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Activity patterns of radio-tracked weasels *Mustela nivalis* in Białowieża National Park (E Poland)

Włodzimierz Jędrzejewski, Bogumiła Jędrzejewska, Karol Zub & Wojciech K. Nowakowski

Jędrzejewski, W., Jędrzejewska, B. & Zub, K., Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża, Poland
Nowakowski, W. K., Faculty of Biology, Warsaw University, Krakowskie Przedmieście 26/28, PL-00-927 Warszawa, Poland; present address: Academy of Podlasie, Institute of Biology, ul. Prusa 12, PL-08-110 Siedlce, Poland

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Diel activity rhythms and factors affecting the duration of daily activity were studied in nine male common weasels *Mustela nivalis vulgaris*, radio-tracked in the pristine deciduous woodland in eastern Poland from April 1990 to August 1991. During the study, mean daily temperature varied from –5.3 °C to 25.5 °C, and densities of forest rodents (bank voles *Clethrionomys glareolus* and yellow-necked mice *Apodemus flavicollis*) ranged from 2 to 270 ind. ha^{-1}. Weasels showed clearly diurnal activity, with a peak around 1000–1300 hrs. On average, weasels were active for 3.8 h day^{-1} (SE = 0.3, range 0–14 h day^{-1}), with 0 to 7 bouts of activity (mean 2.1, SE = 0.1), each bout lasting, on average, 1.8 h (SE = 0.1). Spells of activity were separated by short inactivity bouts (on average 2 h, SE = 0.2). Long (nocturnal) inactivity lasted, on average 17.5 h day^{-1} (SE = 0.7). A remarkable seasonal variation in the duration of weasel daily activity and number of activity bouts per day was related to changes in ambient temperature. In winter, weasels were active in 1–2 bouts day^{-1} each bout lasting 1–2 h; whereas in summer they showed 3–4 (maximally 7) bouts of activity. The highest level of activity coincided with the mating season. Fluctuations of rodent numbers had little effect on weasel activity pattern.

1. Introduction

Activity patterns of small predators can be influenced by food supply, weather, risk of predation, and prey activity (e.g., Curio 1976). Weasels *Mustela nivalis* are rodent specialists and the smallest carnivores with exceptionally tense energy budgets (Casey & Casey 1979). They have been reported as exclusively nocturnal in the laboratory (Price 1971) but diurnal in the field (King 1975). Still, however, the information on weasel activity rhythm is anecdotal and data on duration of their activity is not available.

This paper presents the activity patterns of radio-tracked male common weasels (*Mustela nivalis vulgaris*) in the primeval deciduous forests of Białowieża National Park, eastern Poland. In that woodland, the regular superabundant seed crops of deciduous trees at 6 to 9-year intervals trigger the outbreak-crash 'waves' (lasting 2–2.5 years) of otherwise non-cyclic forest rodents (Pucek *et al.* 1993, Jędrzejewski & Jędrzejewska 1996, Hansson *et al.* 2000). Our study was conducted during outbreak and crash (1990–1991), i.e., under conditions of both overabundant and very scarce prey resources. Detailed information on weasel density, home range size, and hunting tactics was provided by Jędrzejewski *et al.* (1992, 1995).

2. Material and methods

2.1. Study area

The strict reserve of Białowieża National Park (= BNP, 47.5 km^2, 52°43´N, 23°54´E) protects the last remnants of virgin lowland deciduous forests in Europe, still unaltered by timber exploitation and other human activity. The mature woods are dominated by oak *Quercus robur*, hornbeam *Carpinus betulus*, lime *Tilia cordata*, maple *Acer platanoides*, spruce *Picea abies*, black alder *Alnus glutinosa*, and ash *Fraxinus excelsior*. The average age of tree stands is 130 years, and their structure is typical of multi-layer, multi-species forests, with the regeneration of trees taking place under the canopy of the old stand. Numerous windfallen and uprooted trees make the habitat diverse. Live-trapping and radio-tracking of weasels took place in the south-central part of the Park, in the oak–lime–hornbeam forest association. Weasels were the most numerous mammalian predators in the Park. During the winters of 1985/1986 to 1991/1992, their densities varied from 5 to 27 ind. 10 km^{-2}. Summer densities were from 19 to 108 weasels 10 km^{-2} (Jędrzejewski & Jędrzejewska 1993, Jędrzejewski *et al.* 1995). More information on forest vegetation and animal communities of BNP is given by Faliński (1986) and Jędrzejewska and Jędrzejewski (1998).

