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Variation in daily activity of the free-living Eurasian lynx (*Lynx lynx*) in Białowieża Primeval Forest, Poland

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Abstract

The pattern of daily activity of the Eurasian lynx *Lynx lynx* L. was studied by radio-telemetry in the Białowieża Primeval Forest (eastern Poland). Radio-tracking of 18 lynx was done by 24-h continuous observations and by sampling on a daily basis. Lynx were active mostly at night. There was generally one peak of activity between 15:00 and 07:00 which, however, decreased slightly between 20:00 and 22:00. On average, lynx were moving for 6.5 h/day. In males, 73% of locomotory activity occurred at night, whereas females were active as long during the daylight as during the night. Movement bouts of females were shorter than those of males (1.1 h *vs* 2.1 h) but more frequent (4.2 *vs* 3.0 bouts/day). General patterns of activity of females with and without kittens were similar. However, females with kittens were active twice as long per day than non-reproducing females. In May–August (intensive care for kittens), reproducing females were active 26% longer than in September–April. Non-reproducing females showed the opposite pattern; they were active 60% less in May–August compared with September–April. Locomotory activity of adult males was 30–70% longer in January–March (mating season) than in other seasons. The pattern of lynx activity was shaped predominantly by searching for and consuming large prey. The lynx were active for the longest time during the days when they searched for prey but made no kill (12.5 h/day on average) and for the shortest time on the first day after killing a deer (1.6 h/day). Their moving activity increased steadily in the following days, reaching 6.8 h/day on the fourth day of consuming a killed deer. Ambient temperatures and rainfall did not significantly affect lynx activity, but there was little movement most of the time in heavy rain, and all day when the temperature was above 30 °C.

Key words: activity, breeding season, feeding ecology, lynx, *Lynx lynx*, mating season

INTRODUCTION

Animal activity patterns are affected by various environmental and intrinsic factors (Aschoff, 1964). The circadian rhythms of animal activity are persistent features of many species (Cloudsley-Thompson, 1961). According to Curio (1976) activity rhythms of predators follow those of their main prey, and this relationship has been shown in various species, e.g. black-backed jackal *Canis mesomelas* (Ferguson, Galpin & De Vet, 1988) and mountain lion *Puma concolor* (Beier, Choate & Barrett, 1995). However, other factors may also influence both the rhythm and the duration of predator activity. In the temperate zone, the Eurasian lynx *Lynx lynx* hunts large mammals, mainly roe deer *Capreolus capreolus* (Jędrzejewski, Schmidt *et al*., 1993; Okarma *et al*., 1997). Since a large kill provides a predator with enough food for several days (Okarma *et al*., 1997), the need to move (and, in consequence, to hunt) may stop while the prey is eaten.

Lynx exhibit great seasonal and sex-related variation in the size of their territories (Schmidt, Jędrzejewski & Okarma, 1997), and the causes of seasonal variation in territory size are different in male and female lynx. Females respond more to constraints of breeding and rearing of kittens, whereas males are more affected by mating. Supposedly, also diel activity of lynx varies with sex and reproductive status.

Activity rhythms of the Eurasian lynx have not yet been thoroughly investigated. So far, the general characteristics of lynx activity has been provided by Berg, Sommerlatte & Festetics (1978). More detailed studies were done by Bernhart (1990) and Reinhardt & Halle (1999), but, although these reports were based on radio-telemetry, their material was very limited. Moreover, the subjects of these studies were lynx in a reintroduced population. Another study concerning lynx activity was conducted in a zoo by Chubykina & Shilo (1981).

My study, based on radio-telemetry, was carried out in 1991–1996 in the large woodland of Białowieża

Primeval Forest (BPF), the best preserved forest of Europe's lowlands. The lynx population of BPF has been protected since 1989 and coexists with rich communities of potential prey as well as other carnivores (Jędrzejewski, Jędrzejewska *et al.*, 1996). The aims of this paper were to: (1) describe the pattern of the daily activity of Eurasian lynx under natural conditions, (2) show the sexual, age and seasonal variation in lynx activity, (3) find out the factors affecting both the pattern and the duration of lynx activity.

STUDY AREA

BPF is a woodland (1250 km^2) containing large fragments of deciduous and mixed forests of natural character (Faliński, 1986). The forest is located on the Polish–Belarussian borderland. The Polish part (52°30′–53°N, 23°30′–24°15′E, 580 km^2) includes Białowieża National Park (BNP, 47 km^2, a strict reserve since 1921), and the commercial, exploited forest. Timber and wildlife have been harvested in the commercial part of BPF but not in the National Park. Białowieża Primeval Forest is a fairly continuous woodland, with only a few glades with villages and meadows (total area of glades does not exceed 5% of BPF).

