

Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland)

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The movement patterns of free-living lynx, *Lynx lynx*, were studied by radio-telemetry in Białowieża Primeval Forest, Poland. Eighteen lynx were fitted with radio-collars and their movements were recorded by continuous 24-h sequences and daily relocations. On average, lynx moved 7.2 km per day, and males covered longer distances than females (9.0 and 6.8 km, respectively). In males, the daily movement distances were 56% longer during the mating season (January–March) than during the rest of the year. Females moved 43% longer distances during the period of intensive care for kittens (May–August) than in other periods. Males covered longer routes than females and stayed far from the location of the previous day. Females' movements were more concentrated as they moved intensively but stayed close to the previous day's location. The lynx travelled with an average speed of 1.2 km h⁻¹ with males moving faster than females (1.5 and 1.0 km h⁻¹, respectively). Males travelled even faster (on average 1.9 km h⁻¹) during the mating season. During a day lynx utilised an area comprising only 1.7%–2.6% of their annual home range. The home ranges were used with rather low intensity (31 to 50 m of lynx route per 1 km² of home range), still lower in males than in females. The lynx moved the longest distances (14 km day⁻¹, on average) on days when they failed to kill large prey, and the shortest ones (2.8 km day⁻¹) on the first day after making a kill. The results suggest that males tend to maximise their reproductive success by increasing an opportunity to meet receptive females, whereas females increase their reproductive success via adjusting their behaviour to the needs of kittens.

Introduction

Animal movements are related to the needs of foraging, mating, and rearing of young. The area that encloses these movements (home range, *sensu* Burt 1943) is commonly assumed to depend on availability and dispersion of food and other resources (for review *see* Sunquist & Sunquist 1989). The Eurasian lynx, *Lynx lynx*, despite its relatively small size, (rarely above 24 kg, Matjuschkin 1978) use large home ranges (from 130 to 1400 km²; Breitenmoser *et al.* 1993, Schmidt *et al.* 1997, J. Linnell *et al.* unpubl. data) typically for large felids. The lynx feed predominantly on ungulates (Breitenmoser & Haller 1993, Jędrzejewski *et al.* 1993a) whose populations are usually scattered in space, and this may partially explain their holding vast ranges. Although a large kill provides the lynx with food for several days (Okarma *et al.* 1997) and reduces its locomotory activity during the time of consumption, the lynx's activity increases with diminishing amount of meat (Schmidt 1999) as the predator has to search for another prey. This in turn forces the lynx to extend the used area.

The land tenure system in felids (genus *Lynx* included) is based on more or less exclusive territories which are established with priority rights (e.g., Bailey 1974, Smith *et al.* 1987, Breitenmoser *et al.* 1993, Schmidt *et al.* 1997). If resident lynx are to maintain their rights to a territory, they have to move fast and widely enough to advertise their presence over as much area and in as short intervals as possible. However, the larger home range they utilise, the more difficult it could be for them to keep control over the entire territory and to maintain its exclusivity. So far, there is not enough data on movement patterns in felids. The locomotory ability of cats may be one of key factors in our understanding of their land tenure system.

As predicted by Sandell (1989), the spatial organisation in solitary carnivores depends on the sex of the animal and their tactics to maximise reproductive success. Results of previous research on home range size in lynx and its seasonal dynamics seem to corroborate the theory. The home ranges, as in most other mammals, were bigger in males than in females (e.g.,

Breitenmoser *et al.* 1993, Schmidt *et al.* 1997), and they showed seasonal changes specific to males and females as related to their reproductive behaviour (Schmidt *et al.* 1997). Male lynx roamed over a bigger area during and just before the mating period than in the rest of the year, whereas females reduced their ranges after parturition and later they extended the area used in parallel with kittens' development. Similarly, the daily activity pattern of lynx showed variation related to the same factors (Schmidt 1999). Females were generally more diurnal than males, which seems to be influenced by continuous care for young. They were also active longer on each day during the period of most intensive care for kittens than in the rest of a year. Males, on the other hand, showed higher locomotory activity during the mating period as compared with other seasons. On this basis, we suggest that the pattern of lynx movements (e.g., the daily movement distance, speed of travelling, manner of movements) should be affected by factors related to different behavioural strategies in males and females.

The aims of this study were to determine the basic parameters of lynx movements: (1) daily movement distance, (2) straight-line distance between daily locations, (3) speed of movement, (4) area covered by daily movements, and (5) intensity of home range use. Also, we wanted to show, how killing and consumption of large prey influenced the pattern of lynx movements.