2.2. Live-trapping and radio-tracking of weasels

In 1990 and 1991, weasels and forest rodents were trapped in the same area in south-western part of BNP. Weasels were captured with wooden flip-door box traps with a separate bait compartment. Two live laboratory white mice were used as a bait in each trap and were given food and bedding. Traps were placed at ground level under fallen logs or adjacent to root plates and were checked twice daily. Weasels to be radio-collared, were brought to the laboratory. On the first day, they were anaesthetised with ether, their sex was determined, and weight and neck circumference were measured. On the following day, a weasel was sedated with Ketalar® and a radio-collar with a loop antenna was fitted around its neck. The collars (AVM Instrument Co., USA) weighted 3.5 to 4.5 g. A weasel was then released into a semi-natural outdoor enclosure (4.5 × 12 m) with natural vegetation, logs, live rodents, and a nest box with meat and water. During the next 1–3 days, we observed how a weasel adapted to the collar and whether it hunted rodents. When the first killed rodents appeared in the nest box, we released a weasel back to the forest at the place of capture. Weasels are extremely sensitive to handling and collaring (*see* Delattre *et al.* 1985) and such 'ambulatory' treatment was necessary for their survival and undisturbed behaviour after release. In summer 1990, both males and females were caught, but we did not have transmitters small enough for females. In autumn 1990 and in 1991, we were not successful in trapping females.

The range of the signal was 100–400 m, usually 200 m. An observer followed the weasel not farther than 50 m (and occasionally as close as 5 m) but his/her presence did not disturb the behaviour of the weasels (*see* Jędrzejewski *et al.* 1992). Localisation was done at 15-min intervals, hour 0100 including fixes done at 0015, 0030, 0045, and 0100 hrs. Weasels were recorded as active (when running, searching, out of den) or non-active (in a den for at least 15 min). A total of 7 656 fixes from nine male weasels were gathered from April 1990 till the end of August 1991. The body mass of the studied weasels ranged from 75 to 123 g (mean 90.5 g, SD = 15). Data from eight weasels were large enough to analyse individual variation in activity rhythms. For analysing the diel activity rhythm in each weasel, all localisations done during any hour were taken as 100% and percentage of fixes when the weasel found active was calculated. Only hours with 10 or more fixes were included. In seven weasels, continuous radio-tracking sessions covered from 9 to 26 days (24-h cycles) and allowed for the detailed analysis of activity pattern.

2.3. Rodent trapping

Forest rodents (the bank vole *Clethrionomys glareolus* and the yellow-necked mouse *Apodemus flavicollis*) were live-trapped with the Capture–Mark–Recapture method on the 3.24-ha plot in May, July, September, and November 1990, and in April, May, July, and September 1991. Each series lasted 6 days. Traps (Polish wooden box, *see* Olszewski 1968) were distributed in a 15-m grid and baited with oats. Density of rodents was estimated with the Minimum Number Alive method for the entire trapping plot and for the inner square (1.44 ha, two outer trap belts not considered) to check the edge effect (Hansson 1969). Since the two estimates differed, on average, by ± 10% only, we used that for the entire 3.24-ha plot. Combined densities of bank voles and yellow-necked mice were 137 ind. ha^{-1} in May 1990, 270 in July through September, and they declined to 128 ind. ha^{-1} in November 1990 and 2 ind. ha^{-1} in May 1991. Rodent densities increased to 10 ind. ha^{-1} in July and 14 in September 1991.

