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Ecological factors affecting the diel activity of voles in a multi-species community

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Ecological factors affecting the diel activity of rodents in a sedgeland habitat within Białowieża Primeval Forest were examined by live trapping. The results of a short-term but intensive trapping scheme, with checks every 3 hours, confirmed known differences in activity patterns between voles and mice. We observed an even distribution of vole activity around the 24-h cycle, rather than a marked preference for nocturnal activity in summer. Ten-year data from trapping of the same rodent assemblage dominated by *Microtus oeconomus* showed that an increase in population density of the dominant species resulted in more diurnal activity of those voles and the co-occurring bank voles. This shift of activity seemed to result from social tensions in a crowded habitat that mostly affected young root voles, as well as individuals of subordinated species. On the other hand, increased predation pressure exerted by weasels *Mustela nivalis* encouraged more nocturnal activity of voles. The shift was either a direct response of local prey to increased activity of the local diurnal predator, or the ancient anti-predatory response of mammals seeking safety in darkness.

Introduction

Among small mammals, murine species are predominantly nocturnal, while microtines are active day and night (reviews in Madison 1985, Halle & Stenseth 2000). However, under laboratory conditions voles show high levels of wheel-running activity predominantly during the night hours, an observation whose biological significance is still unclear (Daan & Slopsema 1978, Dewsbury 1980, Lehman & Sommersberg 1980, Tavernier *et al*. 2004). Moreover, under field conditions they seem to be more active in the dark phase of the diel cycle in summer, only becoming more diurnal in winter (Erkinaro 1961, Bäumler 1975), though such seasonal changes in activity have not been observed in every study (e.g. Lehman & Sommersberg 1980).

The general conclusion to be drawn from these results is that the optimal temporal behaviour of both mice and voles, as probably shaped by predator–prey interaction at the beginning of mammalian evolution, would be nocturnal activity. However, this pattern can only be employed successfully by mice, since their highly caloric seed-based diet allows them to restrict feeding to the night hours. In contrast, voles with a diet consisting of a large amount of low-quality food and a consequent reliance on the efficiency of a cellulose-decomposing bacterial flora, must feed almost continuously, with only short interruptions (Grodziński 1962, Hansson 1971, Daan &

Slopsema 1978, Weiner 2000). Vole activity patterns may therefore represent one of the clearest cases to be seen among mammals of a trade-off between nutritional demands and predator avoidance on a daily basis. The trade-off, as modified by ecological factors, results in flexibility of temporal behavior, an aspect that is still poorly investigated and understood.

In this paper we analyze diel activity in a free-ranging rodent assemblage, using live-trapping, with special reference to the root vole *Microtus oeconomus*. In the course of the 10-year study, this population experienced significant fluctuations in density and in levels of predation by the weasel *Mustela nivalis*. Our aims were: to test, at the population level, how increased predator pressure affects activity patterns in voles, to evaluate the flexibility of temporal behavior in voles under changing population densities, and to compare responses of other species, voles and mice, to these factors.

Materials and methods

The study was conducted in the years 1997–2006, in sedgeland along the Narewka Valley within the Białowieża Primeval Forest, Poland (52°30´N, 23°30´E). The predominant vegetation in the valley is a sedge *Carex* spp. community with some additions from a humid meadow association, and early stages of forest succession towards *Salici–Franguletum* (Falinski 1986). The root vole, *Microtus oeconomus*, is the dominant rodent species accounting on average for 70% of individuals in the rodent assemblage. The species was accompanied by three others consistently present in the habitat, i.e. the bank vole *Myodes glareolus* (20%), the striped field mouse *Apodemus agrarius* (5%) and the yellow-necked mouse *Apodemus flavicollis* (3%). Other rodent species appeared only sporadically.

Weasels were the main mammalian predators in the studied habitat. Their abundance was estimated three times a year by trapping in the 20-hectare area of marshland that encompasses the rodent trapping plot (K. Zub unpubl. data). The density of the weasel population varied greatly from year to year; from over 15 individuals per km^2 in some years to zero in others (Zub 2004). The number of weasels caught in July was used here as a proxy for predation risk in a given season.

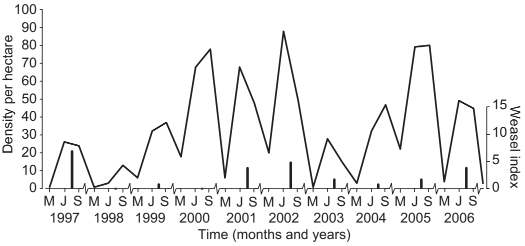

Fig. 1. Population dynamics of *Microtus oeconomus* (line) and abundance index of *Mustela nivalis* (bars) on the sedgeland in Białowieża Primeval Forest. The 10-year period included 4 years of high vole population density (~70 or more ind. per ha) and 6 of low/medium density.

Three times a year (in May, July and September), rodents were live-trapped in a 1-hectare plot with the capture–recapture method using wooden traps and metal cones (50 + 50 in 1997–2004) or wooden traps only (100 in 2005–2006) baited with oat seeds. The change of traps did not affect trappability in any negative way. Rodent abundance was estimated as the MNA (minimum number known alive) on the basis of 6-day trapping. The density of the population of root voles fluctuated greatly but irregularly from one year to another (Fig. 1). The multiannual changes in vole population density and weasel abundance did not correlate with each other ($r = 0.24$, $p = 0.532$, $n = 10$) and could therefore be treated as independent variables (Gliwicz & Jancewicz 2004, Gliwicz 2007).