Study area

The study was carried out in Białowieża Primeval Forest (= BPF), north-eastern Poland, in 1991–1996. The forest, located on the Polish-Belarusian border, contains the largest remnants of deciduous and mixed woodlands of natural origin in European lowlands. Although connected to other large forests in the region, it also has borders with extensive farmland. The study area was limited to the Polish part of BPF (about 600 km², 52°30'–53° N, 23°30'–24°15' E), where coniferous and mixed tree stands dominated by pine, *Pinus silvestris*, and spruce, *Picea abies*, cover 52% of the area, and rich deciduous stands dominated by oak, *Quercus robur*, hornbeam,

Carpinus betulus, and lime, *Tilia cordata*, cover 16%. Wet forests of alder, *Alnus glutinosa*, and ash, *Fraxinus excelsior*, cover 20%. The remaining area is covered with birches, *Betula verrucosa* and *B. pubescens*, and aspen, *Populus tremula*, stands. The Polish part of BPF includes the protected forests of Białowieża National Park (100 km²), and exploited forests managed by State Forestry (500 km²). During the study, winter densities of ungulates preyed upon by lynx were as follows: roe deer *Capreolus capreolus* 3.2–4.9 ind. km⁻², and red deer *Cervus elaphus*, 3.6–6.1 ind. km⁻². The climate is transitional between Atlantic and continental types. In 1991–1996, the mean daily temperature in January was –2.7 °C and in July 19.7 °C. Annual precipitation was 558 mm. Snow cover lasted from 27 to 152 days with maximal depths from 15 to 63 cm. Detailed information about abiotic conditions, physiography, and vegetation of BPF are given by Faliński (1986), and Jędrzejewska and Jędrzejewski (1998).

Methods and material

Lynx movements were studied by radio-tracking. A total of 18 lynx (six adult males, five adult females, two subadult males, one subadult female, and four kittens) were captured and fitted with radio-collars during a research project on lynx ecology (Jędrzejewski *et al.* 1996, Okarma *et al.* 1997, Schmidt *et al.* 1997). One individual was excluded from this analysis due to small sample of locations.

The procedures for capturing and tranquillising the animals are described by Schmidt *et al.* (1997). Movements of radio-collared lynx could be easily followed owing to a dense net of forest roads (every 1 or 2 km along the grid of forest compartments). The compartments (1066 × 1066 m) were further subdivided into 4 quarters, so we aimed to determine in which quarter the focal animal was located. Obtained locations of lynx could then differ from their true position by a maximum of 373 m. However, standard triangulation techniques (Mech 1983), were used mainly when lynx were stationary. In those cases, we tried to take more accurate locations (< 50 m) by approaching the lynx more closely

(≥ 100 m), while still staying on the road. Such accurate locations were used for searching for lynx prey after the lynx had left the area. During continuous radio-tracking, an observer usually stayed 500–1000 m from the focal animal to avoid disturbing it and to minimise his influence on the direction and speed of lynx movement. When the lynx moved, there was no possibility to apply the triangulation correctly and the position of an animal could be less accurate. It was, however, corrected based on signal strength and, later, on comparisons between the last and the next accurate locations taken by triangulation when the lynx stopped.

We collected a total of 7158 radio-locations including 105 sessions of continuous 24-h radio-tracking with locations taken at 30-min intervals. Daily movement distance (DMD) was calculated with the program TRACKER (A. Angerbjörn, Radio Location Systems AB, Huddinge, Sweden) as a straight-line distance between consecutive locations during 24-h sessions of radio-tracking. For calculation of the straight-line distance (SLD) between daily locations we chose 1052 locations taken in consecutive days at approximately 24-h intervals. Speed of lynx travel was estimated during 120 sessions of continuous (from 2 to 13.5 h) radio-tracking when the lynx moved continuously.

We calculated the intensity of lynx movement after Goszczyński (1986) as: $I = \text{DMD} / \text{HR}$, where I = index of home range use (length of lynx route, in metres, per 1 km² of its home range per day), DMD = daily movement distance (km day⁻¹), HR = annual home range of a lynx (km²) calculated as Minimum Convex Polygon with 100% of locations.

Also, we characterised the lynx movement by calculating the area covered by the animal daily movements (100% MCP) as a percentage of a total home range (annual 100% MCP). The methods and material for calculation of home ranges is described in detail by Schmidt *et al.* (1997). Furthermore, we calculated the ratio of SLD/DMD separately for different seasons and sex/age classes of lynx. This index was to describe numerically the manner of lynx movement. Higher values indicated that the animal moved in a more 'direct' fashion, covering its route in an elongated, linear form, and tending

to stay far from a previous day's location. Lower values indicated that the animal moved in a more 'concentrated' fashion, making a winding routes in a small area, and remaining close to the location of a previous day.

To study the pattern of lynx movement in relation to their feeding behaviour we selected 59 lynx prey (44 roe deer, 9 red deer, 5 hares, and a domestic dog) found during the radio-tracking. We measured straight line distances between consecutive kills (PPD = prey-to-prey distance) and a total route covered by lynx between the kills (TR). The latter one was estimated as a sum of straight-line distances between lynx successive daily locations. Then we calculated a ratio between those two indices to reflect the differences in foraging behaviour between lynx sexes and seasons. Based on a sample of 15 prey with known time of having been killed by lynx, we compared the DMD's in consecutive days during prey consumption with those during the days when lynx made no kill. Days with no kill were the days when lynx moved long routes and afterwards killed a prey on the next day.

