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Annual and circadian activity patterns of badgers (*Meles meles*) in Białowieża Primeval Forest (eastern Poland) compared with other Palaearctic populations

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Abstract

Aim The annual and circadian rhythms and duration of activity of Eurasian badger *Meles meles* (Linnaeus 1758) were studied in a low-density population inhabiting the primeval woodland in the European temperate zone. Results were compared with available data from the literature on seasonal changes in body mass and winter inactivity of badgers from across the Palaearctic region.

Location Field work was carried out in Białowieża Primeval Forest, eastern Poland. Biogeographical variation was reviewed based on twenty-three localities in the Palaearctic region (from Western Europe to Central Siberia).

Methods Thirteen badgers were radio-collared in 1997–2001. Their circadian activity was sampled by 24-h sessions of continuous radio-tracking with location taken at 15-min intervals. Annual activity was studied by radio-tracking and inspections of setts. Earthworm (badgers' main food) biomass was estimated in four types of habitats throughout the year.

Results Badgers were nocturnal with one long bout of activity. Their rhythms of diel activity differed between spring and autumn, and between adult and subadult individuals. On average, badgers emerged from setts at 19:00 hours and returned to them at 03:42 hours. The highest level of activity was recorded between 20:00 and 03:00 hours. Duration of daily activity was, on average, 8.2 h day^{-1}, but varied significantly between seasons. The seasonal changes were inversely related to the abundance of earthworms. Duration of activity also depended on daily temperature, especially in the cold season. In winter, badgers stayed inactive for an average of 96 days per year. In autumn, they built fat reserves and their body mass nearly doubled compared with the spring values. The literature review on annual cycle of activity and body mass changes in Eurasian badgers showed that fat storage and duration of winter sleep strongly depended on climate (best approximated by January mean temperature). In regions with warm climates, badgers were active year round and their body mass changed only slightly, while in regions with severe winters badgers increased their body mass twofold from spring to autumn, and stayed inactive for as long as 6 months per year.

Main conclusion We propose that, in the temperate and boreal zones of the Palaearctic region, the ultimate determinant of biogeographical variation in badgers' annual activity is the winter shortage of earthworms, which are the main component of badger diet.

Keywords Activity rhythm, biogeographical variation, body mass change, earthworm abundance, Eurasian badger, winter sleep, intraspecific variation.

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INTRODUCTION

In its wide geographical distribution ranging from Spain to Norway and from the Atlantic coast to Japan (Neal, 1986), the Eurasian badger *Meles meles* (Linnaeus 1758) is adapted to various climates, habitats and feeding conditions. At latitudes with severe winters, badgers build fat reserves in autumn and sleep in winter (Bevanger *et al.*, 1996; Gorshkov, 1997). In southern regions, they are active year round and do not undergo strong seasonal change of body mass (Revilla *et al.*, 1999) and, in contrast to highly variable annual patterns of badger activity in the north, their circadian activity rhythms are more stable. Badgers were always reported as nocturnal, foraging at night and spending daylight hours hidden in their setts (Harris, 1982; Neal & Cheeseman, 1996; Rodriguez *et al.*, 1996). Among factors affecting badger activity, weather conditions and food supply are considered to be the main ones (Neal, 1986; Cresswell & Harris, 1988a). However, factors influencing variation in badger activity have rarely been studied, and most research has been conducted in human-influenced habitats or in captivity (Harris, 1982; Maurel & Boissin, 1983; Cresswell & Harris, 1988b; Fowler & Racey, 1988).

Our study was carried out on radio-collared badgers inhabiting the large woodland of Białowieża Primeval Forest (BPF) in Poland, the best preserved forest in lowland Europe. The badger population in the study area was characterized by low density (0.21 ind km^{-2}), large sizes of group territories (on average 12.8 km^2) and small sizes of social groups (mean: 2.4 adults and 1.5 juveniles) (Kowalczyk *et al.*, 2000; Kowalczyk, 2001). The aims of this work were to: (1) describe the annual and circadian rhythms of badger activity, (2) analyse the duration of daily activity, (3) determine the factors affecting annual and daily activity of badgers and (4) review the data on annual patterns of badger activity and body mass changes in the Palaearctic region.

STUDY AREA

The study area was located on the Polish–Belarusian borderland, in BPF, which is one of the best preserved temperate lowland forests in Europe. The Polish part of the Forest (52°30′–53° N, 23°30′–24°15′ E) covers 595 km^2 and includes Białowieża National Park (BNP) (105 km^2) and the exploited forests. It is fairly continuous woodland with only a few glades with villages and meadows (total area of open habitats is 6% of BPF). The tree stands are composed of spruce (*Picea abies*), pine (*Pinus silvestris*), oak (*Quercus robur*), hornbeam (*Carpinus betulus*), alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and birches (*Betula* spp.), with admixtures of other tree species (Kwiatkowski, 1994; Jędrzejewska & Jędrzejewski, 1998). The study was conducted in the central part of the forest in an area of 130 km^2.