The terrain of BPF is flat, on average 165 m a.s.l. The climate is transitional between continental and Atlantic types with clearly marked cold and warm seasons (Olszewski, 1986). The mean January and July temperatures during the study period were $-2.4\,^{\circ}$C and $20.1\,^{\circ}$C, respectively. The minimum recorded temperature was $-29.6\,^{\circ}$C, and the maximum was $34.6\,^{\circ}$C. Mean annual precipitation amounted to 571 mm. In the winters, snow cover persisted from 27 to 152 days. The length of the light and dark period of the day vary greatly between summer and winter. The minimum (summer) and maximum (winter) duration of the night (time from sunset to sunrise) is 7 h 15 min and 16 h 18 min, respectively.

The most important prey species available to lynx are *C. capreolus*, red deer *Cervus elaphus* and brown hare *Lepus europaeus*. However, hares play a minor role in lynx diet (Jędrzejewski, Schmidt *et al.*, 1993). Lynx have not been hunted in the Polish part of BPF since 1989 but they have been killed in small numbers in the Belarussian part. The main mortality factor of lynx in the Polish part was poaching with snares (Jędrzejewski, Jędrzejewska *et al.*, 1996).

MATERIAL AND METHODS

In 1991–1996, a total of 18 lynx were captured and fitted with radio-collars during the long-term research programme on lynx ecology in BPF (Jędrzejewski, Jędrzejewska *et al.*, 1996; Okarma *et al.*, 1997; Schmidt *et al.*, 1997). Six were adult males, 5 adult females, 2 sub-adult males, 1 sub-adult female and 4 kittens (captured when 7–9 months old). Sixteen lynx yielded enough data to analyse their activity periods; data from 2 individuals (an adult and a juvenile male) were not used because of small samples.

The capturing and tranquillizing methods are described by Schmidt *et al.* (1997). The radio-collared lynx were located from the ground by triangulation (Mech, 1983), using the net of forest roads and the grid of forest compartments of 1066 × 1066 m. The compartments were divided into 4 quarters, so the locations were confined to one of them. The data on lynx activity were collected by both sampling on a daily basis (single records of activity at various times of day or night) and 24-h sessions of continuous radio-tracking of a given lynx conducted for 1–5 days. A total of 7158 radio-locations was collected and 81 24-h sessions of continuous radio-tracking were carried out. During continuous radio-tracking, locations were taken at 30 min intervals.

Activity of lynx was determined by three methods.

(1) When location of a lynx was recorded, the signal was listened to for at least 2 min. Then it was checked a few times until the next record. If the signal strength varied, it indicated that the transmitter on the lynx changed its position in relation to the receiving antenna. This showed any activity of the lynx other than sleeping (movement, feeding, play, scratching, etc.).

(2) Nine transmitters were equipped with 3-dimensional activity sensors that distinguished activity from sleep. The sensors were activated with no time lag. This index of activity included the stationary as well as moving activity of an animal. Moreover, particular transmitters varied somewhat in the threshold of activation.

(3) The movement of a lynx was recognized by the change of location from 1 record to another and it was detected when there was a definite change in position from one quarter of a forest compartment (533 × 533 m) to another. This was the main index of lynx activity used in all analyses in this paper.

Seasonal changes in lynx activity were analysed in different periods for males and females. In males, the mating period (January–March) was distinguished from the rest of the year (April–December). The activity of females with and without kittens was compared in two periods: May–August, when kittens are born and their mobility is very limited, and September–April when kittens are able to follow their mothers during a hunt (Schmidt, 1998). The records were pooled into 2-h periods for analysis of general activity rhythms and into 3-h periods for seasonal analysis. Minimum number of locations per time unit was 20.

Total duration of activity per day was calculated by two methods: (1) percentage of active records in relation to all radio-locations in 2-h periods were summed and recalculated for 24 h, and (2) by summing the duration of activity bouts as recorded by continuous radio-tracking. The bouts of activity were determined when the lynx changed its position between consecutive locations taken every 30 min, thus the minimum recorded bout could have lasted 30 min. Also, duration of activity was calculated separately for days when lynx were

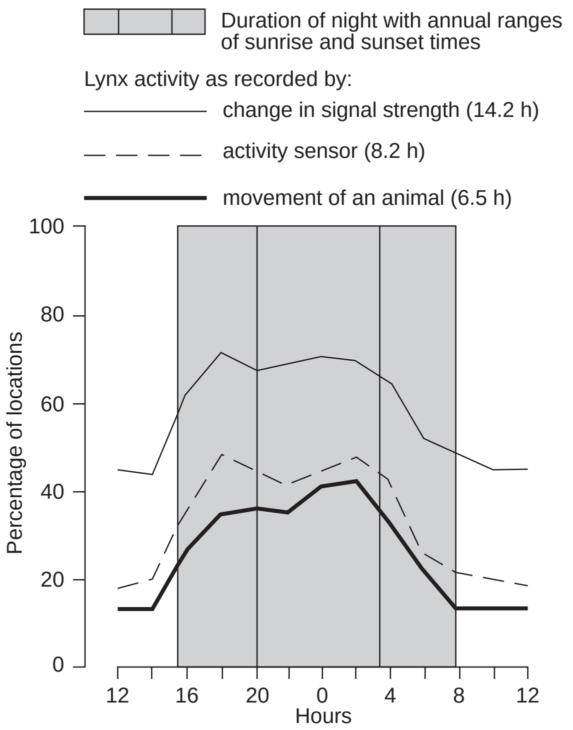

Fig. 1. Patterns of activity of the Eurasian lynx in Białowieża Primeval Forest as recorded by three methods (see text for explanations). Data for 16 lynx are pooled and shown in 2-h periods. Total time of daily activity (h/day) is given in parentheses.