For comparisons of particular movement characteristics between seasons, we distinguished different periods for males and females according to their behaviour related to reproduction. Movement of males was analysed in January–March (mating season) and April–December (the rest of the year). In females, we distinguished May–August (season of parturition and the lowest mobility of kittens) and September–April (kittens accompanying their mothers) (Schmidt 1998). In the statistical analysis we applied non-parametric tests (Mann-Whitney test), because the data deviated from normality of distribution.

Results

Characteristics of lynx movement

The general behaviour of the Eurasian lynx was characterised by 2 to 14-h periods of travelling interrupted by stationary periods lasting from one hour to four days. Daily movement distances (DMD) of lynx were very variable (from 0 to

25 km). We attempted to explain this variation by analysing, in multiple regression, the effects of sex, reproductive status, individual variation of lynx, as well as season and utilisation of a large kill. All these factors together explained 65% of a total observed variation in DMD ($R^2 = 0.65$, $F = 18.054$, $n = 55$, $p < 0.0005$). The time spent by lynx feeding on a large prey contributed most to the total variation explained ($sr^2 = 0.30$, $p < 0.001$), followed by sex of lynx ($sr^2 = 0.03$, $p = 0.05$; semipartial correlation squared calculated according to Tabachnick & Fidell 1983). When prey factor was excluded from the analysis, the remaining independent variables explained only 21% of DMD's variation ($n = 93$, $p < 0.001$), with season ($sr^2 = 0.07$, $p < 0.01$) and sex ($sr^2 = 0.05$, $p < 0.05$) contributing most.

On average, lynx moved 7.2 km per day (Table 1). Adult males moved the longest distances (mean 9 km day⁻¹), whereas non-reproducing females moved the shortest distances (mean 3.7 km). Females with kittens moved significantly longer distances than single females. The longest uninterrupted movement of a lynx covered 31 km and was recorded during 13.5-h continuous radio-tracking (23/24 January, 1996, 16:30–06:00 h) of an adult male.

Daily movement distances were, on average, 2.6–4.5 times longer than distances between locations taken once daily (straight-line distances = SLD) (Table 1). The longest SLD was found in adult males and the shortest in females (with and without kittens). The ratio SLD/DMD was significantly higher in males than females with kittens (Fig. 1) which indicates that males moved in a different mode than females. Males moved more 'directly' as they covered longer routes and tended to end up far from places visited on a previous day. Females with kittens moved intensively, but their movements were more 'concentrated' and they stayed relatively closer to the place visited on a previous day.

The lynx moved with an average speed of 1.2 km h⁻¹. Adult males moved significantly faster (mean 1.5 km h⁻¹) than females with kittens (mean 1.0 km h⁻¹) and subadult males (mean 1.1 km h⁻¹) (Table 1). Single females showed similar speed as those with kittens.

Index of an intensity of home range use (I) by lynx, i.e. the mean length of route per 1 km² of its

home range, was very low in all lynx. It was lowest in adult males (31 m km^{-2}) and highest in females with kittens (50 m km^{-2}) (Fig. 2).

Low intensity of home range utilisation by lynx was especially evident when the area covered by DMD was compared with their annual home ranges. Daily ranges covered 1.7%–2.6% of the entire home range with no significant differences between sexes, though males ranged slightly wider than females. During the longest recorded daily trips (25 and 31 km), male lynx were able to cover up to 18% of their home ranges, only. The range of lynx daily movements increased relatively slowly during 5 consecutive days of 24-h radio-tracking: up to 14.6% and 5.1% of the annual home ranges in males and females, respectively (Fig. 3). It increased more rapidly in males than in females with kittens. The lynx rarely used repeatedly large portions of the areas covered in previous days. On average, ranges of consecutive daily movements overlapped by 28% (SD 30) in males and 31% (SD 25) in reproducing females.

On the basis of our data, it was not possible to determine how long it took a lynx to cover its entire home range. Despite the fact that in a few cases we were able to radio-track lynx day by day for as long as one month, the individuals still covered less than half of their total home

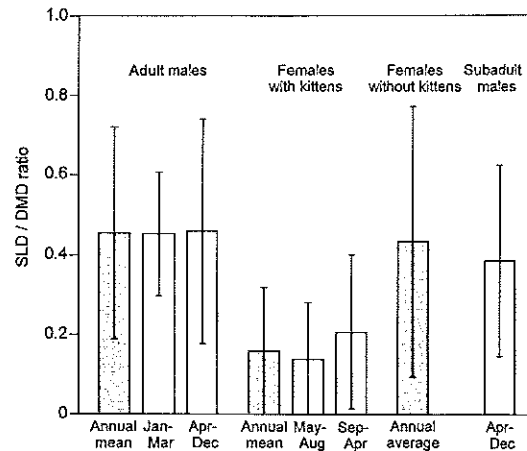


Fig. 1. The average ratios (annual and seasonal means \pm SD) of a straight-line distance (SLD) between daily locations to an actual daily movement distance (DMD) covered by Eurasian lynx, based on 24-h radio-tracking sessions (31 sessions in adult males, 24 in females with kittens, 12 in females without kittens, and 18 in subadult males). The sample of females without kittens was not sufficient for seasonal analysis, and the sample of subadult males contained only one season (April–December). Differences between sex/age lynx groups and seasons were calculated with Mann-Whitney U -test for pairwise comparisons (adult males vs. females with kittens: $U = 623$, $n_1 = 31$, $n_2 = 24$, $p < 0.001$; females with kittens vs. females without kittens: $U = 223$, $n_1 = 13$, $n_2 = 24$, $p < 0.05$; subadult males vs. females with kittens: $U = 347$, $n_1 = 24$, $n_2 = 18$, $p = 0.001$).