The climate of BPF is transitional between Atlantic and continental types with clearly marked cold and warm seasons. The mean annual temperature in 1997–2001 was 7.9° C. The mean daily temperatures varied from −22.1 to 28.8° C. The coldest month was January (mean daily temperature −2.3° C) and the warmest was July (19.3° C). Number of days per year below 0° C varied from 50 to 104, on average 79. Snow cover persisted for an average of 80 days per year (range 60–96) with maximal recorded depth of 23 cm. Mean annual precipitation during the study period was 586 mm. Night length varies from 16 h 18 min on 22 December to 7 h 15 min on 21 June. In BPF, badgers coexist with a rich community of other predators and prey species and they feed mainly on earthworms (Jędrzejewska & Jędrzejewski, 1998).

MATERIALS AND METHODS

In 1997–2001, thirteen badgers (seven adult males, three adult females, and three subadults, the latter ones included one male and two females) were radio-tracked. Subadults were > 1–2 years old, adults were > 2 years old. Badgers were captured in foot snare traps (twelve individuals) and a box trap (one individual), immobilized by an intramuscular injection of ketamine hydrochloride, sexed, weighed, aged and fitted with radio-collars (Advanced Telemetry Systems, Isanti, Minnesota, USA; 125 g). All radio-collared badgers were localized from the ground, three to five times per week, during both daytime and night time. Additionally, sixty-four sessions of 24-h continuous radio-tracking (of non-dispersing badgers) were conducted. During these sessions, the position of an animal was recorded every 15 min. In total, 8370 radio-locations were collected. The average time of radio-tracking of a badger was 459 days (range 37–1101). Activity of badgers was recorded during the tracking. An animal was considered as inactive, if it stayed in the sett (range of the signal was 50–70% shorter compared with periods of above ground activity), and when its spatial position did not change or the amplitude of the transmitter pulse stayed unchanged for at least 2 min. If the animal was out of the sett and its spatial position or amplitude of the pulse did change, we recorded that badger as active.

Duration of daily activity was estimated on the basis of 24-h sessions of continuous radio-tracking, as the time from emergence of an animal from a sett to its return to the sett. To avoid any disturbance of badgers, which sometimes occurs during direct surveys, the time of emergence and return of a badger was estimated on the basis of radio-telemetry (locations taken by observers staying 150–200 m away from the sett). Time of emergence from and return to the sett was estimated based not only on 24-h sessions, but also on shorter (4–8 h) sessions of radio-tracking. Circadian rhythms of activity were drawn on the basis of all fixes (all collared individuals pooled) grouped in 1-h periods. Data were analysed in three seasons: spring (1 March–31 May), summer (1 June–31 August) and autumn (1 September–30 November). Circadian activity of badgers was not analysed in winter because badgers were largely inactive during the cold season (see Results).

The number of days badgers were inactive in winter was estimated on the basis of radio-telemetry, or snow- and ground-tracking. The data were collected at five setts during four winters (1997–2001). Data on badger body mass were collected from badgers captured and recaptured during the study (ten individuals) and two other badgers (not radio-collared) killed by cars.

The meteorological data originated from the weather station of BNP, located in the village of Białowieża (about 1 km from BNP). The temperature records were taken at 07:00, 13:00, and 19:00 hours. For calculation of mean daily temperature relevant to badger activity, the records collected at 19:00 and 07:00 hours were taken. In analysis of the time of emergence and return to the sett, we used temperatures recorded at 19:00 and 07:00 hours, respectively.

Earthworm biomass was estimated in 1997-2000 at randomly selected points by standard methods (Nordström & Rundgren, 1972; Brøseth *et al.*, 1997). Soil samples (of volume $20 \times 20 \times 25$ cm, collected in daytime) were taken in four types of habitats: (1) oak-lime-hornbeam forests ($n = 120$), (2) mixed and coniferous forests ($n = 51$), (3) alder and ash-alder wet forests ($n = 31$) and (4) meadows ($n = 49$). Samples were collected in spring ($n = 77$), summer ($n = 120$), autumn ($n = 20$), and in winter ($n = 8$). The samples were hand-sorted and earthworms were identified to species according to the key by Kasprzak (1986). Their biomass was estimated as fresh weight. Of nine species found, three constituted 90% of earthworm number and biomass (*Allobophora caliginosa, Lumbricus rubellus*, and *Dendrobaena octaedra*). Mean body mass of an earthworm was 0.44 g (range 0.01–3.28 g).