consuming large prey (9 roe deer, 4 red deer, 2 brown hares, 1 domestic dog) and for days when they made no kill. The days when prey was not found were considered to be days with no kills. This was justified because lynx actually killed prey on the following days, after having covered long routes.

RESULTS

Pattern of lynx activity in relation to their sex, age and reproductive status

Data pooled for all individuals showed that lynx were active mostly during the night (Fig. 1). The three methods of recording activity yielded the same circadian rhythm (replicated goodness of fit test, $G=$ from 2.3 to 13.9 in pairwise comparisons, d.f. = 11, $P>0.1$). Percentage of active locations increased after 15:00 (the earliest sunset in winter was at 15:25) and dropped after 07:00 (the latest sunrise in winter was 07:45). In general, there was only one peak of activity. However, the proportion of active locations slightly decreased between 20:00 and 22:00. The duration of lynx daily activity calculated by the three methods varied and it made up from 27% (movements) to 59% (changes in the signal strength) of the day, respectively (Fig. 1).

There were some pronounced differences in the circadian rhythm and duration of lynx activity related to their sex, age, and reproductive status. Henceforth, only actual movements are considered as 'activity'. Adult males showed a typical night activity. During the day (06:00–15:00) movement was recorded in 8–19% of locations only. Between 15:00 and 08:00, up to 47% of male locations recorded movements (Fig. 2). Total time of moving was 6.8 h/day. The 24-h radio-tracking revealed that up to 73% of the time when males were moving occurred at night (Table 1). Although there was no difference in the number of movement bouts between night and day, movement bouts during the night lasted significantly longer than those undertaken during the day ($U=2117$, $P<0.001$, Mann–Whitney *U*-test).

Nocturnal activity was much less pronounced in adult females with kittens than in males (Fig. 2; $G=26.9$, d.f. = 11, $P<0.005$). The locations when females moved were more evenly distributed during day and night (Fig. 2). Females were more active than males between 07:00 and 15:00, but the only significant difference was at 11:00–12:00 ($G=5.8$, d.f. = 1, $P<0.03$). During the night females were slightly less active than males, although there were no statistical differences in particular hours. Also, 24-h sessions of radio-tracking showed that about half of females' daily activity occurred during daylight (Table 1). However, most of the data collected during continuous radio-tracking of females came from summer.

The total duration of females' moving activity was 7 h/day (Fig. 2). Females with kittens that were radio-tracked during 24-h-sessions moved, on average, 4.2 times/day and each time they spent, on average, 1.1 h moving. There were no differences in the number (Student's *t*-test, $t=0.06$, $P=0.95$) and duration ($U=1406$, $P=0.1$) of females' movement bouts as well as the total time spent moving ($t=3.5$, $P>0.5$) between night and daylight (Table 1). Generally, there was no significant variation in the duration of an average single bout among different lynx (Kruskal–Wallis one-way analysis of variance, $H=4.3$, d.f. = 3, $P=0.2$). However, activity bouts at night were shorter in females than in males ($U=1644$, $P<0.005$). The number of bouts per day varied among lynx sex/age classes (Kruskal–Wallis one-way analysis of variance, $H=7.8$, d.f. = 3, $P<0.05$). It was higher in females with kittens than in males ($U=217$, $P<0.05$) (Table 1).

Non-breeding females did not show strong nocturnal activity either (Fig. 2). However, there was a conspicuous decrease in their movements around 14:00 as well as between 06:00–08:00. Their activity increased again between 10:00–12:00. This pattern was significantly different than that of females with kittens ($G=22.2$, d.f. = 11, $P<0.03$). In one female without kittens who was followed during 9 sessions of 24-h radio-tracking the number and duration of movement bouts were similar during the night *vs* daylight (Table 1). There were no statistical differences in these parameters between females with and without kittens, either.

