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Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area

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Hedgehogs *Erinaceus europaeus* Linnaeus, 1758 were radio-tagged and monitored during the summer of 2001 in a Danish rural area with the objective of quantifying home ranges, nightly distances travelled, habitat use, activity patterns, day-nesting habits, and body-weight changes of the five males and five females being recorded. Males had larger home-range sizes and travelled longer nightly distances than females. The two most common habitat types within the home ranges of the hedgehogs were deciduous forest and arable land, whereas the two most frequently used habitat types were deciduous forest and grassland. No differences between the sexes were found in the proportions of different habitat types within the home ranges or in habitat use. Non-random habitat use was found; forested areas and edge habitats seemed preferred to open areas. The most frequently used day-nesting habitat was deciduous forest. Foraging was by far the most time-consuming nightly activity for both sexes. Males lost weight during the study period (May–July), whereas females gained weight. A peak in the frequency of sexual behaviour was found from late-June to mid-July. The high level of male ranging activity and the weight loss of males are interpreted as a consequence of the promiscuous mating system of hedgehogs.

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Introduction

European hedgehogs *Europaeus erinaceus* Linnaeus, 1758 are small secretive nocturnal animals that spend the day in well hidden day-nests. Such characteristics complicate monitoring of the behaviour of free-ranging individuals, contributing to poor understanding of certain aspects of their behavioural ecology. For instance, knowledge of the activity patterns of hedgehog is still limited in spite of the wide distribution of hedgehog in Western Europe and New Zealand. The continuously improving radio-telemetry technology has, however, made comprehensive studies of such animals possible, although the cost of the equipment and the time-consuming form of the method usually still limit the number of study animals involved (eg Morris 1988, Huijser 2000).

Studies of the summer activities of hedgehogs with use of radio telemetry have been conducted in habitats as different as a golf course in Britain (Reeve 1982), a village in Sweden (Kristiansson 1984), an urban botanical garden in Germany (Esser 1984), and a coastal maquis in Italy (Boitani and Reggiani 1984). Only a few studies of hedgehogs have been conducted in rural areas (Morris 1988, Zingg 1994, Huijser 2000). The only existing radio tracking study of hedgehogs in Denmark is a study of hibernation in a rural area during winter (Jensen 2005). Thus, our knowledge of the summer activity of free-ranging hedgehogs in rural areas is relatively sparse.

In the European hedgehog, the sexes have different reproductive strategies due to a promiscuous mating system; females allocate resources into pregnancy and nursing of the young, whereas males, which do not participate in the parental care, allocate resources into finding females and competing with one another to achieve multiple matings (Campbell 1973, Kristiansson 1984, Reeve and Morris 1986). Thus, the hedgehog is characterized by sex differences in the summer activities, which are likely to be reflected in a comparative behavioural study of the sexes.

Here I report on an investigation of the summer activities of hedgehogs monitored in a Danish rural area using radio-telemetry techniques. The aim was to investigate home ranges, nightly distances travelled, habitat use and activity pattern, and analyse for differences between the sexes. Included in the analyses were investigations of day-nesting habits and body-weight changes.

Study area

The study was conducted in a Danish rural area 12 km north of Aarhus (56°15'N, 10°15'E) with a mixture of arable land (53.5%), forests (24.7%), and grassland (12.8%; mainly pastures and fallow fields). Premises only account for a smaller part of the study area (5.9%) and the infrastructure consists of minor roads, where traffic is minimal and road kills of hedgehogs are rare (0.06 hedgehogs/km road/yr). The average annual rainfall in the area is 660 mm distributed approximately evenly over the year. The mean weekly temperature ranges from 12°C to 16°C in the summer with minima as low as 4°C and maxima as high as 29°C (DMI 2005).

Material and methods

Data collection

Between May 28 and July 28 2001, 31 hedgehogs were captured in the study area. Attempts to capture hedgehogs in 10 wire cage traps (75 × 20 × 20 cm) were abandoned after two weeks with only two animals caught, whereas searching in forests and open land with a strong torch turned out to be more efficient with 29 hedgehogs captured using this method. The first five females and five males caught were fitted with VHF radio tags (TW-3, Biotrack Ltd., UK; Table 1), and all data collected in the present

Table 1. Radio-tagged hedgehogs (n = 10) recorded during the summer 2001. [a] Data from No. 7 were only partly used. [b] Data from No. 8 was excluded from all analyses, except calculation of sex ratio.

