or both of these parameters would be greater for wood mice on the sand-dunes compared to woodland, and in the breeding season compared to the nonbreeding season.

The seasonal differences in range area and total distance travelled were attributed to wood mice travelling at over twice the speed in the breeding season as compared to the nonbreeding season. Moreover there was no difference in the time allocated to nocturnal activity, although other components of the time budget differed. During the breeding season wood mice frequently made diurnal forays from the nest, lasting approximately 60 min per diel cycle, whereas in the nonbreeding season they were almost exclusively nocturnal. Moreover, the time spent active at night was positively related to ambient temperature during this latter season only. The nonbreeding season was associated with an approximate 10°C drop in ambient temperatures below those of the breeding season (Corp 1994). Therefore, the reduction in activity may be a means of minimizing the energetic costs of thermoregulation and foraging and consequently energy requirement (Stebbins 1984). However, ambient temperature may have been sufficiently high in the breeding season that its importance as a factor affecting activity was negligible, particularly in comparison to the reduction in length of night.

Diurnal activity has been rarely documented in wood mice (laboratory: Miller 1955; free-living: Bäumler 1975; *A. sylvaticus* or *A. flavicollis*: Halle 1988; Wolton 1983). Why should a predominantly nocturnal species exhibit diurnality? In the breeding season nocturnal activity involves both reproduction and foraging. Balancing the time available at night between these activities is probably critical. If too little time is devoted to foraging the animal will be in negative energy balance, if too much, reproductive success will presumably be diminished. Adding to this dilemma are the short summer nights at this latitude, 426 min (SE = 40.5, range = 210–680 min), which further restricted the time frame for nocturnal activities. The advantages of diurnality are presumably limited, the chances of encountering a mate seem unlikely, while susceptibility to predation is potentially increased, particularly on the sand-dunes, by diurnal predatory birds e.g. kestrels *Falco tinnunculus* and short-eared owls *Asio flammeus*. Consequently we suggest that this activity may be necessary for foraging, to compensate for an energy deficit incurred during the night, due to time allocated to reproductive activity. Further, Wolton (1983) reported that two lactating females regularly spent 2–4 h actively foraging in the middle of the day. Lactation is an energetically demanding period for rodents (Innes and Millar 1981; Weiner 1987; Kenagy et al. 1989) and so further supports the idea that diurnal activity may be required to obtain energy in a situation where foraging time at night may be limited and energy demands elevated.

The time budgets of male wood mice in the breeding season showed pronounced variation between habitats. Mice spent 56% more time active at night on the sand-dunes than in the woodland, although levels of diurnal activity were similar (66 min and 56 min respectively). Assuming the frequency of encounters with potential mates is related to the reproductive success of an individual, then, all else being equal, the latter will increase for animals with longer activity periods. Thus it would be advantageous to be active as long as possible at night in the breeding season. However, site differences in the time spent active at night suggest that “all else” is not equal. If males search for females at random the probability of finding a female at any point within her home range will be an inverse function of her range area. Since females have larger ranges on the sand-dunes (Attuquayefio et al. 1986; Gorman and Akbar 1993) than in woodland (Wolton and Flowerdew 1985; Wilson et al. 1992), in addition to having to increase his home range area to encompass the same number of female ranges as a woodland male, the sand-dune male may need to allocate more time to search for a female within her range. However, males may not search for females entirely at random but use, for example, olfactory cues to locate potential mates. Use of these cues may affect the expected inverse relationship between probability of finding a mate and the home range area. Second, as discussed earlier with regard to range area, sand-dune animals have to spend a longer time foraging to attain an equal amount of food, and may in fact need to attain more given the extra distances travelled.

Wood mice in the woodland did not utilize all the available time at night but instead emerged during the day, presumably to forage. This may indicate that foraging was constrained by an additional factor. One possibility is that gut capacity was a constraint, imposing a limit on the amount of food an animal could ingest. Once the stomach has been filled then before foraging can continue the ingesta must be processed. If this was the function of the rest periods between active sessions, then longer rests would be predicted for wood mice in woodland given their larger gut capacity compared to mice on the sand-dunes (Corp 1994). Although there were insufficient data for statistical analysis, the results indicated that time spent between active sessions by wood mice in the woodland (mean = 100.1 min, SE = 11, $n = 7$) were longer compared to on the sand-dunes (mean = 50.3 min, SE = 20.7, $n = 3$). This result agrees with Wolton (1983), who suggested that 1.5–2.0 h represented the time required by wood mice in his study, also in deciduous woodland, to empty their stomachs.

In conclusion, although the total time active by wood mice in the woodland was not significantly different between seasons, presumably in the breeding season this included time allocated to behaviours associated with reproduction and thus by implication a reduction in foraging time compared to the nonbreeding season. The decrease in home range area, distance travelled and speed, in concert with the lower body masses (Corp 1994), and the length of time active being positively related to ambient temperature suggests that total energy expenditure was being minimized over the winter/nonbreeding season. Lower food availability may account for the larger home ranges, distance and speed travelled, and time active at night and in total, of mice on the sand-dunes compared to the woodland.