Sub-adult males showed similar patterns of activity to adult males ($G=12.4$, d.f. = 11, $P>0.1$), but they exhibited an increase of activity at noon, which was not

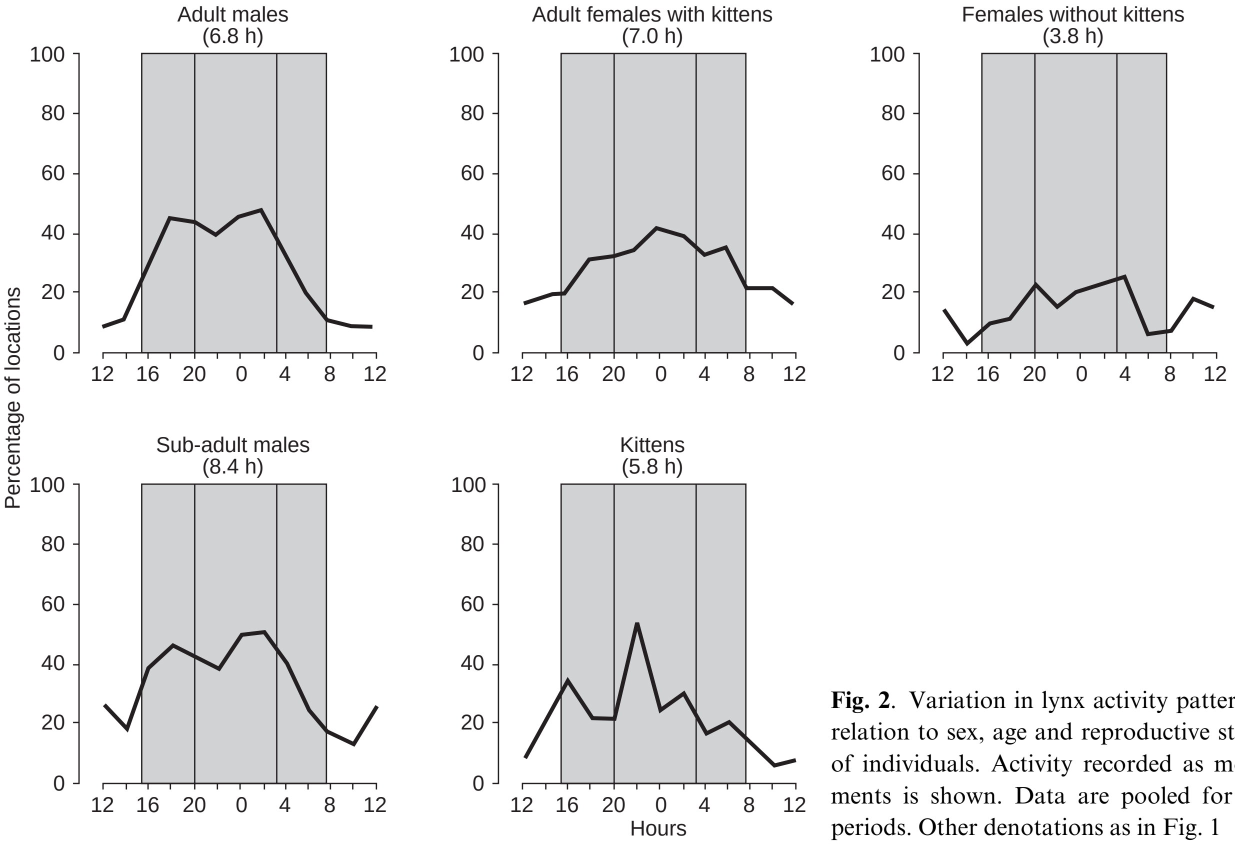

Fig. 2. Variation in lynx activity pattern in relation to sex, age and reproductive status of individuals. Activity recorded as movements is shown. Data are pooled for 2-h periods. Other denotations as in Fig. 1

Table 1. Duration and number of moving activity bouts (mean ± SD) in Eurasian lynx as recorded by 24-h sessions of radio-tracking (77 sessions including 31 for adult males: 14 in May–August, 17 in September–March; 21 for females with young: 16 in June–August, 5 in September–February; 9 for non-breeding females: all in April–May, and 16 for subadult males: 8 in May–July, 8 in September–October). The sample for kittens was too small to count. Variation among sex/age lynx groups were calculated with Kruskal–Wallis one-way analysis of variance (see text) and Mann–Whitney *U*-test for pairwise comparisons. *n* = number of individuals

Activity parameter	Adults males ($n = 3$)	Females with young ($n = 3$)	Females without young ($n = 1$)	Sub-adult males ($n = 2$)
Mean number of activity bouts during:				
Whole day	3.0 ± 2.2[a]	4.2 ± 2.0	4.0 ± 3.8	5.2 ± 2.8
Night	1.6 ± 1.2	2.1 ± 1.4	1.7 ± 1.7	2.6 ± 2.2
Day	1.4 ± 1.5	2.1 ± 1.5	2.3 ± 2.7	2.6 ± 2.2
Mean duration of a single bout (h)				
All bouts	1.6 ± 1.6	1.1 ± 1.1	0.9 ± 0.7	1.4 ± 1.4
Night bouts	2.1 ± 1.7[b,c]	1.1 ± 0.8	1.0 ± 0.7	1.3 ± 1.1
Daylight bouts	0.9 ± 0.5[d]	1.1 ± 1.0	0.9 ± 0.6	1.4 ± 1.2
Percentage of night and daylight activity				
Night	73	48	47	49
Daylight	27	52	53	51