Table 1. Daily movement distances (DMD), straight-line distances (SLD) and speed of movement in radio-tracked Eurasian lynx, *Lynx lynx*, in Białowieża Primeval Forest. DMD is based on continuous 24-h sessions of radio-tracking with locations taken at 0.5-h intervals, SLD on locations taken once daily on consecutive days. Speed was estimated using 2 to 13.5-h bouts of uninterrupted travelling by lynx. n = number of individuals. Differences between lynx groups were tested with Mann-Whitney U -test for pairwise comparisons.

Sex/age group of lynx	DMD (km)		SLD (km)		Speed (km h ⁻¹)	
	Mean \pm SD	(min–max)	Mean \pm SD	(min–max)	Mean \pm SD	(min–max)
Adult males ($n = 5$)	9.0 \pm 7.0	(0–24.8)	3.3 \pm 3.2	(0–16.3) ^{b,c}	1.5 \pm 0.5	(0.7–2.5) ^e
Females with kittens ($n = 4$)	6.8 \pm 4.3	(0–18.6) ^a	1.5 \pm 1.8	(0–10.3)	1.0 \pm 0.4	(0.4–1.7)
Females without kittens ($n = 3$)	3.7 \pm 4.1	(0–11.8)	1.4 \pm 1.6	(0–7.4) ^a	1.2 \pm 0.3	(0.8–1.9)
Subadult males ($n = 2$)	7.4 \pm 4.6	(0–18.4)	2.0 \pm 2.1	(0–10.2)	1.3 \pm 0.4	(0.5–2.0)
Kittens ($n = 3$)	5.8 \pm 2.9	(0.9–10.3)	1.9 \pm 1.8	(0–9.6)	1.0 \pm 0.3	(0.7–1.4)
All lynx ($n = 17$)	7.2 \pm 5.6	(0–24.8)	2.3 \pm 2.7	(0–16.3)	1.2 \pm 0.5	(0.4–2.5)

^a) Different from females without kittens ($U = 115$, $n_1 = 15$, $n_2 = 25$, $p < 0.05$)

^b) Different from females with kittens ($U = 55318$, $n_1 = 423$, $n_2 = 194$, $p < 0.001$)

^c) Different from subadult males ($U = 52652$, $n_1 = 423$, $n_2 = 204$, $p < 0.001$)

^d) Different from subadult males ($U = 17695$, $n_1 = 204$, $n_2 = 149$, $p < 0.01$)

^e) Different from females with kittens and subadult males ($U = 1024$, $n_1 = 45$, $n_2 = 31$, $p = 0.001$)

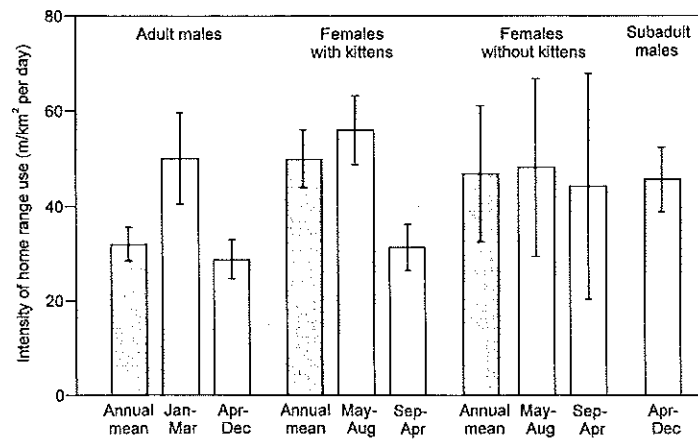


Fig. 2. The intensity of home range use by Eurasian lynx (I index, in metres of route covered daily by an individual per 1 km² of its yearly home range). Annual and seasonal means, based on 24-h radio-tracking sessions (33 sessions in adult males, 24 in females with kittens, 15 in females without kittens, and 20 in subadult males). The sample of subadult males contained only one season (April–December). Differences between lynx groups and seasons were tested with Mann-Whitney U -test for pairwise comparisons (adult males vs. females with kittens: $U = 246$, $n_1 = 33$, $n_2 = 24$, $p < 0.05$, females with kittens in May–August vs. September–April: $U = 85$, $n_1 = 18$, $n_2 = 6$, $p < 0.05$).

ranges. An adult male that was followed during 31 consecutive days (including five days of 24-h radio-tracking sessions) covered 45% of his yearly range, or 27% (if only one location per day was used for calculations). An adult female with kittens covered 43% of her yearly range during 20 days of radio-tracking. A subadult

male covered 43% of his yearly range during 17 days (including five days of 24-h observations) and 5% only during 19 consecutive days of radio-contact. A subadult female was utilising 59% of her yearly home range during 36 days (including two sessions of 5-day continuous observations).