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References

Akbar Z (1990) Effect of supplementary food on the ecology of wood mice (*Apodemus sylvaticus* L.) living in a sand dune habitat. PhD Thesis, University of Aberdeen

Akbar Z, Gorman ML (1993a) The effect of supplementary feeding upon the demography of a population of woodmice *Apodemus sylvaticus*, living on a system of maritime sand-dunes. J Zool Lond 230: 609–617

Akbar Z, Gorman ML (1993b) The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. J Zool Lond 231: 233–237

Andreassen HP, Ims RA, Stenseth NC, Yoccoz NG (1993) Investigating space use by means of radiotelemetry and other methods: a methodological guide. In: Stenseth NC, Ims RA (eds) The biology of lemmings. Academic Press, London, pp 589–618

Attuquayefio DK (1984) Home range and patterns of activity in a sand dune population of the woodmouse *Apodemus sylvaticus* L. MSc Thesis, University of Aberdeen

Attuquayefio DK, Gorman ML, Wolton RJ (1986) Home range sizes in the wood mouse *Apodemus sylvaticus*: habitat, sex and seasonal differences. J Zool Lond 210: 45–53

Bäumler W (1975) Activity of some small mammals in the field. Acta Theriol 20: 365–377

Benhamou S (1990) An analysis of movements of the wood mouse *Apodemus sylvaticus* in its home range. Behav Process 22: 235–250

Boggs CL (1992) Resource allocation: exploring connections between foraging and life history. Funct Ecol 6: 508–518

Boutin S (1990) Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can J Zool 68: 203–220

Brown LE (1969) Field experiments on the movements of *Apodemus sylvaticus* L. using trapping and tracking techniques. Oecologia 2: 198–222

Brown TN (1985) Brown's nautical almanac. Brown, Son and Ferguson, Glasgow

Bubela TM, Happoid DCD, Broome LS (1991) Home range and activity of the broad-toothed rat, *Mastacomys fuscus*, in subalpine heathland. Wildl Res 18: 39–48

Burt WH (1943) Territoriality and home range concepts as applied to mammals. J Mammal 24: 346–352

Canova L, Maistrello L, Emiliani D (1994) Comparative ecology of the wood mouse *Apodemus sylvaticus* in 2 differing habitats. Z Säugetierk 59: 193–198

Cody CBJ (1982) Studies on behavioural and territorial factors relating to the dynamics of woodland rodent populations. DPhil Thesis, University of Oxford

Corbet GB, Harris S (1991) The handbook of British mammals, 3rd edn. Blackwell, Oxford

Corp N (1994) Ecological energetics of male wood mice *Apodemus sylvaticus* in two contrasting habitats. PhD Thesis, University of Aberdeen

Crawley MC (1969) Movements and home-ranges of *Clethrionomys glareolus* Schreber and *Apodemus sylvaticus* L. in north-east England. Oikos 20: 310–319

Fridell RA, Litvaitis JA (1991) Influence of resource distribution and abundance on home-range characteristics of southern flying squirrels. Can J Zool 69: 2589–2593

Garson PJ (1975) Social interactions of woodmice (*Apodemus sylvaticus*) studied by direct observation in the wild. J Zool Lond 177: 496–500

Gompper ME, Gittleman JL (1991) Home range scaling: intraspecific and comparative trends. Oecologia 87: 343–348

Gorman ML, Akbar Z (1993) A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. J Zool Lond 229: 385–396

Green R (1979) The ecology of wood mice (*Apodemus sylvaticus*) on arable farmland. J Zool Lond 188: 357–377

Greenwood PJ (1978) Timing of activity of the bank vole *Clethrionomys glareolus* and the wood mouse *Apodemus sylvaticus* in a deciduous woodland. Oikos 31: 123–127

Grodziński W (1985) Ecological energetics of bank voles and wood mice. Symp Zool Soc Lond 55: 169–192

Halle S (1988) Locomotory activity pattern of wood mice as measured in the field by automatic recording. Acta Theriol 22: 305–312

Harestad AS, Bunnell FL (1979) Home range and body weight – a reevaluation. Ecology 60: 389–402

Harris S, Cresswell WJ, Forde PG, Trewhella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Rev 20: 97–123

Hayne DW (1949) Calculation of size of home range. J Mammal 30: 1–18

Ims RA (1987) Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. J Anim Ecol 56: 585–596

Innes DGL, Millar JS (1981) Body weight, litter size, and energetics of reproduction in *Clethrionomys gapperi* and *Microtus pennsylvanicus*. Can J Zool 59: 785–789

Jones EN (1990) Effects of forage availability on home range and population density of *Microtus pennsylvanicus*. J Mammal 71: 382–389