Hedgehog id	Sex	Initial weight (g)	Date of tagging	Nights recorded	No. of records	∑ days tagged
1	M	1214	28 May	18	216	58
2	M	1288	1 June	15	307	49
3	M	858	2 June	12	238	46
4	M	820	4 June	13	192	43
5	F	629	5 June	15	210	43
6	F	638	9 June	12	262	41
7[a]	M	886	14 June	6	140	6
8[b]	F	844	25 June	8	154	23
9	F	893	28 June	19	276	34
10	F	917	2 July	18	292	30

study relate only to these 10 animals, except for the recordings of sex and sexual behaviour which include all hedgehogs encountered. The radio tags were glued to the spines between the shoulders on the back of the hedgehogs. The entire backpack used weighed 10–11 g and was removed at the end of the study. In order to observe the focal animal during continuous tracking sessions from a distance at night, luminous plastic rods (Euro lite, 1–2 g, 4.5 × 39 mm) were attached with tape around two-three spines just above the tail. The light lasted for 10 hours and could easily be spotted from a minimum distance of 20 m in the darkness.

Prior to the tracking session an ethogram consisting of eight identified behavioural categories was composed (Table 2), and eight habitat types were identified in the study area; deciduous forest, coniferous forest, forest edge, hedgerow, grassland (pasture, fallow field, meadow, moor), cropland (wheat, barley, oil-seed rape), premises, and other (road, lake, stream). The forest edge was defined as the 10 m zone on both sides of the outer line of trees. Whenever a day-nest was located it was described at two different levels; in which habitat type it was located and the type of principal nesting materials used for construction (leaves, grasses, or man-made materials).

The tracking period lasted from May 28 – July 30. Approximately every second night in the tracking period (34 nights in total), continuous tracking of a focal animal was conducted throughout the night. The focal animal was selected among the 10 radio-tagged hedgehogs according to a predetermined schedule. The day-nest site of the focal animal was located by use of the VHF signal approximately an hour before sunset in order to obtain the exact duration of the activity period. When the focal animal left the day-nest, time and body weight (± 1 g) were recorded. The focal animal was tracked continuously during the entire night from a maximum distance of 40 m until it returned to a day-nest. During tracking the behaviour and GPS position of the focal animal as well as the habitat type at the location point were obtained using five-minute intervals. In addition, approximately every fourth night (in total 13 nights) during the tracking period was spent on discontinuous tracking, where the position, behaviour, and habitat type of all the radio-tagged hedgehogs were recorded at least three times during the night with body weight measured on the first sighting. Finally, discontinuous day tracking was performed on an irregular basis to determine whether any activity occurred during the day.

Data analysis

All GPS positions were analysed using the Geographic Information System (GIS) software ArcView 3.2 with the extension Animal Movement Program (Hooge and Eichenlaub 1997). Unfortunately, all radio contact to No. 7 was lost after six days of data collection. Thus, data from No. 7 were excluded from the analyses of growth, home range size, and habitat use. No. 8 continuously lost weight during the radio tracking period. It was apparently ill and found dead 23 days after the initial observation. Due to the risk that it might have exhibited abnormal behaviour caused by its illness, data from this hedgehog were excluded from all analyses, except for the calculation of the sex ratio.

The applied home-range estimators were the 100% Minimum Convex Polygon (100% MCP) and the 95% and 50% Kernel method (Kernohan *et al.* 2001). The 95% Kernel excludes 5% of the outermost radio locations, whereby occasionally sallies are separated from the "true home range". The 50% Kernel is the core of the home range, ie the range where the probability of locating the animal is 0.5. To estimate whether a sufficient number of radio locations had been collected to give a realistic estimate of the home-range sizes, 100% MCP-area estimates were plotted against the number of radio locations (Odum and Kuenzler 1955). The overlaps between home ranges were calculated as the percentage the home range of each radio-tagged hedgehog

Table 2. Ethogram dividing the activity of the hedgehog into eight behavioural categories.

