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Home ranges of brown hares in a natural salt marsh: comparisons with agricultural systems

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This is the first study on spatial behaviour of brown hares *Lepus europaeus* Pallas, 1778 based on radio-telemetry in a natural system, which we contrast with data from agricultural systems. Radio tracking took place in a Dutch salt marsh over a 10-month period, with intensive tracking sessions during April/May and December/January. Six hares could be followed in both periods and in total 1224 fixes were collected. Average home range size was calculated as 28.7 ± 8.5 ha when using Adaptive Kernell method (Mimimum Convex Polygon: 27.3 ± 9.0 ha) on 90% of all fixes. Such values are in the lower end of the range of those obtained for agricultural systems. Home range size did not differ between sexes, day and night, or across seasons. However, the size of the core range (50% of fixes) was twice as large in May compared to the winter period, and thus inversely related to food availability. Unlike in agricultural systems, use of space by hares did not change over the course of the season. This probably reflects the patchy nature of the natural habitat which provides food and shelter throughout the year in a confined area.

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Introduction

During the last three decades, populations of brown hare *Lepus europaeus* Pallas, 1778 have declined substantially throughout Europe (Tapper 1992). Although changes in weather, hunting pressure, predation and disease have locally contributed to this decline (Hutchings and Harris 1996), it has largely been attributed to changes in agricultural land use and related conversion of the countryside (Tapper and Barnes 1986, Slamecka 1991). Except for set-aside programs, there is little scope for substantial improvement in agricultural areas to change to such an extent that hares can profit from it and have a revival. Therefore, nature reserves are expected to become increasingly important for hares. However, knowledge

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about hares is largely derived from agricultural systems, and little is known from natural systems.

We focus on hares inhabiting a natural salt-marsh system and test whether habitat use parallels the behaviour of hares in agricultural systems. Based on radio-telemetry data, we established size and position of home ranges, and studied changes over the season.

Since the size of home ranges in *Lagomorphs* was found negatively related to food supply (Boutin 1984, Swihart 1986, Hulbert *et al*. 1996), we expected home ranges in the salt-marsh system to be larger than in agricultural habitat. Moreover, we hypothesised that home ranges are extended in winter, when food is in short supply.

Study area

The study was carried out in the central part of a 550-ha undisturbed natural salt marsh in the eastern part of the Dutch island of Schiermonnikoog (53°30'N, 6°18'E). Brown hares were introduced in 1898 and the species is currently well established. Based on the number of shot hares, the population was remarkably stable over the period 1971–1994 (Hunting Corporation Schiermonnikoog, unpubl. data). Soon after the area obtained the status 'national park' in 1995, hunting was prohibited. Annual autumn counts (line transect counts involving around 30 people) have revealed that in the first year after cessation of hunting, the number of hares increased from about 0.5 hare ha^{-1} to 1 hare ha^{-1}, but in subsequent years no further increase has been observed. Densities compare with optimal agricultural habitat from the past (Broekhuizen 1975). There are no foxes *Vulpes vulpes* on the island, but feral cats *Felix silvestris catus* and birds of prey, particularly hen harriers *Circus cyaneus* and marsh harriers *Circus aeruginosus* regularly attack both adult and juvenile hares and therefore have to be considered a potential threat (Van der Wal *et al*. 1998).

Methods

Ten hares were captured and radio-tagged with collar transmitters in April 1996. Hares were caught by driving them into an approximately 1-m high and 800-m long net positioned perpendicular to the east-west axis of the island. Simultaneous radio tracking was performed from fixed positions on two dune tops which were 220 metres apart, and were on either side of the place where the catching net had been up. The position of radio-tagged hares was determined by intercepting the signal with two Yeasu FT-290 receivers with loop antennas tuned on 30 MHz. The collar transmitters (made by the Institute for Forest and Nature Management, IBN-DLO Arnhem, the Netherlands) had a range of about 1 km. Each transmitter weighed 40 grams (including collar), and fitted batteries were predicted to last for at least 800 days. Half of the transmitters had a dip switch which allowed the pulse frequency to double when the hares' neck and head bend downwards. Although we did not use the change of pulse frequency as such, its rapidly changing nature indicated that hares were active during both at night and day.

Accuracy of tracking was tested in advance by placing transmitters on four different locations in the field at 100–500 metre distance from the receivers, where after position was determined 30 times. All fixes fell within an area of 0.002 to 0.4 ha.