To examine the biogeographical pattern of variation in annual activity of Eurasian badgers, we reviewed the data from twenty-three localities in the Palaearctic ranging from 37° to 65°N, and from 7°W to 110°E, for which the data on length of inactivity in the cold season and body mass changes throughout the warm season were available (Appendix 1). The percentage increase in body mass was calculated as percentage difference between the highest and the lowest mean body mass recorded in the annual cycle. The length of cold season inactivity was calculated as the mean number of days per year during which badgers did not emerge at all from their setts. The localities represented various climatic conditions. We chose the mean temperature of the coldest month (January) as a measure of winter severity in various regions (data from World Weather Records 1971–1980, 1987; and World Climate Database, www.worldclimate.com). Data on the duration of winter inactivity by badgers were available for thirteen localities, on body mass increase for fifteen study areas, and on both parameters for six localities. More complex analysis of the circadian activity of badgers across Palaearctic was not possible due to limitation of this kind of data to Western Europe, only.

RESULTS

Rhythm of annual activity and body mass changes of badgers in BPF

From April to October badgers were active on 100% of days (Fig. 1). In November, they decreased their activity to, on average, 47% of days per month. In December and January, badgers were largely inactive (short-time and short-distance emergences were recorded on 2–6% of days). From February they increased their activity again to 42% of days, and by March, badgers were active on 83% of days. In the autumn–winter season, percentage of days with badger activity per month was strongly dependent on mean monthly temperatures ($Y = 38.490 + 10.018X$, $r^2 = 0.55$, $n = 16$, $P = 0.001$). Badgers did not emerge from their setts when monthly temperatures were below −4° C, and were active every day in months with mean temperatures > 5° C. In 1997–2001, the total length of winter inactivity of badgers varied from 79 to 116 days per year, on average 96 (SD = 12, $n = 11$ sett-years), which was equivalent to 26% of the year.

Badger body mass also showed strong seasonal variation (Fig. 2). In spring adult badgers weighed, on average, 10.2 kg (SD = 0.9, $n = 14$) and subadults 8.4 kg (SD = 1.1, $n = 3$). By late summer their body mass increased, and in late autumn adults weighed 19 kg. During winter badgers lost about 9 kg, i.e. 46% of their autumn body mass.

Circadian rhythm of badger activity in BPF

In BPF, badgers were nocturnal with one long bout of activity, not interspersed with any resting periods. From

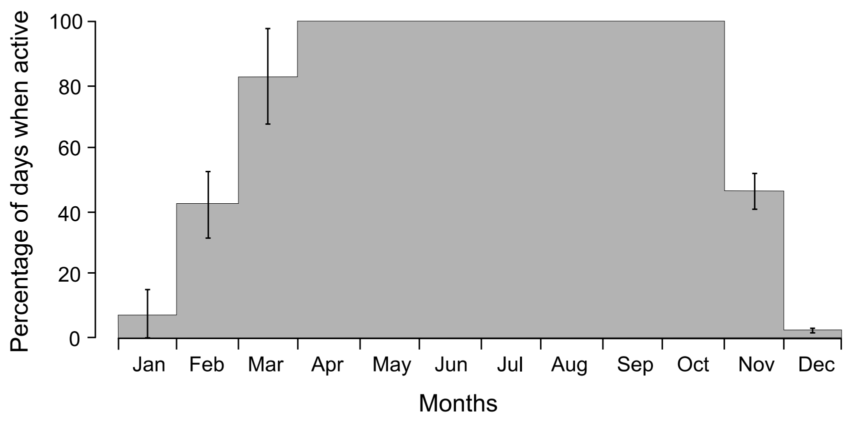

Figure 1 Annual pattern of badger *Meles meles* activity in Białowieża Primeval Forest in 1997–2001. The percentages of days per month with activity were estimated on the basis of radio-tracking of badgers as well as snow- and ground-tracking at the main setts occupied by radio-collared animals. The average values ± SD are given.

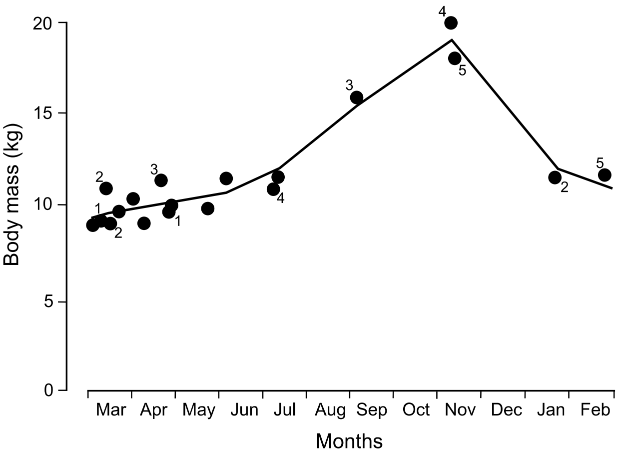

Figure 2 Seasonal changes of body mass in adult badgers from BPF in 1997–2001. Each point denotes one weighing ($n = 19$ measurements collected from twelve badgers: ten captured and recaptured during the study and two other killed by cars). The same numbers (1-1, 2-2 etc.) denote body mass of one individual in different seasons or years.