Meteorological data were collected at the Białowieża meteorological station and included mean daily temperature (records at 0700 hrs, 1300 hrs, and doubled record at 1900 hrs averaged), mean daily snow cover, and daily rainfall.

3. Results

3.1. Diel activity rhythms of weasels

Out of nine radio-tracked weasels, five were followed during several day-and-night periods (males 1, 2, 16, 10, 8). They all were active during the day, reduced their activity at dark, and were completely inactive during some night hours (Fig. 1). Also, in the three weasels of which the data were too small to show the whole 24-h cycle (males 7, 14, and 12), the course of activity indicated lower activity towards the dark period (Fig. 1). All weasels adjusted the period of high daily activity to seasonally changing span of daylight, which varied from 7.7 h on 23 December to 16.8 h on 22 June (Fig. 1).

Data pooled for all weasels (including observations too scarce to show activity in each weasel separately) revealed a clear daylight activity rhythm with a peak around 1000–1300 hrs (Fig. 2). Very little activity was recorded between 2100 hrs and 0400 hrs (below 10%) and all localisations taken between 0115 hrs and 0200 hrs showed inactivity of weasels.

3.2. Factors affecting duration of weasels' daily activity

Mean duration of weasels' daily activity was 3.8 h that is 16% of the day (Table 1). Out of 96 days, weasels were found wholly inactive on 4 days (4%). On all other days, weasels were active in 1 to 7 bouts, lasting on average 1.8 h (Table 1). Activity bouts shorter than one hour were most often recorded (35%). Spells of activity were separated by short periods of inactivity (from 1 to 6 per day) lasting on average 2 h. Most frequently, diurnal inactivity bouts were shorter than 1 hour (32%). Weasels were usually non-active during the night. The mean duration of long (nocturnal) inactivity bout was 17.5 h (Table 1) and the longest recorded inactivity of a weasel staying in a den covered 46 h.

There was a remarkable seasonal variation in the duration of weasel daily activity. It was longest but also most variable in spring–summer and it became shorter in autumn and winter (Fig. 3). Duration of weasel daily activity correlated positively with both the day length (from sunrise to sunset; $r = 0.575$, $n = 96$, $p < 0.0005$) and the mean daily temperature ($r = 0.484$, $p < 0.0005$). As these two variables were strongly mutually correlated ($r = 0.88$, $p < 0.0005$), we chose the temperature for further analysis. Mean daily tem-