In the periods 1 April – 28 May 1996 ('spring') and 1 December 1996 – 15 January 1997 ('winter'), tracking sessions were held on a close to daily basis, at different times during the 24 h period. In each session a single hare was tracked from both location points within the same three minute period, after which the next hare was located. This procedure was repeated three times in each session, and all three locations of a single hare during a session were treated as independent observations in the analyses. Three hares died during the study periods and one transmitter failed, so data of six hares were eventually used in the analysis. All positions found further than 1 km from a receiver were marked as errors and were excluded, as it exceeded the range of the transmitters used. In total, 1224 positions (fixes) were used in the analysis. Home ranges were constructed using the Adaptive Kernel method (Worton 1989). To allow comparison with other studies also the Minimum Convex Polygon method (Mohr 1947) was used.

The data were divided into three time periods: April, May and December/January. To overcome the methodological problem of increasing estimates of home range size with the number of fixes used (Broekhuizen 1975, Marboutin and Aebischer 1996), data for each hare were subdivided into units of 40 fixes per time period. For each unit of 40 fixes the size of the home range and core range were determined, and for each period, the averages of these estimates were taken. Home range size was estimated on 90% and core ranges on 50% of the fixes excluding the outermost points first. The time of sunrise and sunset was used to separate day-time locations from night-time only.

The vegetation in the study area was mapped in the field in June 1996, aided by false-colour photographs. Six different vegetation types were recognised, ranging from frequently inundated lower salt marsh communities to elevated dune vegetation. The map was made in a Geographical Information System and the percentage of all radio fixes of hares in each vegetation type was determined by making an overlay of the hare data on the vegetation map. The study area is described in more detail in Van der Wal *et al*. (1998).

Results

Average home range size for the total study period was 27.3 ha (SD = 9.0) when using the Minimum Convex Polygon method, and 28.7 ha (± 8.5) when using the Adaptive Kernel method on 90% of all fixes (Table 1). Home range size did not differ between sexes (Mann Whitney U-test: Adaptive Kernel $U = 6$, $n_1 = 3$, $n_2 = 3$, $p > 0.2$; MCP $U = 5$, $n_1 = 3$, $n_2 = 3$, $p > 0.2$). The home ranges of the six hares showed considerable overlap (mean 51 ± 9% on an area basis).

Home range size did not differ significantly across seasons (Fig. 1; Kruskal--Wallis: $\chi^2 = 2.05$, df = 5, $p = 0.36$). However, the size of the core range varied from

Table 1. The home range size of the six hares followed throughout the research period. Home range size is calculated on 90% of the fixes following the Mimimum Convex Polygon (MCP) and Adaptive Kernel method.

Hare	Sex	Body mass	Home range size (ha)		Fixes (n)
			(MCP)	(Ad. Kernel)	
1	M	3100	27.9	32.7	227
2	F	4030	34.8	29.1	187
3	M	3050	35.2	39.8	224
4	F	3100	24.6	29.4	205
5	F	3100	30.1	27.4	143
6	M	3100	10.9	14.0	238
Mean		3250	27.3	28.7	204
SD		380	9.0	8.5	35

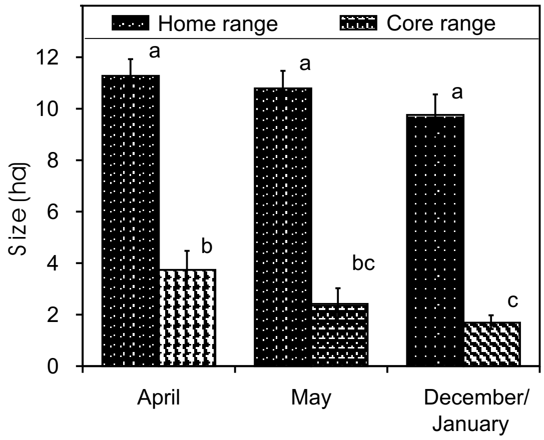

Fig. 1. Average size of home range (± SE) and core range for hares during the three time periods of the study. Adaptive Kernel method based on 90% (home range) and 50% (core range) of the fixes, respectively. Bars with different letters differed significantly from each other.