spring to autumn the highest level of activity (over 80% of active fixes) was recorded between 20:00 and 03:00 h (Fig. 3). The rhythms of activity of all badgers differed between spring and autumn ($G = 26.15$, $P < 0.025$, d.f. = 14, G-test for homogeneity of percentages calculated for hours 17:00–07:00) but not between spring and summer or summer and autumn ($P > 0.1$). Pair-wise comparison of hours showed that in autumn badgers were significantly more active at dawn (04:00–05:00 hours) and dusk (18:00 hours) (Fig. 3).

Activity rhythms of adult males and females did not differ ($P > 0.1$), but both of them were statistically different from that of subadult badgers (adult males – subadults: $G = 35.82$, $P < 0.005$, d.f. = 14; adult females – subadults: $G = 43.82$, $P < 0.001$, d.f. = 14; G-tests calculated for hours 17:00–07:00). Subadults started their activity about 2 h later than adults (Fig. 3).

Average time of badger emergence from a sett was 19:00 hours, and that of return to the sett 03:42 hours, however, some seasonal variation was noticed (Fig. 4). In spring and autumn, badgers started their activity around 1 h after sunset, and finished over 2 h before sunrise, while in summer they emerged almost 1 h before sunset, and returned to sett half an hour after sunrise. Time of emergence did not vary seasonally as much as did the time of return (Fig. 4).

From March to November, badgers were active from 0.5 to 14.7 h per day, on average 8.2 h (Table 1). Differences in duration of activity were significant for seasons, but not for sex/age groups (two-way ANOVA, seasons: $F_{2,59} = 12.278$, $P < 0.0005$; sex/age group: $F_{2,59} = 1.277$, $P > 0.25$). In spring, badgers were active for an average of 6.8 h, increased their activity to 9.4 h in summer, and reduced it again to 7.6 h in autumn. The seasonal changes in duration of

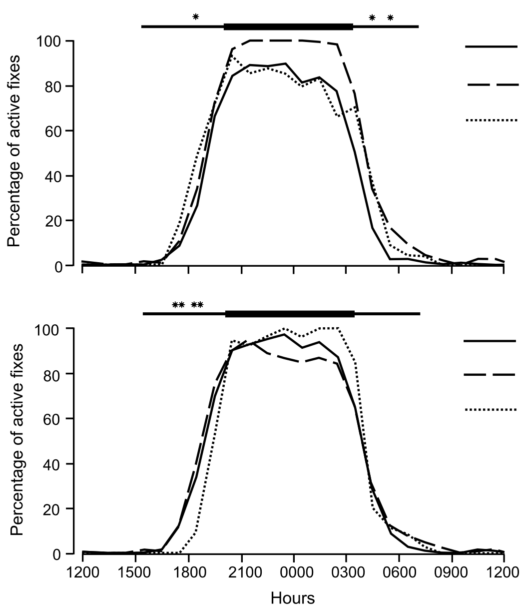

Figure 3 Circadian activity rhythms of badgers radio-tracked in BPF in 1997–2001: seasonal variation (upper panel) and age/sex variation (lower panel). For each 1-h period fixes when badgers were found active, were calculated as percentage of all fixes. Total number of fixes in 1-h periods varied from twenty-two to 266. Black horizontal bars indicate the shortest and the longest time from sunset to sunrise. Asterisks mark hours for which the differences in percentages of fixes were significant (*$P < 0.05$, **$P < 0.001$).