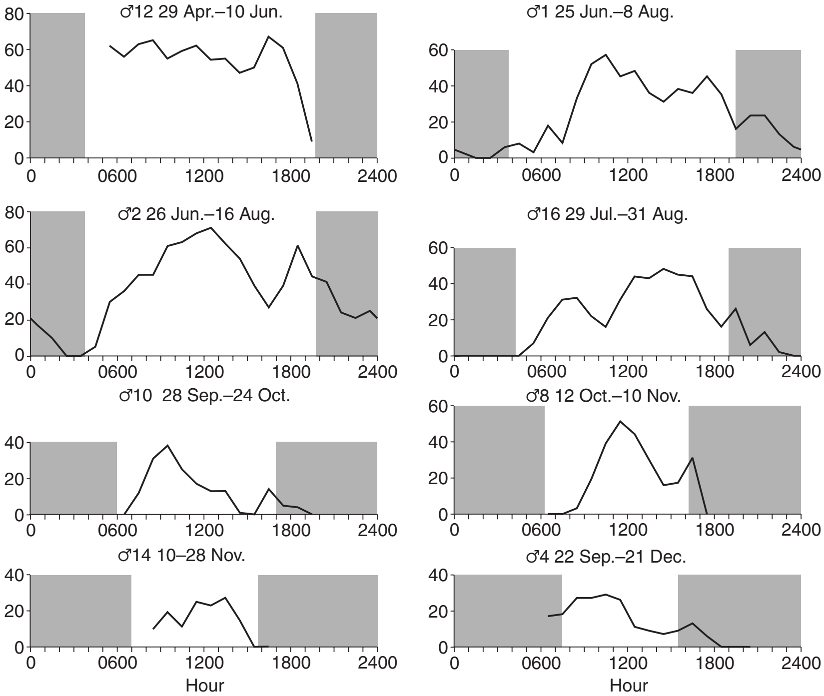

Fig. 1. Diel activity rhythms of eight weasels *Mustela nivalis* radio-tracked in April 1990–August 1991 in Białowieża National Park. Dates by weasel numbers are time spans of their radio-tracking. Shaded bars denote night-time (from sunset to sunrise, averaged for each weasel). Solid lines mark percentage of locations with weasels found active outside their dens. If total number of locations in any hour was < 10, data were considered too small for presentation. Total samples for various weasels ranged from 243 to 1 951 locations taken at 15-min intervals.

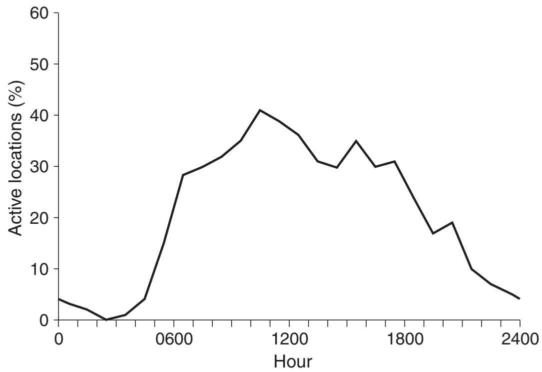

Fig. 2. Diel activity rhythm of weasels — data pooled for all weasels and all seasons of a year; totally 7 656 locations taken at 15-min intervals.

perature appeared the most important factor explaining the observed variation in weasel activity pattern (Table 2). Weasels prolonged their activity from an average of 1.4 h on frosty nights (–5 °C) to an asymptote of nearly 6 hours on very warm days (> 20 °C) that is from 6% to 25% of the day (Fig. 3). Interestingly, the dramatic change in forest rodent numbers (from peak densities in 1990 to a crash in 1991) had little consequences for weasel activity (Table 2, *see* also Fig. 3). The daily time of activity in spring–summer 1990 (peak of rodents, data on two weasels pooled) and in spring–summer 1991 (crash of rodents, two weasels pooled) did not differ statistically (p = 0.15, Mann-Whitney U-test). In the rodent crash year, the range of variation in weasel activity time was somewhat wider (0–14 h day^{-1}) than in the rodent peak year (1–10 h).

The mean duration of a single activity bout and a short (diurnal) inactivity bout did not change seasonally and remained fairly stable in the range of ambient temperatures from –5 °C to 25 °C, although their ranges of variation were much wider on warm days (>10 °C) than on cool days (Fig. 4). It was the number of activity bouts (and, consequently, of short inactivity bouts separating them) that significantly increased with higher temperatures (Table 2). The rate of increase was highest in temperatures > 10 °C (Fig. 4).

The summed duration of short (diurnal) inactivity periods increased with ambient temperature but the time of long period of night inactivity declined from an average of 25 h on frosty winter days to less than 8 h on warm summer nights (Fig. 5). Again, the change in rodent numbers did not have any effect on weasel inactivity (Table 2). In summary, while being entirely diurnal year round, weasels typically changed their pattern of activ-