Behavioural category	Description
Locomotion	Movement in a relatively straight line with the nose lifted from the ground.
Foraging	Eating/handling food, rooting, digging or moving slowly in a non-straight line with the nose close to ground.
Stationary behaviour	Outside a day-nest, either resting or alert.
Sexual behaviour	Courtship and mating.
Agonistic behaviour	Aggressive and submissive behaviour displayed during fights.
Active behaviour	Unspecified active behaviour; out of sight, but movement is registered due to changes in radio signal strength.
Day-nesting	Resting in a day-nest or the like.
Others	Drinking, grooming, self-anointing, swimming.

formed part of the home ranges of the other radio-tagged hedgehogs of the same sex.

Nightly movements were estimated by calculating the linear distance between the consecutive radio locations recorded with 5-minutes intervals. Because of the varying topography and the non-linear routes between points followed by the hedgehogs, the calculated distances are minimum estimates. Only data from nights, when an animal was followed throughout the entire night, were used.

The proportion of home range area occupied by each habitat type was calculated. In addition, the use of the different habitat types was estimated as the proportion of radio locations within each type of habitat. Compositional analysis was applied to test for non-random habitat selection, ie the proportions of the different habitat types within the 100% MCP home ranges were compared to the proportions of the different habitat types available within the study area (Aebischer *et al.* 1993). Appointing the study area as the available habitat was judged to be reasonable, as the study area was mainly surrounded by natural and human created barriers (eg highway, streams). A similar analysis was conducted to test for differences between the proportions of radio locations within each habitat type with the proportions available within the 100% MCP home ranges. In cases where non-random selection is found, a matrix can be constructed to establish habitat rankings reflecting habitat preference (Aebischer *et al.* 1993).

The proportions of time spent on the various activities were estimated from the number of sample points allocated a particular behavioural category as compared to the total number of sample points. The data on sexual behaviour are also presented using a histogram of the frequency distribution of the observed sexual behaviour over 16-day time periods.

Statistical analyses

When averages are provided below, they are followed by the ± standard deviation. The chi-square test was applied for analysis of deviation from parity of the sex ratio of the captured hedgehogs. The Mann-Whitney *U*-test was applied for comparison of home ranges, nightly distances travelled, habitat use, activity patterns, and body-weight changes between the sexes, as data were found not to follow the normal distribution. For the test of correlation between cessation/ /initiation of activity and sunrise/-set, the Spearman Rank Correlation Coefficient (r_s) was applied. The multivariate analysis of variance (MANOVA) was used for test of non- -random habitat use. Finally, the *t*-distribution was used to test for significance in habitat type preference. Although the MANOVA and the *t*-distribution test are parametric tests and assume multivariate normality of the residuals after model fitting, the use of data failing to meet this assumption has only a slight effect on the result (Zar 1999). They have been tested in the compositional analysis of habitat use, where they were found suitable for evaluating whether habitats are used non-randomly and for testing for statistical significance in the ranking of habitat types irrespective of the distribution of data (Aebischer *et al.* 1993).

Results

Twenty four males and seven females were captured during the field work. The sex ratio was 3.43 and deviated highly significantly from 1:1 (Chi-square test: $\chi^2 = 9.32$, df = 1, $p = 0.002$).

In total, 1993 location points were available for the home-range analysis (Table 1). The 100% MCP area-location point curves revealed that a sufficient number of location points had been collected from four males and four females, ie the home-range estimates each reached an asymptote. The average home-range size (± SD), determined by the 100% MCP method, was 96 (± 24) ha for males and 26 (± 15) ha for females. Using the 95% Kernel method, the average home-range sizes were found to be 74 (± 35) ha for males and 17 (± 7) ha for females. The differences in home-range size were found to be statistically significant (Mann-Whitney *U*-test: $U_{100\%\mathrm{MCP}} = U_{95\%\mathrm{Kernel}} = 26$, $p = 0.03$). The core areas, determined as 50% Kernel estimates, were found to be 12 (± 8) ha for males and 3 (± 0.8) ha for females ($U = 23$, $p = 0.193$). No sex specific spatial separation of the home ranges was found; the mean overlap between the recorded males was found to be 61.1 (± 20.7) %, whereas the mean overlap between the recorded females was 6.8 (± 9.8) %, which was significantly less than for the males ($U = 26$, $p = 0.029$). The average distance travelled by the five males was 2042 (± 860) m/night, whereas the four females travelled an average of 1187 (± 538) m/night ($U = 173$, $p = 0.009$). The longest recorded distance covered in one night was 3211 m for males and 2046 m for females.