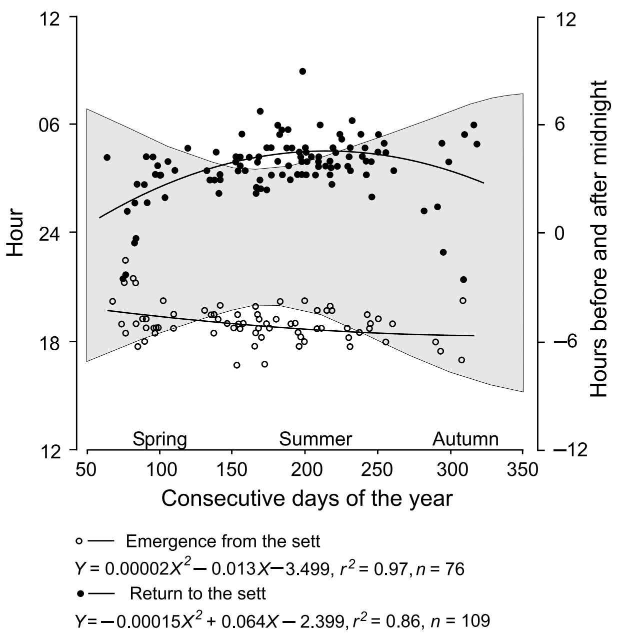

Figure 4 Time of emergence (open circles) and return to the sett (black circles) by radio-tracked badgers, data from 4 to 24-h sessions of continuous radio-tracking, during which fixes were taken in 15-min intervals. Nonlinear (quadratic) lines appeared to be the best fit regression lines; equations show emergence and return time calculated as the number of hours before or after midnight in relation to the consecutive days of the year. Shaded area denotes night length.

Table 1 Mean standing crop of earthworm biomass (kg ha^{-1}) and duration of daily activity (in hours) of badgers *Meles meles* radio-tracked in Białowieża Primeval Forest in 1997–2001; based on sessions of 24-h continuous radio-tracking. Numbers of radio-tracked individuals in parentheses. Seasons: spring (1 March–31 May), summer (1 June–31 August) and autumn (1 September–30 November)

	Standing crop of earthworm biomass (kg ha^{-1})	Duration of activity (h)							
		Adult males (7)		Adult females (3)		Subadults (3)		All badgers (13)	
Season/period	Mean ± SE	Mean ± SD	(Range)	Mean ± SD	(Range)	Mean ± SD	(Range)	Mean ± SD	(Range)
Spring	486 ± 84	6.0 ± 2.5	(2.0–9.5)	6.7 ± 3.1	(0.5–10.0)	8.5 ± 1.2	(7.7–10.3)	6.8 ± 2.7	(0.5–10.3)
Summer	106 ± 30	9.2 ± 1.4	(6.5–12.5)	9.8 ± 1.9	(6.7–14.7)	8.8 ± 0.4	(8.5–9.3)	9.4 ± 1.6	(6.5–14.7)
Autumn	204 ± 89	7.5 ± 2.0	(4.5–9.3)	7.0 ± 2.1	(5.5–8.5)	9.3	–	7.6 ± 1.8	(4.5–9.3)
Whole year	–	8.0 ± 2.3	(2.0–12.5)	8.3 ± 3.9	(0.5–14.7)	8.7 ± 0.8	(7.7–10.3)	8.2 ± 2.4	(0.5–14.7)

activity were inversely related to differences in earthworm abundance (Table 1). Badgers were active longest in summer, when standing crop of earthworm biomass was the lowest, and they were active shortest in spring, when earthworms were abundant. In winter, when earthworms were not available at all, badgers retreated to their setts for winter sleep.

Duration of badger's daily activity was also strongly correlated with mean daily temperature ($r^2 = 0.97$, $n = 64$, $P < 0.0005$) (Fig. 5). The relationship was nonlinear: badgers increased their activity from below 0° C to about 15–17° C, and then slightly curtailed it on still warmer nights.

Comparative seasonal changes in body mass and cold season inactivity in badgers across the Palaearctic

In the wide Palaearctic range of Eurasian badgers, the mean temperature of January, used here as an index of winter length and severity, ranged from −27.5° C to 11° C (Appendix 1). The duration of winter inactivity in badgers was strongly negatively correlated with January temperature, which explained 81% of the observed biogeographical variation in the length of badger winter sleep (Figs. 6 and 7). Seasonal increase of badger body mass ranged from 25–27% in Western Europe to as much as 117% in the north-eastern regions of the European part of Russia (Fig. 6). Also, the mean temperature of January was the main factor shaping the observed variation: the colder the winter, the larger the percentage increase of body mass from spring to autumn (Fig. 7). Although data on both winter inactivity and body mass changes were available for only six localities, they showed a strong positive correlation: badgers had to store more fat, if they were to survive long periods of winter sleep. In the warmest, south-western part, badger activity and body mass level were rather stable year round. In their northernmost quarters (> 60° N), badgers were active for only 6 months per year, and during that time they had to double their weight in order to survive another 6 months.