1.6 ha in winter to 3.7 ha in April (Fig. 1; Kruskal-Wallis: $\chi^2 = 6.54$, df = 5, $p < 0.05$). During night time, hares had home ranges and core ranges the size equal of those in day-time (Mann Whitney U-test: home range $U = 20$, $n_1 = 6$, $n_2 = 6$, $p > 0.2$; core range $U = 21$, $n_1 = 6$, $n_2 = 6$, $p > 0.2$).

No large-scale movements of radio-tagged hares were observed; individuals were faithful to their home ranges throughout the year. However, the centre of activity moved for all six hares between spring and winter in N to NE direction towards the dunes by 108 m (± 12.9) on average. Females showed a relatively large shift based on night time observations (248 ± 81 m), and almost no displacement on the basis of fixes in day time (24 ± 2 m; Mann Whitney U-test: $U = 9$, $n_1 = 3$, $n_2 = 3$, $p < 0.1$). Males had comparable shifts in their activity centre between spring and winter based on either day-time (104 ± 31 m) or night-time (149 ± 29 m) observation.

Habitat use of hares as based on the proportions of fixes in the different vegetation types did not differ significantly across seasons ($\chi^2 = 12.31$, df = 8, $p = 0.25$). Also, no significant differences in habitat use between day and night were found ($\chi^2 = 7.19$ df = 5, $p = 0.20$).

Discussion

No large-scale movements of radio-tagged hares were observed over the 9-month study period despite large changes in food availability due to both flooding and seasonality. Biomass of the grass *Festuca rubra*, which is an important food item for hares throughout the year (Van der Wal *et al.* 2000), was 43.1 ± 5.7 g/m^2 in May

1994 and dropped to 11.6 ± 1.4 g/m^2 in December 1994 (R. Van der Wal, unpubl. data). This study supports the view that hares have a non-migratory way of live (Broekhuizen and Maaskamp 1982, Pépin and Cargnelutti 1985). Large-scale movements have been observed elsewhere following periods of heavy snowfall (Grzimek 1972), which is likely to be linked to a poor accessibility of food. Large parts of our study area are regularly flooded by the sea, which impedes foraging opportunities for a period of hours up to several weeks. During extreme high tides, hares have been observed to gather on the tops of nearby dunes, rather than migrate to areas where the overall probability of inundation is lower. However, for all six hares the activity centre had shifted N to NE towards the dune ridge between spring and winter. This shift might be induced by floodings which are most dramatic during winter.

Home range size of hares in the natural salt-marsh system was found to be comparable to those in agricultural areas (Table 2). Only in the most large-scale agricultural area of all studies (Table 2, study no. 7), Marboutin and Aebisher (1996) report home ranges which seem greater than average. It appears that most variation in the size of home ranges is due to the proportion of fixes taken into account when calculating home range size, as the size of the home range of an animal is strongly influenced by occasional sallies. In our study, home range size was linearly related to the percentage of fixes included in the calculation, but this relationship turned exponential when more than 90% of the fixes were included. By following Burt (1943) and defining home range as that area where the majority of the activities take place, we excluded the outermost 10% of the fixes when calculating home range size. In our study, estimated home range size using Adaptive Kernel was 55 ha when 100% of the valid fixes were included, and dropped to 44 ha and 29 ha when calculated on the basis of 95% and 90% of the fixes respectively. Reitz and Léonard (1994) indicate an even more extreme drop in home range size when reducing the number of fixes included (Table 2). Similar to studies in agricultural areas (Broekhuizen and Maaskamp 1982, Kovacs and Buza 1992) home ranges of the hares in the salt marsh greatly overlapped, which indicates a high degree of tolerance.

In our study, home range size did not differ across seasons. However, we found the size of the core range (50% of the fixes) smallest in winter, when food availability is lowest due to natural dieback (R. Van der Wal, pers. obs.). Similarly, Reitz and Léonard (1994) found that average home range size tended to be smallest in winter, which is contrary to expectation if food availability is determining home range size (Hulbert *et al*. 1996). Large core ranges in April may be related to peak sexual activity, since 'March madness' is delayed by about a month in the salt-marsh system. Alternatively, small core ranges during winter might reflect low activity as a strategy to save energy when food is in short supply, and weather conditions often poor. By minimising movements and maximising the time in shelter (Thirgood and Hewson 1987), wind chill and associated high energetic costs are likely to be kept low.