In total, 1993 locations were available for the habitat-use analysis (Table 1). Similar proportions of the different habitat types within the home ranges were found for males ($n = 4$) and females ($n = 4$) ($U_{\mathrm{dec.forest}} = 8$, $U_{\mathrm{con.forest}} = 4$, $U_{\mathrm{forest.edge}} = 7$, $U_{\mathrm{hedgerow}} = 8$, $U_{\mathrm{arable.land}} = 5$, $U_{\mathrm{grassland}} = 6$, $U_{\mathrm{premises}} = 3.5$, and $U_{\mathrm{other}} = 8$; $p > 0.05$). Data from both sexes were thus pooled. The two habitat types constituting most of the home ranges were deciduous forest (37.3 ± 28.0%) and arable land (25.6 ± 23.2%), whereas hedgerows (0.6 ± 0.7%) formed the least part of the home ranges (Fig. 1). The proportional use (ie the number of radio locations) of the different habitat types within the home ranges was similar for males and females ($U_{dec.forest}$ = 8, $U_{con.forest}$ = 6, $U_{forest.edge}$ = 5, $U_{hedgerow}$ = 7.5, $U_{arable.land}$ = 6, $U_{grassland}$ = 7, $U_{premises}$ = 3.5, and U_{other} = 4; $p > 0.05$), and data from both sexes were thus pooled. The two most frequently used habitat types were deciduous forest (57.3 ± 33.2%) and grassland (17.2 ± 21.8%), and the least used habitat type was the category "Other" (1.0 ± 1.4%), consisting of roads, streams, and lakes (Fig. 1).

Non-random habitat use within the study area was found (MANOVA: $\Lambda = 0.04, \chi^2 = 29.8$, df = 7, $p < 0.01$), ie the habitat composition in the 100% MCP home ranges differed significantly from that in the study area as a whole. The relative use of the habitat types within the study area was ranked in the following order: forest edge > deciduous forest > hedgerow > conifer forest > other > premises > grassland > arable land, indicating a selection of forested areas and edge habitats at the expense of open areas. However, the rankings were not significantly different (t-distribution: $0.04 > t < 1.23$, df = 7, $p > 0.05$). The habitat use within the home ranges was found to be random ($\Lambda = 0.38, \chi^2 = 8.5$, df = 7, $p > 0.05$), ie the proportion of radio locations within each habitat type did not differ from the proportions of the different habitat types available within the 100% MCP home ranges. In total, 75 observations on day-nests were obtained from 63 different day-nests. Nine day-nests were reoccupied at least once by the same individual. Simultaneous nest sharing was never observed, but on one occasion non-simultaneous nest sharing occurred; a male used a nest formerly occupied by a different male. The habitat types used for day-nesting were found to be similar for males and females ($U_{dec.forest}$ = 17, $U_{con.forest}$ = 18, $U_{forest.edge}$ = 17.5, $U_{hedgerow}$ = 22, $U_{arable.land}$ = 20.5, $U_{grassland}$ = 25, and $U_{premises}$ = 20.5; $p > 0.05$), and data were thus pooled. Day-nests were mainly built in forested areas and premises with leaves as the principal nesting material (Table 3).

In total, 1914 observations were available for the analysis of activity pattern. Day-time tracking revealed no activity, and the hedgehogs were always found in the same day-nest at night as they had entered in the morning earlier the same day. The average duration of the nightly activity period was 370 (±41) minutes for males ($n = 5$) and 356 (± 26) minutes for females ($n = 4$). The difference was not statistically significant