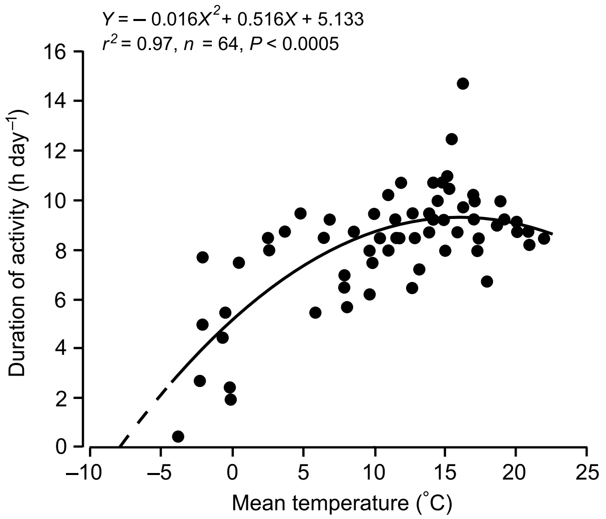

Figure 5 Duration of daily activity (out of sett) of badgers in relation to mean daily temperature. Each point denotes one day ($n = 64$ days). The duration of activity estimated on the basis of 24-h continuous sessions of radio-tracking. Nonlinear (quadratic) line appeared to be the best fit regression line.

DISCUSSION

Circadian activity of badgers in Białowieża Forest was characterized by high activity in a single period of several hours and an absence of any distinct, short-lasting peaks of activity. In other European populations, one or two clearly marked peaks of activity may occur (Harris, 1982; Maurel & Boissin, 1983; Fowler & Racey, 1988). Duration of badgers' daily activity in BPF was among the longest reported from Europe (3–9.7 h day^{-1}; Harris, 1982; Maurel & Boissin, 1983; Cresswell & Harris, 1988b; Revilla & Palomares, 2002), and – unlike in many other regions – their activity bouts were not interspersed by resting periods. A single bout of activity was also observed in badgers inhabiting an agricultural-woodland mosaic in Central Poland, but the duration of activity was shorter there than in BPF (Goszczyński *et al.*, 2000a). In BPF, the duration of daily activity did not vary between age/sex classes, which has also been found in England (Cresswell & Harris, 1988b.

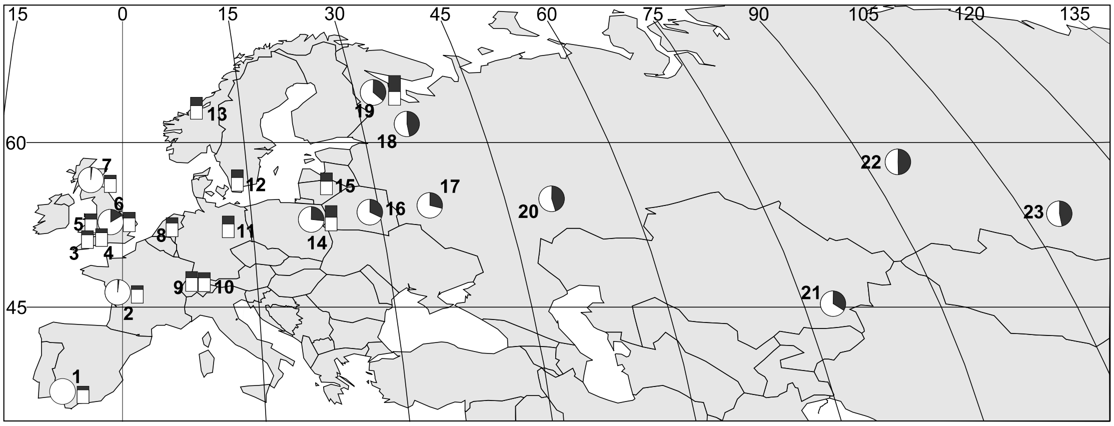

Figure 6 Biogeographical variation in the duration of winter inactivity and body mass changes over annual cycle in Eurasian badgers. Numbers refer to localities of the studies listed in Appendix 1. Circles denote a year and their black parts – proportion of time spent by badgers for winter sleep. Bars mark body mass changes; their white fields (the same size in all localities) denote the smallest body mass recorded in the annual cycle, black fields of the bars show the percentage increase in body mass in an annual cycle in relation to the minimum recorded mass.