Table 2. Seasonal changes in movement parameters of lynx in BPF. Seasons for males and females are different due to specific feature of their reproductive behaviour (see Methods). Differences between seasons were tested with Mann-Whitney U -test for pairwise comparisons. Denotations as in Table 1.

Season	DMD (km)		SLD (km)		Speed (km h ⁻¹)	
	Mean ± SD	(min–max)	Mean ± SD	(min–max)	Mean ± SD	(min–max)
Adult males ($n = 5$)						
January–March	17.2 ± 7.5	(7.5–4.8) ^{a)}	3.0 ± 3.1	(0–16.3)	1.9 ± 0.5	(1.1–2.5) ^{d)}
April–December	7.5 ± 5.9	(0–21.3)	3.3 ± 3.2	(0–14.5)	1.4 ± 0.5	(0.7–2.2)
Females with kittens ($n = 4$)						
May–August	7.7 ± 4.7	(0–18.6) ^{b)}	1.6 ± 2.1	(0–10.3)	1.1 ± 0.4	(0.5–1.7)
September–April	4.4 ± 1.7	(2–6.7)	1.4 ± 1.6	(0–7.6)	1.0 ± 0.3	(0.4–1.4)
Females without kittens ($n = 3$)						
May–August	4.0 ± 4.4	(0–11.8)	1.2 ± 1.3	(0–5.1)	1.2 ± 0.3	(0.8–1.9)
September–April	3.3 ± 3.9	(0–7.9)	1.6 ± 1.7	(0–7.4)	1.1 ± 0.5	(0.8–1.8)

^{a)} Different from April–December ($U = 119$, $n_1 = 5$, $n_2 = 28$, $p < 0.05$)

^{b)} Different from September–April ($U = 97$, $n_1 = 18$, $n_2 = 7$, $p < 0.05$)

^{c)} Different from April–December ($U = 277$, $n_1 = 10$, $n_2 = 35$, $p = 0.005$)

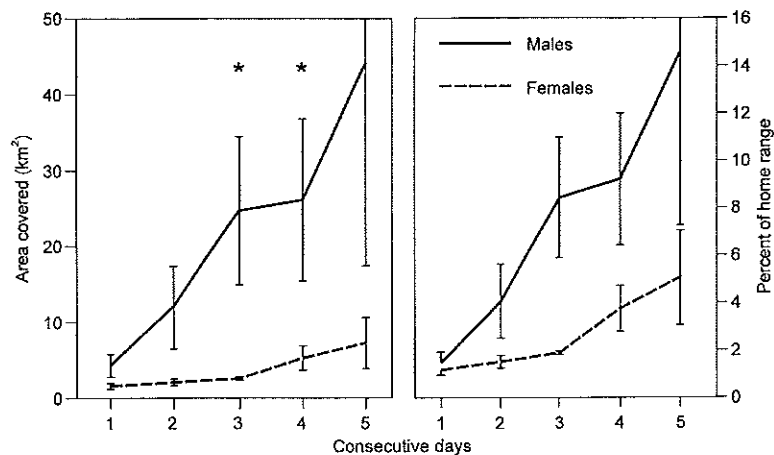


Fig. 3. The increase of home range area used by lynx during 5 days of continuous radio-tracking shown as the cumulative area covered (left graph) and the cumulative percentage of total home range size (right graph). Vertical lines show \pm SE. Statistical differences between males and females: * $p < 0.05$ (Mann-Whitney U -test). Sample size from 3 to 6 sessions of consecutive days.

Changes in lynx movements related to reproduction

Adult male lynx showed significantly higher mobility during the mating season (January–March) than during the rest of a year. Mean DMD of males was 56% longer during this period (Table 2). They also moved faster by 0.5 km h⁻¹. The straight-line distance between consecutive days, however, was the same in both periods. There was a significant increase (by 57%) in the intensity of home range use (I) in males during the mating period (Fig. 2). Notably, the mode of males' movements was similar in both periods with SLD/DMD ratios being equally high (0.45–0.46, Fig. 1), which means that males always tended to cover long daily routes and to stay far from the previous day's locations.

Females with kittens moved longer DMD (by 43%) during May–August than in other periods (Table 2). Their speed of travelling and SLD did not change between seasons. However, their intensity of home range penetration (I) was by 55% higher in May–August (Fig. 2). Females showed similar mode of movements in both seasons, with low values of SLD/DMD ratios (0.14 and 0.22). This indicates that even after the denning period (when kittens' mobility increased), they still tended to stay close to the

previous day's locations after moving long daily routes (Fig. 1). Females without kittens showed no seasonal variation in any of the recorded movement parameters (DMD, SLD, speed and I in Table 2 and Fig. 2).

Influence of foraging behaviour on the lynx movements

DMD of lynx was greatly influenced by hunting and foraging activity. Lynx moved longest distances (mean 14 km, SD = 3.4 km) during the days when they made no kill (Fig. 4). The DMD's in all consecutive days after making a kill were significantly shorter (Mann-Whitney U -test, $p < 0.05$) than in the day without kill. DMD's gradually increased from the first till the fourth day of prey consumption, though there was no statistical differences among consecutive days with prey (Mann-Whitney U -test, $p > 0.1$).