[a] Different from females with young and sub-adult males ($P < 0.05$).
[b] Different from females with young ($P < 0.005$), females without young and sub-adult males ($P < 0.05$)
[c] Different from daylight bouts ($P < 0.001$).
[d] Different from sub-adult males ($P < 0.05$).

found in adults ($G = 11$, d.f. = 1, $P < 0.005$) (Fig. 2). Generally, sub-adult males moved more frequently (more bouts per day) than adult males ($U = 134$, $P < 0.01$). During 24-h radio-tracking, sub-adult males were active as long during the night as during the daylight (Table 1).

The activity of kittens was characterized by two peaks: at 16:00–17:00 and 22:00–23:00. From 00:00 till 14:00 they became less active (Fig. 2). This activity rhythm was significantly different from that of their mothers ($G = 30.6$, d.f. = 11, $P < 0.001$)).

There was also some individual variation in the

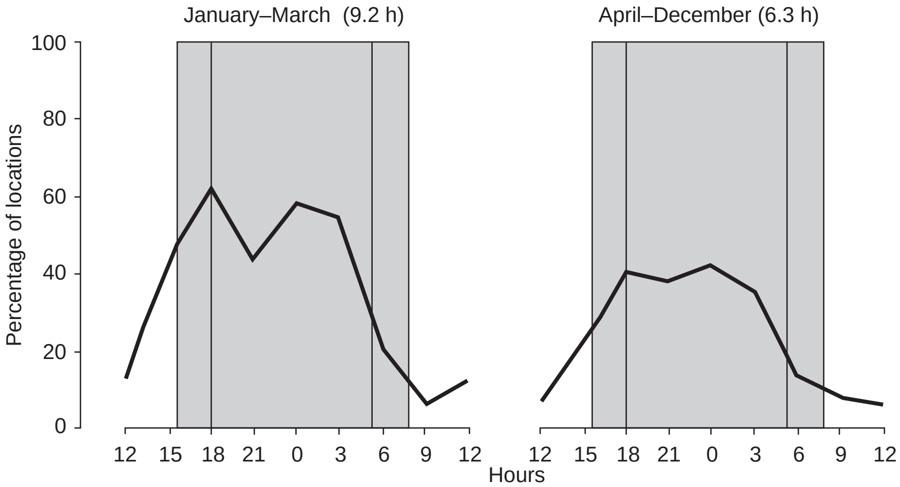

Fig. 3. Seasonal changes in the activity of adult male lynx (*n* = 5). Data are pooled into 3-h periods. Total time of daily activity (h/day) is given in parentheses.

rhythms or levels of activity among various lynx of the same sex, age and reproductive status. In males (both, adult and sub-adult), there was a significant difference in the total time of activity per day (adults: 4.0 and 8.0 h; $G = 81.9$, d.f. = 1, $P < 0.001$, sub-adults: 8.9 and 7.7 h; $G = 5.8$, d.f. = 1, $P < 0.03$). The rhythm of activity in adult females with kittens differed significantly between the two studied individuals ($G = 20.8$, d.f. = 7 $P < 0.005$) as one of them was more nocturnal than the other one. They differed also substantially in the total time of activity (5.6 and 7.6 h; $G = 27.6$, d.f. = 1 $P < 0.001$).

Seasonal changes in lynx activity

In males the rhythm of activity did not change significantly between January–March (mating period) and the rest of the year (April–December) ($G = 4.8$, d.f. = 7, $P > 0.1$) (Fig. 3). There was a slight decrease (not significant) in their activity around 21:00 in January–March. On the other hand, the total time of male activity during the mating period was 30% longer than during other months ($G = 31.0$, d.f. = 1, $P < 0.001$).

Reproducing females showed a significantly different activity rhythm in May–August than in September–April ($G = 14.7$, d.f. = 7, $P < 0.05$, Fig. 4). In May–August they were more active at 18:00–20:00 and 06:00–08:00, compared to September–April. The total time of their activity was 26% longer in May–August when kittens were small, compared to September–April ($G = 10.7$, d.f. = 1, $P < 0.001$, Fig. 4).

Also females without kittens showed great variation in the rhythm of their activity between May–August and September–April ($G = 23.6$, d.f. = 7, $P < 0.005$, Fig. 4). They were active for much shorter time per day in May–August, than in September–April ($G = 24.6$, d.f. = 1, $P < 0.001$, Fig. 4).