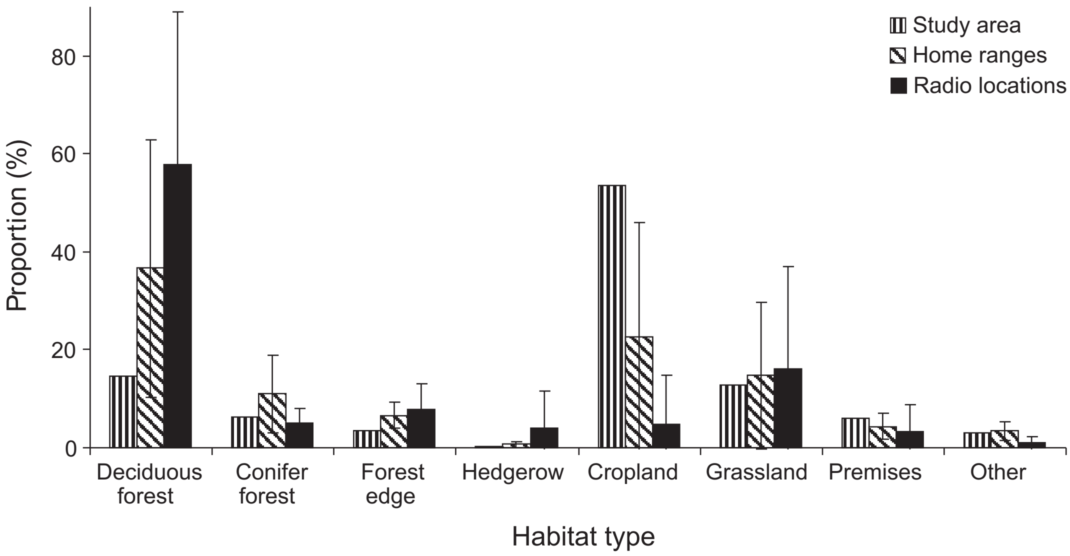

Fig. 1. Habitat type compositions (mean ± SD) within the study area, within the 100% MCP home ranges of the radio-tagged hedgehogs ($n = 8$) and of the radio locations from the eight radio-tagged hedgehogs ($n = 1993$) during the study period (May 28 – July 30 2001).

Table 3. The location and composition of 63 day-nests used by 9 hedgehogs during the period May 28 – July 30 2001.

Material	Habitat							Total (No.)	Total (%)
	Deciduous forest	Coniferous forest	Forest edge	Hedge-row	Grass-land	Crop-land	Pre-mises		
Leaves	27	4	5	5	0	0	1	42	66.7
Grasses	2	0	1	0	6	4	0	13	20.6
Man-made	6	1	0	0	0	0	1	8	12.7
Total (No.)	35	5	6	5	6	4	2	63	100
Total (%)	55.6	7.9	9.5	7.9	9.5	6.3	3.2	100	

(U = 92, p = 0.463). No correlations between either cessation of activity and sunrise (n = 31), or between initiation of activity and sunset were found (n = 26) (Spearman Rank Correlation: $r_{S(sunrise/end)}$ = 0.141, p = 0.451 and $r_{S(sunset/start)}$ = –0.29, p = 0.146). A peak in the frequency of sexual behaviour (n = 21) was found in the period from late-June to mid-July (Fig. 2). The proportions of time spent on the different activities are shown in Fig. 3 for males (n = 5) and females (n = 4). Foraging was by far the most time-consuming nightly activity for both sexes. Only males spent time on interactions with the same sex ($U_{agonistic.beh.}$ = 10, p = 0.015). No statistically significant differences between males and females were found in the remaining behavioural categories ($U_{foraging}$ = 27, $U_{locomotion}$ = 14, $U_{stationary.beh.}$ = 16, $U_{sexual.beh.}$ = 24, $U_{active.beh.}$ = 26.5, and U_{other} = 21; p > 0.05).

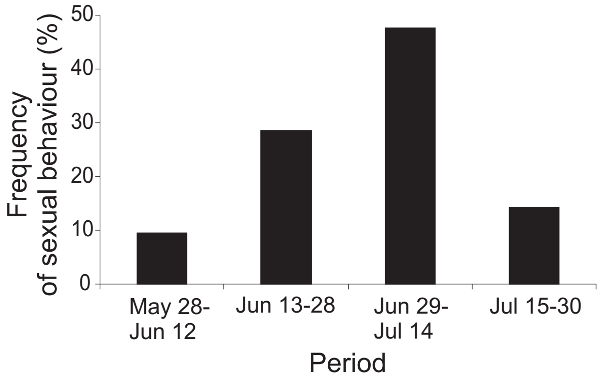

Fig. 2. Frequency of recorded sexual behaviour (n = 21).

Males (n = 4) lost on average 1.9 (± 1.6) g/day, corresponding to a daily weight loss of 0.2 (± 0.1)%. The mean total weight loss during the study period was 8.4 (± 5.6)% for the males. In contrast, females (n = 4) gained 1.2 (± 1.3) g/day, corresponding to a daily weight gain of 0.2 (± 0.1)%. The mean total weight gain for the females was 5.2 (±4.7)%. The daily weight changes in percentages were found to be significantly different between males and females (U = 10, p = 0.03).