Straight-line distances between consecutively killed prey (PPD) varied from 2.9 km in reproducing female lynx to 6.4 km in adult males (Table 3). In males, these distances were longer during the mating season, whereas in females, they were longer during the period of kittens' high mobility than during the rest of a year (the difference was significant in females only; Table 3). The actual distance travelled by

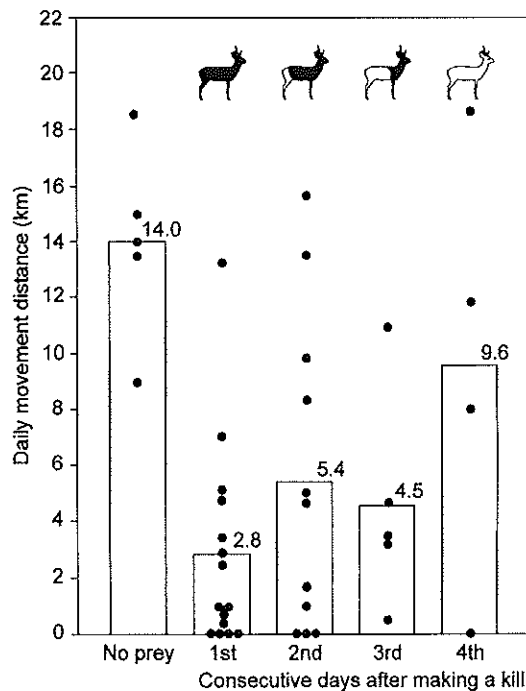


Fig. 4. Daily movement distances of Eurasian lynx on days with and without kills. Bars and numbers show mean values. Each point denotes one session of 24-h radio-tracking. Roe deer silhouettes symbolise the amount of prey left uneaten in consecutive days after a kill.

lynx between consecutive kills (based on 9 radio-tracking sessions with 0.5 hour location intervals) varied from 3 to 86 km (mean 22 km, SD = 26). These data, however, were too few to calculate sexual and seasonal differences in prey-to-prey distances. Therefore, the estimated total route (TR) based on SLD between daily locations was taken for that analysis. Females moved more linearly during hunting passages from kill to kill than males, as indicated by higher values of PPD/TR ratio (Table 3, Fig. 5). In females, that ratio was at the same high level in both seasons, whereas in males it was lower (though not significantly) in January–March. In adult males, three types of hunting strategies may be distinguished: (1) long winding route, (2) long straight route (both typical for mating season), and (3) short straight route (often recorded in summer) (Fig. 5). In females, type (2) could occur in winter, whereas type (1) was absent in both seasons.

Discussion

Since the study was based on radio-tracking alone, the daily movement distances of lynx may be somewhat underestimated. To increase

Table 3. Straight-line distances between consecutive prey killed by lynx (prey-to-prey distance, PPD) in km, and a ratio of PPD to total route (TR) covered by lynx between kills (total route was measured as a sum of straight-line distances between locations taken once a day). Differences between lynx groups and seasons were tested with Mann-Whitney *U*-test for pairwise comparisons. *n* = number of individuals.

Season	PPD (km)		PPD/TR ratio
	Mean ± SD	(min–max)	
Adult males (<i>n</i> = 5)			
January–March	8.4 ± 3.4	(3.0–12.3)	0.47
April–December	4.3 ± 4.5	(1.5–13.4)	0.61
Annual average	6.4 ± 4.4	(1.5–13.4) ^{a)}	0.54 ^{b)}
Females with kittens (<i>n</i> = 4)			
May–August	1.3 ± 0.6	(0.6–2.1) ^{c)}	0.90
September–April	4.3 ± 2.1	(1.5–7.2)	0.89
Annual average	2.9 ± 2.2	(0.6–7.2)	0.90
Females without kittens (<i>n</i> = 3)			
Annual average	5.3 ± 2.4	(3.4–8.7)	0.74
Subadult males (<i>n</i> = 2)			
Annual average	4.3 ± 3.2	(0.8–10.3)	0.59

^{a)} Different from females with kittens ($U = 99$, $n_1 = 12$, $n_2 = 11$, $p < 0.05$)

^{b)} Different from females with kittens ($U = 26$, $n_1 = 12$, $n_2 = 11$, $p = 0.01$)

^{c)} Different from September–April ($U = 1.5$, $n_1 = 5$, $n_2 = 6$, $p = 0.01$)

accuracy of reflecting a real distance travelled by a radio-collared animal, it may be useful to shorten intervals between locations to 15 min as it was done in wolves (Musiani *et al.* 1998). However, we considered 30-min intervals as sufficient for studying lynx because they moved slowly, so shorter intervals between locations would have not detected movements far enough to obtain accurate radio-location.