Although there was no significant difference in the activity rhythms between females with and without kittens in May–August ($G = 9.4$, d.f. = 7, $P > 0.1$), the total time of activity of reproducing females was over twice as long as that of non-reproducing ones ($G = 120.6$, d.f. = 1, $P < 0.001$, Fig. 4). In September–April, the duration of daily activity in reproducing females remained still longer ($G = 8.0$, d.f. = 1, $P < 0.005$), and the rhythms of activity diverged significantly in the two groups of females ($G = 25.3$, $P < 0.005$) (Fig. 4). There were clear pauses in the activity of non-reproducing females between 15:00–17:00 and 06:00–08:00, whereas in females with kittens the percentage of active locations never dropped below 20%.

Lynx activity in relation to food supply and weather conditions

An essential factor shaping the variation in lynx activity was the process of searching for and consuming an ungulate prey. The 24-h radio-tracking revealed that lynx were active longest during the days when they searched for but apparently made no kill (Fig. 5). During the first day after killing a prey, the duration of lynx activity was minimal (1.6 h/day), but it increased steadily until the fourth day after the kill when it was 4.3 times longer (Fig. 5). The number of activity bouts (NAB: overall and during daylight) also varied on particular days (Kruskal–Wallis one-way analysis of variance, $H = 16.9$, d.f. = 3, $P < 0.001$) and it increased significantly during the third and fourth days (Table 2). Lynx were, however, most frequently active during the days with no kill. Interestingly, NAB was especially high during the daylight on the days with no kill and in the third and fourth days after a kill. There was no significant variation in the total duration of activity bouts (DAB) on days before and after a kill ($H = 2.6$, d.f. = 3, $P = 0.5$). However, the DAB at night during the third and fourth days was significantly longer than that

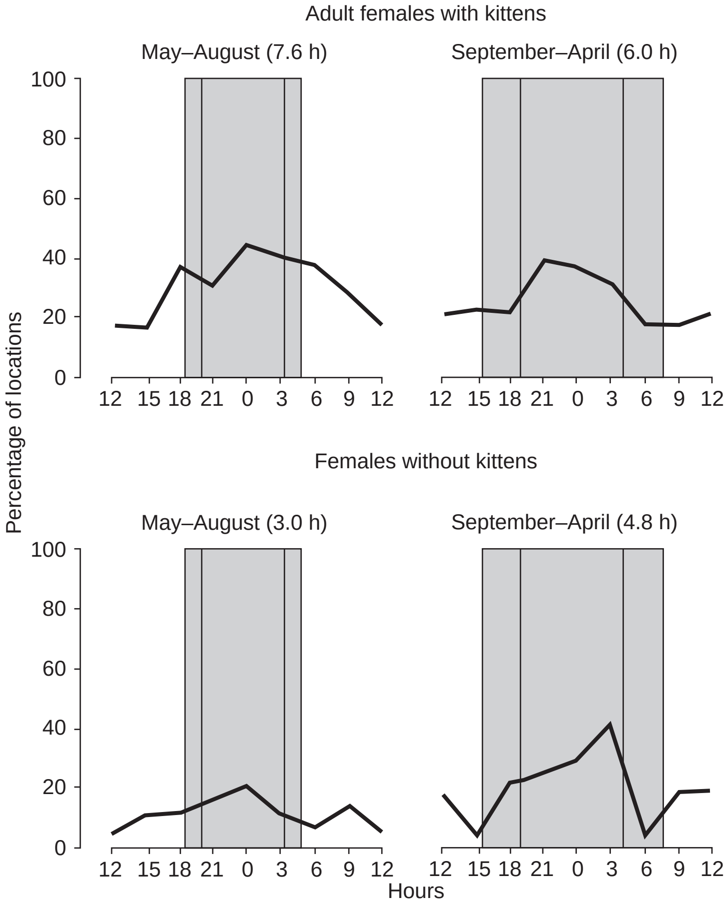

Fig. 4. Seasonal changes in the activity of female lynx with ($n = 3$ females) and without ($n = 3$) kittens. Total time of daily activity (h/day) is given in parentheses.

during the daylight. Generally, in consecutive days after killing a large prey, the number of active bouts increased during daylight and the duration of active bouts increased at night (Table 2).

Sessions of 24-h continuous radio-tracking covered the range of mean daily temperatures from –8.2 to 24.1 °C. There was no correlation between temperature and duration of lynx activity (simple regression analysis, $R^2 = 0.02$, $n = 81$ days, $P = 0.2$). Extremely high and low temperatures were recorded very rarely. On 9 days with temperature above 30 °C, the lynx did not move. During 12 days with the temperatures below −15 °C, they moved in 41% of cases. Rainfall (range from 0 to 24.7 mm/day) did not affect the duration of lynx daily movement either ($R^2 = 0.02$, $n = 81$ days, $P = 0.2$). Lynx were, however, not moving in 76% of the time when there was heavy rain ($n = 86$ h of the rainy periods).

DISCUSSION

The lynx studied appeared to have a generally nocturnal rhythm of activity, which, however, varied markedly with sex and reproductive status of the individuals. All methods used to determine lynx activity showed the same pattern. Longer duration of activity that was estimated by either signal strength or motion sensor rather than by records of actual movements resulted from inclusion of any stationary activity (eating, scratching) into total activity. Thus, movement which was easy to detect, was the major consideration in this analysis. Movement seems the most important indicator of lynx activity as it is often unequivocally related to hunting behaviour (Jędrzejewski, Schmidt *et al.*, 1993).