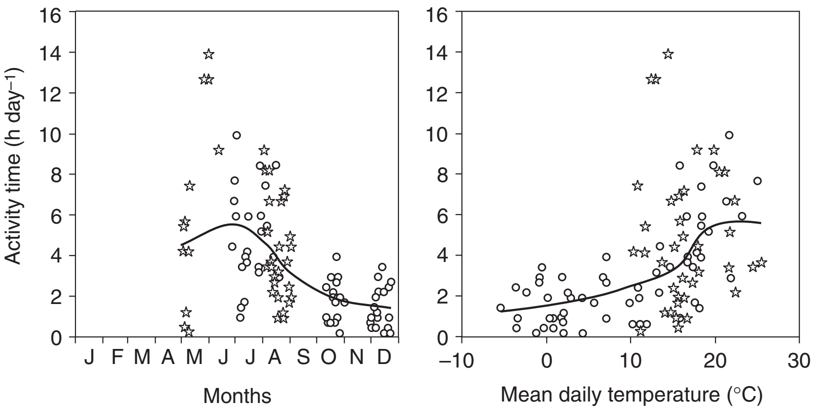

Fig. 3. Duration of daily activity (out of den) in weasels in relation to season (left panel) and mean daily temperature (right panel). Each point denotes one day (n = 96 days): circles — year 1990 (outbreak of forest rodents), stars — year 1991 (crash of rodents). Scatterplots of data were smoothed (solid lines) with Lowess method (Cleveland 1979) to show the most probable shape of relationship. *See* Table 2 for statistical significance.

ity from 1–2 bouts of activity, each lasting 1–2 h in winter to 3–4 (maximally 7) bouts on very warm summer days. Spells of activity were usually separated by 1–2 h of rest.

Since tracking days as sample units may not be fully independent observations, we repeated the statistical analyses using mean values for seven weasels as data points. The results were similar. Mean duration of weasel daily activity, numbers of activity bouts and short inactivity bouts per day positively correlated with ambient temperature (r from 0.70 to 0.86, p from 0.08 to 0.01, $n = 7$). The average duration of long inactivity bout was negatively related to temperature ($r = -0.92$, $p = 0.003$). Mean duration of an activity bout and that of a short inactivity bout were not correlated with temperature ($p > 0.4$).

4. Discussion

Weasels live-trapped by King (1975) in an English woodland were captured twice as often during the daylight as during the night. In summer, stoats studied by radio-tracking in Sweden (Erlinge 1979) and in Quebec (Samson & Raymond 1995) had a diurnal rhythm of activity. In winter, however, stoats tended to be nocturnal (Erlinge 1979). In Białowieża Forest, weasels typically hunted bank voles and yellow-necked mice when they were resting in their tunnels and nests (Jędrzejewski *et al.* 1992). Thus, weasel hunting was independent of the activity rhythm of forest rodents, which are active predominantly at night (*A. flavicollis*) or during the whole day (*C. glareolus*) (Buchalczyk 1964, Wójcik & Wołk 1985).

Table 1. Parameters of weasel activity in Białowieża National Park. Data based on 96 days of continuous radio-tracking of seven male weasels in 1990–1991.

Parameter	Duration (in hours) or number per day		
	Mean	SE	Range
Duration of daily activity	3.8 h	0.3	0–14.0
Number of activity bouts	2.1	0.1	0–7
Duration of an activity bout	1.8 h	0.1	0.25–14.0
Number of short inactivity bouts	1.1	0.1	0–6
Duration of a short inactivity bout	2.0	0.2	0.25–10.7
Duration of long inactivity bout	17.5 h	0.7	5.5–29.5