The Eurasian lynx moved relatively long distances during 24 h, but their travels highly depended on hunting success, time elapsed from killing prey (degree of its consumption), sex of the lynx, and season of the year. So far, there were no data on the Eurasian lynx's DMD based on radio-tracking. However, average values obtained by snow-tracking fall in the range of DMD's found in our study (Haglund 1966: 19.2 km; Zheltukhin 1984: 10.1 km). The DMD of radio-tracked Canada lynx *Lynx canadensis* ranged from 12.9 to 13.5 km (Breitenmoser *et al.* 1992). Even when multiplied by a correction factor derived by the authors from snow-tracking, those values (16.1–21.1 km) still remained in the range of DMD for Eurasian lynx.

Although data on DMD in other large felids are scarce, they are consistent with values obtained by us for the Eurasian lynx. Leopards, *Panthera pardus*, moved from 9.6 to 29 km daily (Bothma & Le Riche 1994, Jenny 1996), jaguars, *Panthera onca*, 11 km (Schaller & Crawshaw 1980), tigers, *Panthera tigris*, 2.7–9.6 km (Sunquist 1981), and Iberian lynx, *Lynx pardinus*, 5.7–9.2 km per day (Ferrerias *et al.* 1997).

Most often the straight-line distance (SLD) between consecutive daily locations has been used as an index of cats movements in various studies. The use of SLD for interspecific comparisons is not recommended as it is usually not correlated to real movement (Laundré *et al.* 1987). Nonetheless, the range of mean SLD values for different species of felids is relatively narrow: from 1.5 km in leopards (Bailey 1993), to 2.3 km in Eurasian lynx (this study), to 4 km in jaguars (Schaller & Crawshaw 1980), and 4.6 km in mountain lions, *Felis concolor* (Beier *et al.* 1995). Other studies of Eurasian lynx reported an average SLD 4.6 km in a boreal zone of northern Sweden (Pedersen *et al.* 1999) and 4.9 km in southern Norway (J. Odden *et al.* unpubl. data).

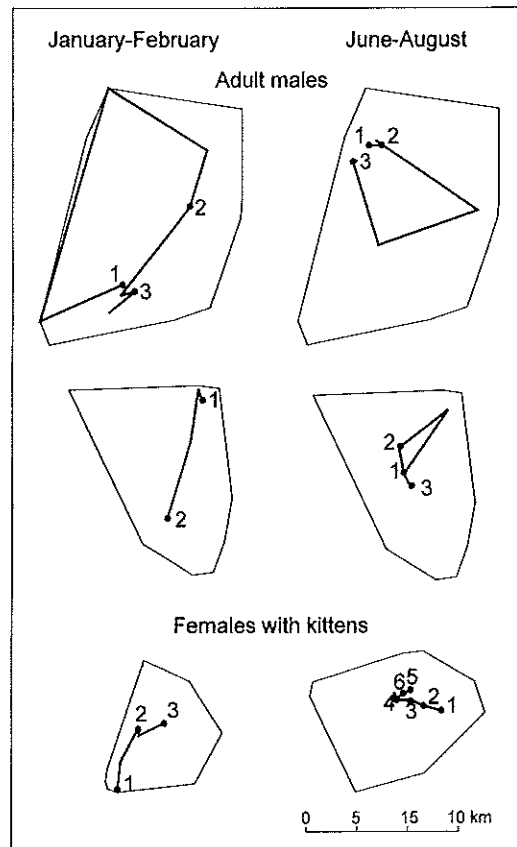


Fig. 5. Examples of lynx movements in relation to the distribution of their consecutive kills (roe and red deer, marked by solid points). The lines represent straight-line distances between consecutive daily radio-locations. In contrast to days with kills, during days with no kill (indicated by bends of lines) lynx stayed there only one day. Polygons show home ranges of particular individuals. Numbers indicate consecutive kills.

Low mobility of the Eurasian lynx, especially expressed by the *I* index, stands in a striking contrast with their vast home ranges and territorial behaviour (Breitenmoser *et al.* 1993, Schmidt *et al.* 1997, J. Linnell *et al.* unpubl. data). Our results show that patrolling the territory by lynx is a very slow process. Thus, parts of lynx home ranges remained unattended for relatively long periods. Comparisons with other felid species show that their land tenure system is very flexible. In ocelot, *Felis pardalis*, the entire home range boundaries were visited every 2–4 days (Emmons 1988). Tigers and leopards visited

most parts of their ranges at intervals of 5–14 days (Sunquist 1981, Bailey 1993). The home ranges in these species were much smaller than that of the Eurasian lynx, so those felids were able to cover their territories in a relatively short time to maintain exclusive rights to the areas. On the other hand, Ferreras *et al.* (1997) found that despite the Iberian lynx were able to patrol their small ranges (20–25 km²), they could not keep them exclusive intrasexually, possibly due to shortage of optimal habitat.

As available data on DMD's and SLD's in felids show relatively constant movement rate, we suggest that patrolling the territory and deterring intruders may become difficult if the home range increases above some threshold. In such a case, the overlap among home ranges of resident individuals should increase, too. This indeed was found in Białowieża Forest (Jędrzejewski *et al.* 1996; Schmidt *et al.* 1997). However, we are aware that, because of high inter- and intraspecific variation in size and overlap of felid home ranges, this explanation is not sufficient to fully understand their spatial organisation. Nonetheless, it seems that the mechanisms of land tenure system in felids are basically the same. A key factor responsible for home range size appears to be availability of food (Macdonald 1983). If home range increases with decreasing prey population, the frequency of owner's visiting and scent-marking of the whole range cannot remain regular. Then, land tenure system should become less tight, and individuals maintain residence in the range, utilising the overlapping area at different times.