In vertebrates, the factors governing activity time are predation or availability of food (Cloudsley-Thompson, 1961). In large predators, risk of being predated upon is usually negligible, and their coexistence with other species of predators should be considered in terms of competition rather than predation (Seidensticker, 1976; Sunquist, 1981). In the Białowieża Forest, lynx co-exist with wolves *Canis lupus*, and preliminary data indicate that the period of prevailing locomotory activity of wolves is at night (W. Jędrzejewski and co-workers, pers. comm.). Therefore, the lynx's rhythm of activity cannot be a consequence of avoiding competition with the wolf.

There is much evidence that predators adjust their circadian rhythm of activity to that of their main prey (Curio, 1976; Ferguson, Galpin & De Vet, 1988). The activity rhythm of roe deer, the main prey of lynx in

Table 2. Changes of lynx activity bouts (h: mean ± SD) between the days with no kill and consecutive days since killing a large prey. Variation among activity bouts on particular days was calculated with Kruskal–Wallis one-way analysis of variance (see text) and Mann–Whitney *U*-test for pairwise comparisons. n = number of 24-h sessions of continuous radio-tracking. NAB = number of activity bouts. DAB = duration of activity bouts

	Consecutive days after killing prey			
Activity parameter	No prey $n = 5$	Day 1 $n = 15$	Day 2 $n = 11$	Day 3 and 4 $n = 9$
NAB	8.2 ± 2.2^{a}	1.5 ± 1.4^{b}	1.9 ± 1.6	3.4 ± 2.0
NAB at night	2.3 ± 1.0^{a}	0.5 ± 0.7	0.7 ± 0.7	1.0 ± 0.7
NAB during daylight	5.9 ± 2.2^{a}	0.9 ± 0.9^{b}	1.3 ± 1.4	2.5 ± 1.6
DAB	1.5 ± 1.5	1.1 ± 1.1	1.8 ± 2.3	1.6 ± 1.9
DAB at night	1.6 ± 1.0	1.5 ± 1.6	2.4 ± 2.5	2.8 ± 2.5^{c}
DAB during daylight	1.4 ± 1.2	0.8 ± 0.6	1.4 ± 1.8	0.9 ± 0.7

[a] Different from 1, 2, and 3–4 days ($P < 0.01$).

[b] Different from day 3 and 4 ($P < 0.03$).

[c] Different from DAB during daylight ($P < 0.005$).

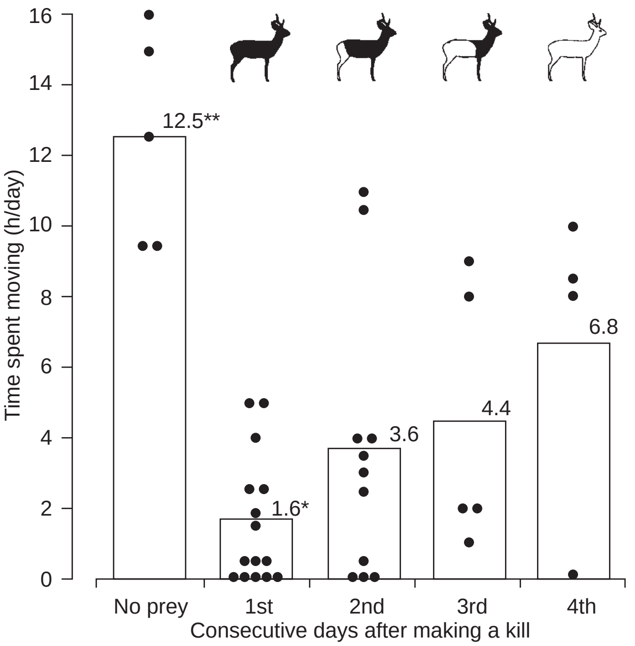

Fig. 5. Duration of lynx daily activity on days spent searching for prey and on consecutive days since the kill of a large prey. Bars and numbers show mean values. Each point denotes one day (24 h). Roe deer silhouettes symbolize amount of prey left uneaten. Differences were calculated with Mann–Whitney *U*-test. ** Days with no prey differ from all other days after kill ($P < 0.01$). * First day after making a kill differed from days 3 and 4, pooled because of small samples ($P < 0.03$).