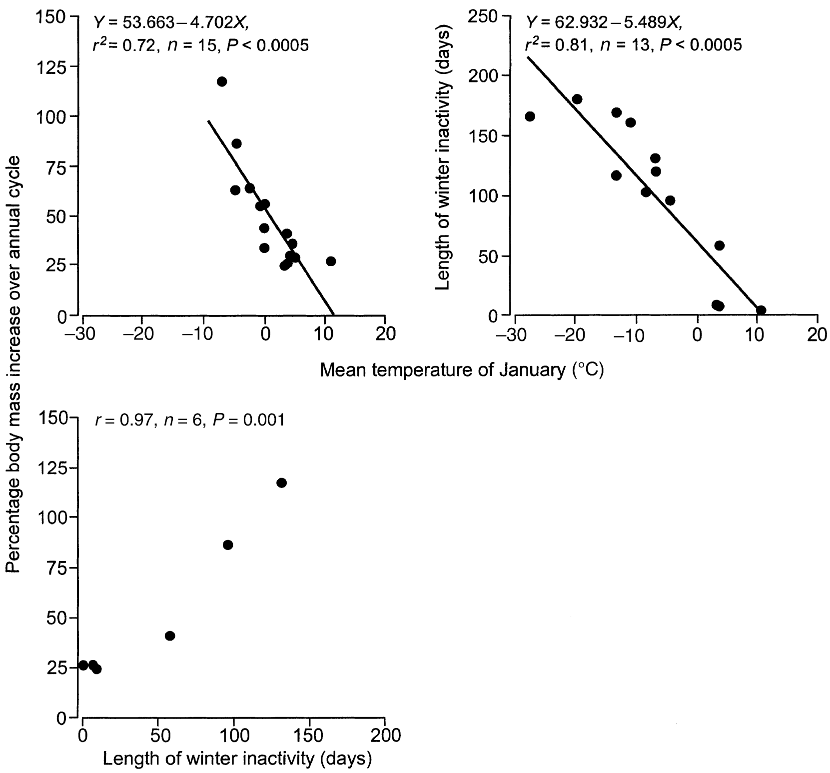

Figure 7 Duration of winter inactivity and body mass changes in Eurasian badgers in the Palaearctic region. Upper left: percentage increase in body mass in relation to the mean temperature of January in fifteen localities in Europe. Upper right: length of winter inactivity in relation to January mean temperature in thirteen localities in Europe and Asia. Lower panel: percentage increase in body mass of badgers in relation to the duration of their winter inactivity length (six localities in Europe). See Fig. 6 for geographical distribution of data points and Appendix 1 for the list of data and sources.

Long daily activity seems typical for badger populations living in low densities and was interpreted as badgers' response to low and seasonally varying food resources (Revilla & Palomares, 2002). Typically for the temperate and boreal zone, in BPF badgers fed mainly on earthworms (Jędrzejewska & Jędrzejewski, 1998; Goszczyński *et al.*, 2000b), the supply of which strongly varied across seasons. Most earthworm species are active within a temperature range of 0–20° C (Nordström, 1975). Therefore, in Białowieża Forest, the period of poor supply or inaccessibility of earthworms to badgers lasted nearly 4 months, a time span corresponding well to the mean duration of badger inactivity in the cold season. Moreover, during summer droughts earthworms decrease their activity and may discontinue reproduction (Nordström, 1975; Rundgren, 1975; Kasprzak, 1986). Badgers could compensate for the summer decline of earthworms by devoting a longer time to foraging and preying more on alternative foods such as amphibians and fruit (Jędrzejewska & Jędrzejewski, 1998; Kowalczyk, 2001).

Several authors reported that during periods of low abundance or low availability of earthworms, badgers' foraging efficiency declined. Kruuk (1978) found that the efficiency of catching earthworm by badgers was threefold lower in summer than in spring and autumn, and that during nights with high earthworm availability, badgers were able to fulfil their daily food requirement in 1 h. Henry (1984) reported that, when earthworms were scarce on frosty nights, the effectiveness of badger foraging was over ten times lower than during warmer nights. Neal (1986) noted earlier emergence of badgers from setts during dry periods when worm supply was short.

Prolonged activity of badgers in autumn can also result from the necessity to build fat reserves and prepare the setts for wintering. Göransson (1983) found that, in autumn, badgers spent over 2–5 h daily digging and collecting material for bedding. Similar patterns of seasonal changes in badger circadian activity to those in BPF were reported in France and Switzerland (Maurel & Boissin, 1983; Ferrari, 1997).

Many animals (e.g. insectivores, bats, dormice and bears) exposed to periods of food scarcity exhibit adaptation in the form of inactivity periods in these conditions (hibernation and winter sleep) which can last even a few months (e.g. Swan, 1974; Johnson & Pelton, 1980; Erkert, 1982; Gillies *et al.*, 1991). As suggested by Boyce (1979), winter inactivity in animals is an adaptation to environmental seasonality rather than to cold temperatures as such. In the case of badgers, unavailability of earthworms during winter appears to be the ultimate factor influencing the duration of their winter sleep. The annual pattern of activity has profound ecological consequences for badger populations. Kowalczyk *et al.* (in press) documented that, in the temperate and boreal zones of Europe, badger densities are largely determined by the abundance of earthworms and annual temperature (positive correlations with density in both cases). Thus, given a similar standing crop of food resources, badgers attain lower densities in regions with prolonged cold seasons. The mechanisms underlying this, besides an obviously shorter time to exploit available resources, may be high winter mortality, especially in juvenile badgers. This conclusion is in line with the results of large-scale analysis conducted by Johnson *et al.* (2002), who found that the annual difference in minimum and maximum temperature was correlated with badger densities in Europe; the wider the temperature range between the warm and the cold season, the lower badger densities.