Discussion

Males were found to have larger home ranges than females in the present study, which has generally been found in previous studies during the mating season, although the actual home--range sizes seem to be quite variable (Reeve 1982, Kristiansson 1984, Morris 1986, 1988, Zingg 1994). Direct comparisons between studies of home ranges are impeded by differences in purpose and methodology. The strongest resemblance in methodology and season was found between the present study and a study conducted by Zingg (1994). The average male home-range size found by Zingg (1994) was similar to the one found in the present study, whereas the home-range size of females was almost half the size found in the present study. In addition, the male home-range size found by Zingg (1994) outside the mating season was similar to the core area found in the present

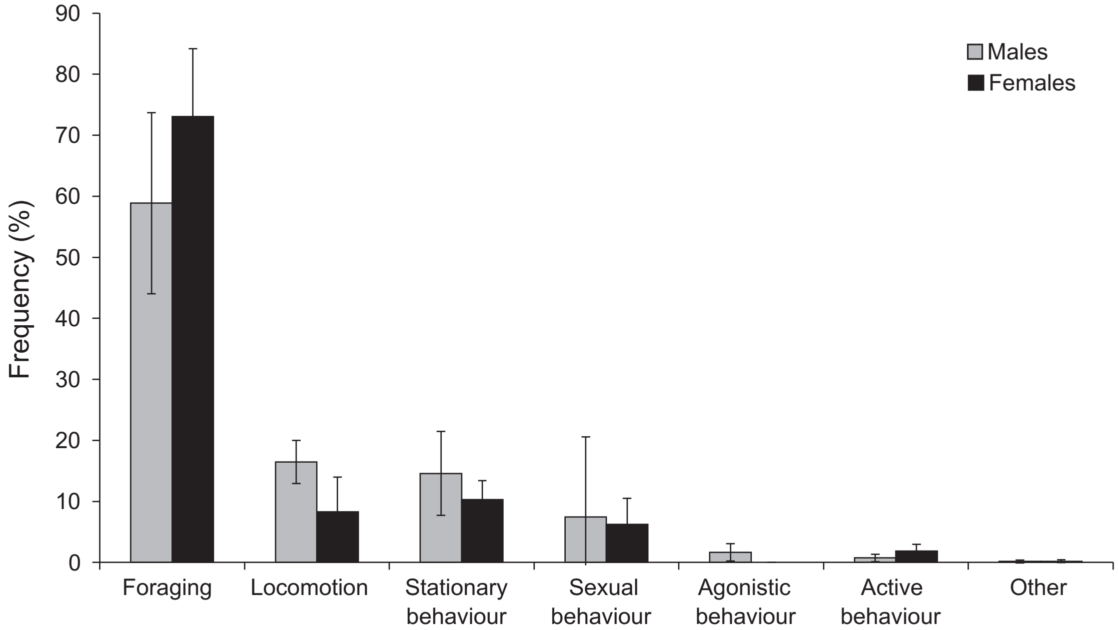

Fig. 3. Proportions of time (mean ± SD) spent by males (n = 5) and females (n = 4) on the different nightly activities (May 28 – July 30 2001; cf Table 1).

study during the mating period. The recorded distances travelled by both males and females are slightly longer than the previously reported 1200–1800 m for males and 600–1000 m for females recorded during the mating season (Reeve 1982, Kristiansson 1984, Morris 1988, Zingg 1994). This is likely to be due to the fact that the sampling interval in the present study was more frequent than in the previous studies (except Zingg 1994), providing a more exact mapping of the individual movements. Differences in habitat compositions between the study areas may also be an important factor influencing the distances travelled as large proportions of unsuitable habitat for hedgehogs may result in longer distances travelled for sufficient amounts of food to be found.