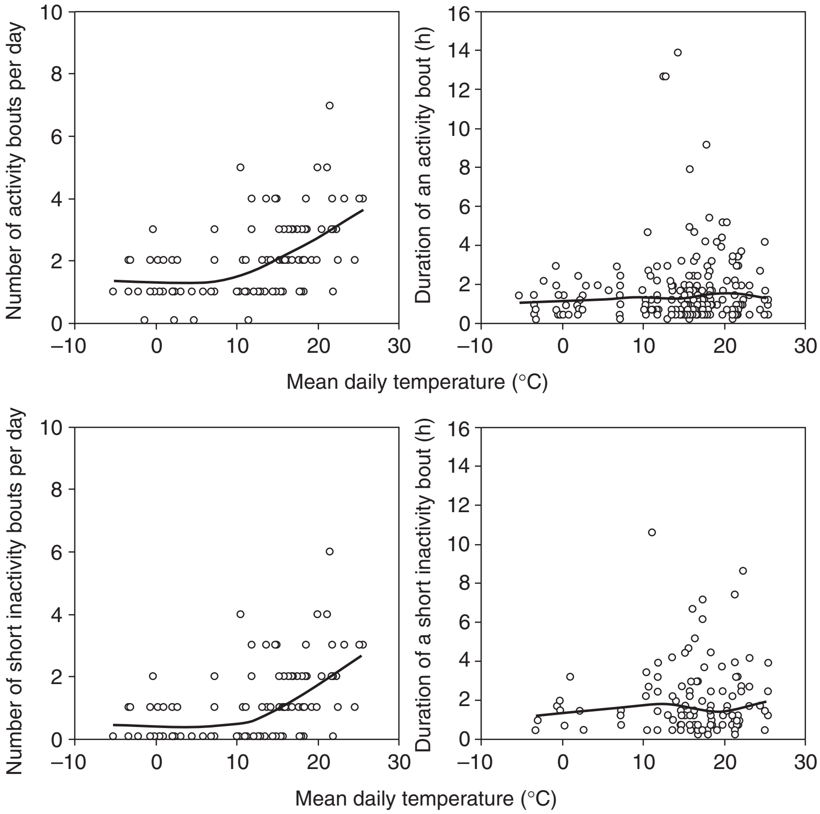

Fig. 4. Upper panels: number of activity bouts per day and their duration in relation to mean daily temperature, as studied in radio-collared weasels. Sample size: 202 activity bouts recorded in 96 days. Lower panels: number of short inactivity bouts per day and their duration in relation to mean daily temperature. Sample size: 110 short inactivity bouts recorded in 92 days. Solid lines are smoothed relationships (Lowess method; Cleveland 1979). *See* Table 2 for statistical significance.

Being active on daylight, Białowieża's weasels more frequently fell as prey to diurnal raptors (e.g., common buzzard *Buteo buteo*, lesser spotted eagle *Aquila pomarina*) than to owls (e.g., tawny owl *Strix aluco*) (Jędrzejewska & Jędrzejewski 1998). Generally, however, diurnal activity of weasels makes them less susceptible to predation, because the most numerous predators in BPF are tawny owls (Jędrzejewska & Jędrzejewski 1998).

The pattern of weasel activity, i.e. a number of short spells of movements separated with short rests was very similar to that described in stoats.

Table 2. The roles of mean daily temperature and densities of forest rodents in shaping daily activity of weasels — results of multiple regression analysis. sr^2 = contributions by each of the two independent variables to the total variation explained (Tabachnick & Fidell 1983). (+) positive relationship, (–) negative relationship. ***p < 0.001. *See* Figs. 3–5 for data points.

Parameter	Sample size (n)	Total variation explained (R^2)	Contributions by independent variables (sr^2): Mean daily temperature	Contributions by independent variables (sr^2): Density of forest rodents
Duration of daily activity	96	0.243***	(+) 0.225***	(–) 0.008
Number of activity bouts per day	96	0.247***	(+) 0.247***	0
Duration of activity bout	202	0.014	0	0
Number of short inactivity bouts per day	92	0.215***	(+) 0.215***	0
Duration of short inactivity bout	110	0.004	0	0
Duration of long inactivity bout	64	0.421***	(–) 0.397***	(–) 0.029