Karulin BE, Nikitina NA, Khlyap LA, Litvin VY, Okhotsky YV, Albov SA, Sushkin ND, Pavlovsky YS (1976) Diurnal activity of common field-mice (*Apodemus sylvaticus*) and utilization of territory by them, with reference to observations of animals marked by ^{60}Co (in Russian, English summary) Zool Zh 55: 112–121

Kenagy GJ, Sharbaugh SM, Nagy KA (1989) Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78: 269–282

Kenagy GJ, Stevenson RD, Masman D (1989) Energy requirements for lactation and postnatal growth in captive golden-mantled ground squirrels. Physiol Zool 62: 470–487

Kenward R (1987) Wildlife radio tagging: equipment, field techniques and data analysis. Academic Press, London

Kikkawa J (1964) Movement, activity and distribution of the small rodents *Clethrionomys glareolus* and *Apodemus sylvaticus* in woodland. J Anim Ecol 33: 259–299

Lambin X (1988) Social relations in *Apodemus sylvaticus* as revealed by video-observation in the wild. J Zool Lond 216: 587–593

Mares MA, Lacher JTE (1987) Social spacing in small mammals: patterns of individual variation. Am Zool 27: 293–306

Masman D, Daan S, Beldhuis HJA (1988) Ecological energetics of the kestrel: daily energy expenditure throughout the year based on time-budget, food intake and doubly labeled water methods. Ardea 76: 64–81

Masman D, Daan S, Dijkstra C (1988) Time allocation in the kestrel (*Falco tinnunculus*), and the principle of energy minimization. J Anim Ecol 57: 411–432

Miller RS (1955) Activity rhythms in the wood mouse, *Apodemus sylvaticus* and the bank vole, *Clethrionomys glareolus*. Proc Zool Soc Lond 125: 505–519

Mohr CO (1947) Table of equivalent populations of North American small mammals. Am Midl Nat 37: 223–249

Morris PA (1988) A study of home range and movements in the hedgehog (*Erinaceus europaeus*). J Zool Lond 214: 433–449

Nikitina NA, Karulin BE, Litvin VY, Khlyap LA, Albov SA, Sushkin ND, Okhotsky YV (1977) On the size of daily territory and probable structure of individual ranges in some species of rodents (in Russian, English summary). Zool Zh 56: 1862–1869

Randolph SE (1977) Changing spatial relationships in a population of *Apodemus sylvaticus* with the onset of breeding. J Anim Ecol 46: 653–676

Ricklefs RE (1991) Structures and transformations of life histories. Funct Ecol 5: 174–183

Rogers LM, Gorman ML (in press) The home range size of wood mice *Apodemus sylvaticus* living in set-aside agricultural land and surrounding arable and semi-natural habitats. J Zool Lond

Saint Giron MC (1967) Etude du genre *Apodemus* Kaup, 1829 en France. Mammalia 31: 55–100

Stebbins LL (1984) Overwintering activity of *Peromyscus maniculatus*, *Clethrionomys gapperi*, *C. rutilus*, *Eutamias amoenus*, and *Microtus pennsylvanicus*. In: Merritt JF (ed) Winter ecology of small mammals (Special publication). Carnegie Museum of Natural History, Pittsburgh, pp 301–314

Taitt MJ (1981) The effect of extra food on small rodent populations: I. Deermice (*Peromyscus maniculatus*). J Anim Ecol 50: 111–124

Tew TE (1992) Radio-tracking arable-dwelling woodmice. In: Priede IG, Swift SM (eds) Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, Chichester, pp 561–569

Weiner J (1987) Limits to energy budget and tactics in energy investments during reproduction in the Djungarian hamster (*Phodopus sungorus sungorus* Pallas 1770). Symp Zool Soc Lond 57: 167–187

White GC, Garrott RA (1990) Analysis of wildlife radio-tracking data. Academic Press, San Diego

Wilson WL, Montgomery WI, Elwood RW (1992) Range use in female woodmice (*Apodemus sylvaticus*) in deciduous woodland. In: Priede IG, Swift SM (eds) Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, Chichester, pp 549–560

Wolton RJ (1982) The social ecology of the wood mouse (*Apodemus sylvaticus*). PhD, Aberdeen

Wolton RJ (1983) The activity of free-ranging wood mice *Apodemus sylvaticus*. J Anim Ecol 52: 781–794

Wolton RJ (1985) The ranging and nesting behaviour of wood mice, *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radio-tracking. J Zool Lond 206: 203–222

Wolton RJ, Flowerdew JR (1985) Spatial distribution and movements of wood mice, yellow-necked mice and bank voles. Symp Zool Soc Lond 55: 249–275

Wolton RJ, Trowbridge BJ (1985) The effects of radio-collars on wood mice, *Apodemus sylvaticus*. J Zool Lond 206: 222–224

Worton BJ (1987) A review of models of home range for animal movement. Ecol Model 38: 277–298