A remarkable observation in the present study is the extensive use of deciduous forest, which is unlike previous findings (Berthoud 1982 cited by Huijser 1999, Morris 1986, Doncaster 1994, Huijser 2000). This may reflect the quality of the forests in the study area. Intensive forestry was not conducted, leaving the forests with a high degree of diversity, consisting of clearings and a variable degree of cover, undergrowth, and species composition. The clearings within the deciduous forests constituted additional edge habitat, and hedgehogs were found to spend a great deal of time in these clearings. Hedgehogs may be flexible to some extent in their habitat choice due to variations in the microclimate in the different habitat types, which influences availability of the main components of the hedgehogs' diet: ground invertebrates. This has been proven to be the case with badgers (*Meles meles*) that, like the hedgehogs, forage to a great extent on earthworms (Kruuk 1978). July was found to be drier than on average (29 mm in 2001 vs 64 mm mean 1961–1990; DMI 2005). Forests retain humidity for a longer time during dry periods than open areas because the tree cover shields against sun and wind and may therefore supply better options for invertebrates during dry periods.

The non-random habitat use found in the present study is in contrast to the result found by Huijser (2000), a dissimilarity which is likely to be due to differences in the composition of preferred and avoided habitats in the home ranges. A great proportion of arable land in the study area was rarely visited by the hedgehogs, a result found in previous studies (Berthoud 1982 cited by Huijser 1999, Doncaster 1992, 1994, Huijser 2000). The tendency of hedgehogs to prefer edge habitats has frequently been recorded (present study, Reeve 1981 cited by Huijser 1999, Morris 1986, Zingg 1994, Huijser 2000), and is related to the richness of invertebrates and nearby cover found in edge habitat, which are valuable qualities to hedgehogs (Esser 1984). In agreement with the present study, Zingg (1994) found no difference between males and females in the use of the various habitat types as day-nesting sites. Over 80% of all day-nests found in the present study and by Huijser (2000) were in hedgerows or forests, whereas Zingg (1994) found only 26% of the day-nests in forested areas. The use of leaves as the principal day-nesting material is consistent with the findings of Reeve and Morris (1985). Hitherto, non-simultaneous day-nest sharing has only been recorded as males or females using a day-nest previously occupied by a female (Reeve and Morris 1985), whereas in the present study it was found that males will also use day-nests formerly occupied by other males.

The lack of correlation between activity, sunset and sunrise found in the present study may be related to the fact that hedgehogs were often recorded to have shorter activity periods on cold or rainy nights, an observation also noted by Esser (1984). In addition, on nights with courtships or mating hedgehogs were often recorded to retreat to day-nests well after sunrise. If adding the five week long pregnancy of hedgehogs to the observed frequency of sexual behaviour, then the resulting estimated birth distribution is consistent with the frequency distribution of hedgehog litters found in Denmark in a previous study (Walhovd 1984). Zingg (1994) found a marked difference between the sexes in the time spent moving around during summer; males spent 21% of their active period on locomotion, whereas females only spent 6%, corresponding to the results in the present study. However, a statistical significance could not be proven in the present study, possibly due to the small sample size. The males' high level of movement in the mating season is also indicated by the numerous previous records of sex ratios biased towards males during the mating season (present study, Brockie 1974, Esser 1984, Reeve and Morris 1986, Huijser 2000) and the fact that traffic-kills during the mating season are mainly males despite an unbiased yearly sex ratio in the population (Göransson *et al.* 1976, Huijser 2000). Thus, the skewed sex ratio is likely due to a non-representative sample of the population owing to the fact that the males are ranging further than females during the mating period. The extensive movements and the weight loss of males during the mating season reflect their effort put into the search for females. The absence of any agonistic encounters between females, along with their overlapping home ranges, is a strong indication of non-territoriality. Defence of home ranges has never been observed in hedgehog populations (Brockie 1974, Parkes 1975, Kristiansson 1984, Zingg 1994).

The body-weight changes found in the present study are in accordance with previous studies (Kristiansson 1984, Huijser 2000). The weight loss of the males reflects their increased activity level during the mating season. Females, on the other hand, gain weight during the mating season partly because they recover from the weight loss during hibernation and partly because of pregnancy.

The promiscuous mating system of hedgehogs, which instigates males to put much effort into the search for females willing to mate, resulted in the present study in larger male home ranges, longer nightly distances travelled by males than by females and a weight loss in males compared to a weight gain in females. The extensive use of forested areas is in contrast to previous findings and may be explained by 1) the biodiverse forests in the study area, ie possibly high density of ground invertebrates and 2) temporary variation in climate, affecting food availability in the various habitat types.

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