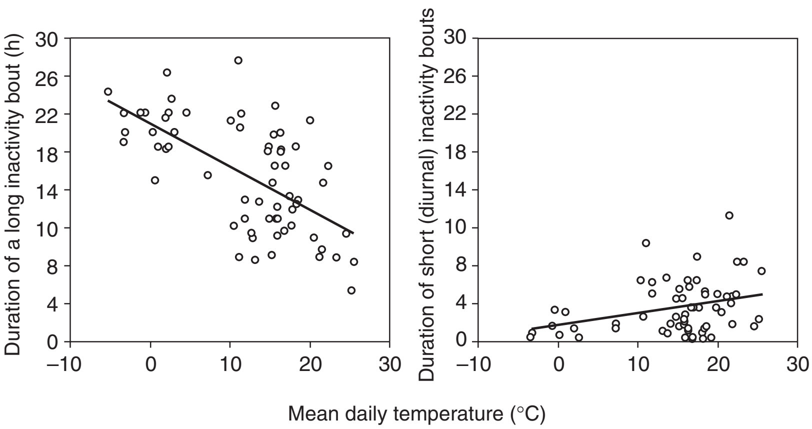

Fig. 5. Duration of weasels' long inactivity bout (recorded during the night, n = 64) and summed duration of short (diurnal) inactivity bouts in relation to mean daily temperature. Lines are linear regressions. *See* Table 2 for statistical significance.

In Quebec, stoats showed, on average, 5 bouts of activity during the day and one bout during the night, with most of the bouts lasting less than 40 minutes (Samson & Raymond 1995). In southern Sweden, stoats radio-tracked in all seasons of a year showed spells of activity lasting 10–45 minutes, alternated with periods of rest (Erlinge 1979).

Gillingham (1984), who studied the meal size and feeding rate in the least weasels in laboratory conditions, documented that even when exposed to food *ad libitum*, weasels cannot eat more than one meal of a few grams every few hours. To survive they must eat five to ten meals per day and this is the strongest constrain of their daily activity.

The total duration of weasels' 'outdoor' activity in Białowieża (from an average of 2 to 6 h day^{-1} in various seasons) was similar to that reported for stoats: 5 h day^{-1} (Samson & Raymond 1995), 6–9 h day^{-1} (Erlinge 1979, Sandell 1985). Reduction of activity in winter and its correlation with ambient temperature as a thermoregulatory behaviour, is a common phenomenon in small and medium-sized mustelids. It was reported for e.g. American stoats and European weasels in outdoor enclosures (Robitaille & Baron 1987, Jędrzejewska & Jędrzejewski 1989), free-living European pine martens *Martes martes* (Zalewski 2000), American martens *Martes americana* (Buskirk *et al.* 1988). It is obviously 'the cost of being long and thin' (Brown & Lasiewski 1972). On the other hand, the longest activity of weasels in Białowieża was recorded in spring, not in hot summer, which we interpret as the additional effect of reproductive activity. The mating season in Polish weasels lasts from April until July or August (Jędrzejewska 1987), and during that period male weasels searching for mates may exhibit elevated locomotory activity, as was documented in stoats (Robitaille & Baron 1987).

Surprising was the small impact of rodent fluctuations on weasel activity in Białowieża. We had expected that in 1991, a rodent crash year, duration of weasel daily activity would be markedly longer due to lower efficiency of hunting. This was suggested by the laboratory experiments. Price (1971) evidenced that food deprivation lasting 8 hours did not change the activity of least weasels, but 24-h deprivation of food had nearly doubled weasels' activity. Indeed, in Białowieża, during rodent crash year we observed extraordinarily long spells of uninterrupted activity by weasels (up to 14 h day^{-1}), which might have indicated long, unsuccessful hunting efforts. On average, however, weasel activity was negligibly affected by rodent fluctuations. This is in contrast to data on weasel densities, home range size, and length of daily movements, which were profoundly influenced by rodent densities (Jędrzejewski *et al.* 1995, Jędrzejewski & Jędrzejewska 1996). The possible explanation for the observed lack of differences may be that weasels were lavishly active during rodent outbreak when prey was superabundant.

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