The tendency to maintain some control over the territory was evident in a comparison of movement pattern (SLD/DMD ratio) in male and female lynx. Males moved faster and their routes were more linear than those of females, which suggests that they tended to cover as much area as possible, presumably to mark their presence. Females with kittens moved in a more concentrated fashion as they were more focused on kittens' needs. It is remarkable that these patterns were maintained year round in both sexes. 'Directional' movements by males outside the mating season suggest that this was a typical behaviour of male lynx to patrol as many places in their ranges as possible year round.

During the mating season males additionally increased their chances of meeting females by moving faster, covering longer routes, holding wider ranges, and being active longer during the day (Schmidt 1999).

The seasonal variation in female movements reflected their reproductive status. During May–August, when kittens were born and were least mobile (Schmidt 1998), females moved the longest distances and used their home ranges most intensively despite a drastic reduction of their home range size, during two months after parturition (Schmidt *et al.* 1997). Such movement patterns in females resulted from their short but frequent travels undertaken in search for food while kittens stayed in a lair. Those changes in female behaviour in May–August were also reflected by their increased daily activity which prolonged into daylight hours at that time of year (Schmidt 1999). Interestingly, despite the fact that female's home ranges increased with kittens' age (Schmidt *et al.* 1997), female lynx continued to move in a similar manner, staying close to locations of the former day. This was possible, because females always stayed with kittens at the kill site (Schmidt 1998) and they were efficient enough to kill prey at very short time intervals and distances (Okarma *et al.* 1997).

The results of the analysis of the lynx movements in relation to prey indicate that the main hunting strategy of the lynx was active searching for and presumably stalking prey. It is also possible that they killed prey at occasional encounters, as was found in the African lion *Panthera leo* (Elliott *et al.* 1977) and the Eurasian lynx in Sweden (Pedersen *et al.* 1999). Lynx locomotory activity in BPF was divided into short (1–2 hours) bouts interspersed with stationary periods (Schmidt 1999), during which they could ambush prey as well, but it was not possible to determine what was the actual cause of inactivity. On the other hand, the ambush seemed unlikely as this strategy may be efficient mainly in places with high probability of encountering prey (e.g., at waterholes in dry tropical climate; Bailey 1993) or in cases of extremely high densities of prey (Nellis & Keith 1968). Although ambush may be used by most felids (Kruuk 1986), active searching for prey seems the most effective hunting strategy for felids

living in environments with low visibility and scattered distribution of prey. Mountain lions, for instance, must seek a set of conditions for successful attack (Hornocker 1970). Furthermore, Beier *et al.* (1995) distinguished short and long travel bouts in mountain lions and speculated that they included stalking and moving to the next hunting site, respectively.

The movements of lynx between consecutive kills varied greatly in terms of direct distances and hunting routes. This variation indicated distinct life strategies in male and female lynx which was earlier shown by the differences in seasonal changes in their home range sizes (Schmidt *et al.* 1997) and daily activity patterns (Schmidt 1999). Males focused not only on providing food for themselves, but also on maintaining access to as many areas of their territories as possible. Therefore, males usually made a new kill relatively far from the previous one and covered much longer routes than the straight-line distances between kills. Females rearing kittens, attempted to secure enough food for their families. Thus, not only direct distances between kills were short, but also routes of females' movements during hunting were not much longer.

Yet another problem related to predator's hunting routes is the necessity to deal with adaptations of prey to avoid predation. Visiting the same parts of territory too often may diminish hunting success regardless of local density of prey. It was evidenced experimentally that small rodents reacted to carnivore odours by changes in behaviour and spatial distribution (e.g., Gorman 1984, Jędrzejewski *et al.* 1993b, Borowski 1998). Some behavioural response to predator odour was shown in ungulates, too (e.g., Müller-Schwarze 1972: black-tailed deer, *Odocoileus hemionus*), but it is even more difficult to record it in the field. Breitenmoser and Haller (1993) suggested that roe deer and chamois, *Rupicapra rupicapra*, exposed to predation of reintroduced lynx after a long time of a large predator absence redeveloped an anti-predator behaviour and became more alert. In effect, their vulnerability to predation decreased (behavioural depression of prey availability *sensu* Charnov *et al.* 1976) and the distance covered by lynx to make a new kill increased as the time after

reintroduction progressed. In our study area, the roe deer coexists with lynx almost uninterruptedly for ages (Jędrzejewski *et al.* 1996). Thus, we were not able to directly document if the behavioural depression of prey had discernible effect on lynx movements in their natural population. Nonetheless, the pattern of home range use by lynx conformed to the predictions of prey depression hypothesis. We found that lynx tended to visit various parts of their territories on consecutive days as their succeeding daily ranges overlapped only by 30%.

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