BPF (Jędrzejewski, Schmidt *et al.*, 1993; Okarma *et al.*, 1997), has not been studied in Białowieża. Roe deer studied in Sweden showed irregular patterns of activity, with males in spring and summer exhibiting peaks around sunrise and sunset (Cederlund, 1981). The synchronization of predator and prey activity would occur more closely in species that rely on small or medium-sized prey which rest hidden in burrows, because such prey are detectable only when active outside their dens. In roe deer, one may expect that they would be even less vulnerable to predation when active, as they would then be more alert. In the Białowieża Forest, snow-tracking revealed lynx's successful attacks on both feeding or lying roe deer (Jędrzejewski, Schmidt *et al.*, 1993). Thus, it is not the pattern of prey activity but the conditions that increase its vulnerability that affect the time when the lynx hunts. For example, the African lions *Panthera leo* may be active at night in the plains with little cover to stalk the prey and may be diurnal in the woodlands during the dry season when the prey gathers along the rivers (Schaller, 1972).

Finally, human activity in the forest might have also affected lynx activity, as evidenced by two females with kittens. One of them, with activity distributed fairly evenly during the 24 h, moved mainly in the strictly protected part of the BPF (i.e. in the Białowieża National Park) and along the state border, which is rarely visited by people. The other female, whose movements were more nocturnal, occupied the area in the part of the forest used for logging. Human disturbance has been reported as a factor affecting the rhythm of activity in black bears *Ursus americanus* (Larivière, Huot & Samson, 1994) and red foxes *Vulpes vulpes* (Weber, Meia & Aubry, 1994).

Nocturnal activity was less conspicuous in females than in males. It was especially evident during the early period of rearing kittens. Females that have to secure food for kittens must extend their hunting into the daytime. A female Eurasian lynx radio-tracked by Reinhardt & Halle (1999) was also active as long during the daylight as during the night. Similarly, Wassmer, Guenther & Layne (1988) found that, in summer, female bobcats were more active than males during the daylight hours.

Interestingly, the overall time of activity per day in female lynx was not longer than in males. Males hold territories twice as big as females (Schmidt *et al.*, 1997). Thus, they have to allocate proportionally more time to patrolling their large territories and less time to hunting. Indeed, they were killing on average 1.5 times fewer deer per time unit than females with kittens (Okarma *et al.*, 1997). Similarly, male mountain lions that occupied home ranges twice as large as females were travelling longer daily distances than females (Beier *et al.*, 1995).

Longer duration of activity of male lynx in January–March, i.e. during the mating season, coincides with the fact that males roamed more widely from December till March, covering up to 1.9 times larger areas than during autumn (Schmidt *et al.*, 1997). Also Bernhart (1990) recorded that the activity level of an adult male lynx from a Swiss reintroduced population increased in March. Higher movement rate was found also in the Iberian lynx during winter (Beltran, 1988). It was, however, suggested to be a result of decreasing availability of rabbits rather than the ongoing mating season. In contrast, there was a characteristic lack of seasonal variation in the movements of mountain lions in the California population that did not exhibit a determined mating season (Beier *et al.*, 1995).

In females with kittens, the size of territory increased from May to autumn (Schmidt *et al.*, 1997) but it was not followed by an increase in duration of their activity (contrary to the reintroduced female lynx: Bernhart, 1990; Reinhardt & Halle, 1999). In fact, these females were active longest in May–August, when their territories were smallest. As females with no kittens showed exceptionally low activity at that time, it seems that the reproductive status of females determined the levels of their activity. Female black bears with cubs also showed generally higher activity levels, than adult females without cubs (Garshelis & Pelton, 1980). Very long duration of locomotory activity in the reproducing female lynx in May–August was apparently related to their care for young and frequent travels between the den and the prey (Schmidt, 1998). It was also clearly reflected in the high number and short duration of their activity bouts. The difference in duration of activity between females with and without kittens decreased in September–April, when the area covered by the lynx family was largest (Schmidt *et al.*, 1997). The kittens accompanied their mothers so that the females did not need to move frequently between the den and a distant prey. On the other hand, the activity bouts might remain short as females were killing prey at much shorter time intervals and within closer distances than the males (Okarma *et al.*, 1997), and they spent much time near the prey with their kittens. The travel bouts in female mountain lions were also shorter and more frequent than in males (Beier *et al.*, 1995).

The amount of time a lynx spent moving was most dependent on whether or not it had a prey and how much of it was already consumed. The general behaviour of lynx was to feed on a large carcass until it was finished and then to leave it and search for another one (Okarma *et al.*, 1997). This pattern, however, changed sometimes when lynx were killing and feeding on two carcasses at a time. The decrease in lynx activity after killing prey has been shown also for reintroduced individuals by Bernhart (1990) and Reinhardt & Halle (1999). In my study, however, it was evidenced that the duration of the lynx's locomotory activity increased in the days following the kill. This suggests that the diminishing amount of food evoked stronger hunting behaviour. The mountain lions studied by Beier *et al.* (1995), on the other hand, showed very little movement during the time when they were feeding on a previously killed large mammal. In contrast to the lynx, the hunting behaviour of the mountain lions was suspended after they made a kill until the carcass was totally consumed. This feast-or-famine pattern of behaviour (Curio, 1976) is apparently not fully represented in the lynx.

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