The physiological and ecological consequences of long winter inactivity for individuals and populations of badgers are little known. These aspects are worthy of further investigation, because they represent examples of great biogeographical plasticity in physiology and ecology in a carnivore species for which most information comes from Western Europe.

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BIOSKETCHES

Rafał Kowalczyk has completed a PhD on the ecology of European badgers in Białowieża Primeval Forest. He also conducted field studies on the impact of alien, introduced predator (raccoon dog) on native fauna. He is currently studying habitat use and foraging strategies of semiaquatic mustelids.

Bogumiła Jędrzejewska, Associate Professor in animal ecology, has conducted long-term studies on predator–prey relationships and population regulation of mammals. She has published a book *Predation in vertebrate communities* with Włodzimierz Jędrzejewski (Springer, 1998). She is currently conducting research on ungulates and forest regeneration.

Andrzej Zalewski has completed a PhD on the ecology of pine martens in Białowieża National Park. His current research is focused on the influence of introduced American mink on native fauna and its competition with native predators.

Appendix 1 Body mass increase in annual cycle and length of winter inactivity in badgers in the Palaearctic

No.	Country (locality)	Latitude and longitude	Body mass increase in annual cycle (%)	Length of winter inactivity (days)	Mean temperature of January (°C)	Source
1	Spain (Donana)	37°N, 6°30′ W	27	0	10.8	E. Revilla (unpublished data)
2	France (Chize Forest)	46°19′ N, 0°24′ W	26	7	3.7	Maurel & Boissin (1983)
3	England (Devon and Somerset)	50°15′–51°15′ N, 2°30′–4°30′ W	29	–	5.0	Kruuk & Parish (1983), after Neal & Harrison (1958)
4	England (Wales – Dyfed, Avon, Gloucestershire, Wiltshire, Dorset)	50°45′–52°30′ N, 1°30′–5°W	36	–	4.6	Cresswell *et al.* (1992) and Page *et al.* (1994)
5	England (Gloucestershire)	51°53′ N, 2°14′ W	30	–	4.1	Cheeseman *et al.* (1987, 1993)
6	England (Wytham Wood, Waddesdon)	51°46′ N, 1°18′ W	41	58*	3.7	Lindsay & Macdonald (1985) and da Silva *et al.* (1993)
7	Scotland (Banchory)	57°6′ N, 2°30′ W	25	8	3.2	Fowler & Racey (1988)
8	The Netherlands (Northern Brabant)	51°40′ N, 5°45′ E	34	–	3.2	Lüps & Wandeler (1993)
9	Switzerland (Bern)	47°09′ N, 6°56′ E	44	–	−0.1	Lüps (1981)
10	Switzerland (Neuchâtel)	47°02′ N, 7°E	34	–	−0.1	Ferrari (1997)
11	Germany (eastern part)	51°30′ N, 12°W	56	–	0.0	Ebersbach & Stubbe (1994)
12	Sweden (Lund)	55°45′ N, 13°30′ E	55	–	−0.6	G. Göransson (unpublished data)
13	Norway (Trondheim)	63°36′ N, 10°25′ E	64	–	−2.5	Bevanger *et al.* (1996)
14	Poland (Białowieża Forest)	52°41′ N, 22°52′ E	86	96	−4.6	This study
15	Lithuania (Ukmerges)	55°20′ N, 24°45′ E	63	–	−4.8	Maldziunaite (1960)
16	Belarus (Berezinskii Reserve)	54°30′ N, 28°15′ E	–	120	−6.9	Serzhanin (1955)
17	Russia (Tula Forest)	54°55′ N, 36°58′ E	–	103	−8.5	Likhachev (1956)
18	Russia (Kivach Reserve)	62°15′ N, 34°12′ E	–	161	11.0	Ivanter (1973)
19	Russia (Leningrad region)	65°N, 32°E	117	131	−7.1	Danilov & Tumanov (1976)
20	Russia (Tatarstan)	55°N, 51°E	–	169	13.4	Gorshkov (1997)
21	Kazakhstan (Dzhungarskii Alatau)	45°30′ N, 80°30′ E	–	117	13.3	Lobachev (1976)
22	Russia (Motygino)	58°15′ N, 94°43′ E	–	180	19.8	Shaparev (1977)
23	Russia (Buryatya)	53°N, 110°E	–	166	27.5	Smirnov & Noskov (1977)

*Number of days badgers stayed inactive was calculated on the basis of Fig. 3 in Lindsay & Macdonald (1985), but the nights when sett entrances had been blocked by people were excluded from calculations.