Table 2. Overview of home range studies on brown hares. For the current study, three different calculation methods were used to facilitate comparison with other studies. Size of home ranges (± SD) is in hectares. Sources: 1 – Broekhuizen and Maaskamp (1982), 2 – Parkes (1984, 3 – Tapper and Barnes 1986, 4 – Kovacs and Buza 1992, 5 – Reitz and Léonard 1994, 6 – Marboutin and Aebisher 1996, 7 – this study.

Country	Habitat	Home range	Calc. method	Fixes per hares	Hares (n)	Tracking method	Tracking period (months)	Source
1. The Netherlands – river IJssel	small-scale grassland	26 (19)	MCP (<100%)	40 (19)	10	2 synchronous bearings + spotlight views	1–6″	1
2. Netherlands – Noordoostpolder	arable land	39 (30)	MCP (<100%)	27 (12)	3	2 synchronous bearings + spotlight views	[illegible]–4	1
3. New Zealand – Avocado River	retired country range	53 (13)	MCP (90%)	> 600	5	2 synchronous bearings	12 months	2
4. England – Hampshire	mixed arable land and pasture	38 (14)	harm. mean (90%)	78 (54)	15	2 non-synchronous bearings	1–7 months	3
5. Hungary – Fuzesabony	large-scale arable land	37 (41)	MCP (100%)	65 (11)	6	2 synchornous bearings	4–7 months	4
6. Hungary – near Budapest	forested agricultural land	45 (51)	MCP (100%)	86 (23)	6	2 synchornous bearings	3–5 months	4
7. France – near Paris	intensive farmland	123 (74) 109 (101) 54 (37) 38 (–)	MCP (100%) adapt. kernel (100%) adapt. kernel (95%) adapt. kernel (90%)	221 (14)	6	2–3 non-synchornous bearings	9–10 months	5
8. France – North east	large-scale agricultural land	190 (53)	MCP (95%)	195 (53)	20	3 synchronous bearings	5 months	6
9. The Netherlands Schiermonnikoog	natural salt marsh	142 (48) 43 (13) 27 (9) 55 (10) 44 (12) 29 (9)	MCP (100%) MCP (95%) MCP (90%) adapt. kernel (100%) adapt. kernel (95%) adapt. kernel (90%)	204 (32)	6	2 synchronous bearings	9 months	7

We did not find differences in the size or location of home ranges between night and day, suggesting weak differences in habitat use between day and night. Habitat use, as based on the number of fixes in the various vegetation types, also did not differ across seasons. This is in contrast to the general patterns observed in agricultural areas and indicate a different use of natural habitat. In their classical study, Tapper and Barnes (1986) showed that hares shifted their activities between fields according to crop development, usually preferring the early stages of development. Similarly, hares in France were shown to incorporate stubble fields successively in their home range after harvest (Reitz and Léonard 1994), and in New Zealand rangeland there were distinct seasonal differences in the use of different vegetational units by hares (Parkes 1984). Generally, night-time ranges of hares in agricultural area are significantly larger than day-time ranges (Reitz and Léonard 1994, Marboutin and Aebisher 1996), reflecting a wider area for foraging (Homolka 1986, Tapper and Barnes 1986). The diet of hares in the salt marsh of Schiermonnikoog changes over the season, with large amounts of the lower salt marsh shrub *Atriplex portulacoides* consumed in winter, at the expense of the grass *Festuca rubra*, which grows in higher parts of the marsh (Van der Wal *et al*. 2000). However, this major switch in the use of food plants did not lead to detectable changes in spatial use of the salt marsh, which probably reflects the patchy structure of the system. Without extending their home ranges, hares have access to most of their food plants in a relatively small area. In agricultural areas the daily resting areas are often clearly separated in space from the nightly feeding areas (Tapper and Barnes 1986, Reitz and Léonard 1994), leading to differences in the size of night and day range and contrasting habitat use. This salt marsh offers foraging and resting places in close vicinity. Throughout the year, home range size has frequently shown to increase as fields with different crop species or management regime are included sequentially. We hypothesize that due to the heterogeneity of the salt-marsh vegetation, use of space by hares within a day and throughout the year are relatively invariable. The fact that the average home range size in our study is among the smallest of all studies, suggests that this high level of patchiness guarantees food availability and shelter throughout the year in an area of limited size.

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