The standard trapping procedure consisted of two trap controls each day, at 8:00 and 20:00. In order to ensure comparisons of exactly the same periods in different years, and to exclude variability resulting from seasonal changes in temporal behaviour, analysis was confined to data from summer trapping, which was usually carried out between 15 and 25 July. In July, animals present in traps at the time of the evening checks were clearly active only during the daylight phase, whereas those present in the mornings could partly have been caught during daytime since the true phase of darkness accounted for only about 60% of "nights". The percentage of captures made between mornings and evenings

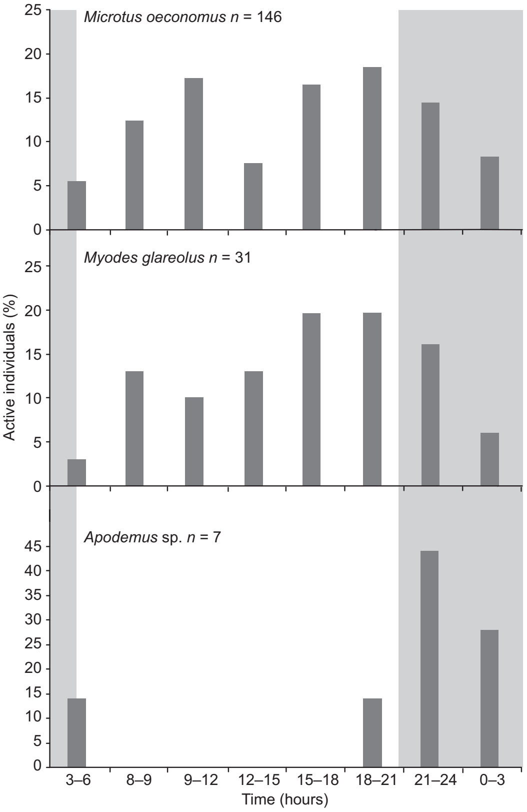

Fig. 2. Diel activity of the rodent assemblage comprising voles and mice, as revealed by intense live trapping over 3 days in July 2006. Data for *Apodemus flavicollis* and *A. agrarius* were pooled. Shaded area corresponds to the period of darkness; *n* indicates number of captures.

in each July trapping session was therefore used as a conservative proxy for rodents' diurnal activity. The long-term analysis of activity patterns presented here is based on 1606 captures of *Microtus oeconomus*, 456 captures of *Myodes glareolus*, 90 of *Apodemus agrarius* and 81 of *A. flavicollis*.

Additionally, short-term trapping based on a different time schedule was carried out in July 2006, the aim being to establish more detailed patterns of activity for the studied rodents. This trapping was performed for three days (16–18 July) during a regular session in the standard plot and, in addition, in a second 1-ha plot located in the same habitat at a distance 0.5 km away. During this experiment, traps were checked every 3 hours, at 00:00, 3:00, 6:00, 9:00, 12:00, 15:00, 18:00 and 21:00 h. The data from this trapping were used to establish whether the live-trapping method accurately reflected known interspecific differences in activity patterns, as well as how the results of live-trapping based on eight checks corresponded to the results of standard trapping based on just two.

Results

Short-term study

The distribution of rodent captures at 3-hour intervals offered an effective illustration of the polyphasic activity in the microtine species *Microtus oeconomus* and *Myodes glareolus*, as well as the nocturnal activity of *Apodemus* spp. (Fig. 2). The patterns of activity of the two vole species were almost identical, with minima at midday and at dawn. The percentage distribution of captures of the two species between the light and dark phases of the diel cycle did not differ significantly from those expected on the basis of the relative durations of day and night in July (70.8% of daylight hours as compared with 74.6% and 74.2% of root voles and bank voles captured during daylight hours, respectively). In the case of the root vole, a comparison of activity patterns revealed by captures of males ($n = 81$) and females ($n = 65$) indicated that males were slightly more active in the daylight phase than females (79.0% and 63.1% of captures respectively), though the difference in the distributions of captures at 3-hour intervals did not achieve statistical significance ($\chi^2 = 5.79$, df = 7, $p > 0.05$). The numbers of captures of bank voles and mice were too small to permit such analysis.

Long-term data

The analysis of the 10-year data served to assess inter-annual differences in the activity patterns of *Microtus oeconomus*, as well as to estimate flexibility of response to changing ecological factors. The factors in question were multi-annual variations in the root vole density, the density of all rodents, and predator pressure measured in terms of the abundance of weasels.

Diurnal (8:00–20:00) activity, measured as the percentage of captures in the evening, varied between years with a range of 34%–49%, the average being 44.5% and was significantly lower than the expected 50% (proportion test: $z = 4.44$, $p < 0.001$). (Note that the difference in the percentage diurnality in this analysis *vs*. short-term data analysis resulted from different definition of a "day" that here spanned for 12 hours, and in the short-term experiment — over 16 hours). In years of high population density voles were significantly more active during the day than in those of low population density (Table 1). This relationship was confirmed by a statistically significant positive correlation between the densities of root voles and their diurnal activity over the 10 years. This variation in population density accounted for about 40% of the observed variability in voles' temporal behavior (Table 1). The increased diurnal activity at high population density was more evident among young (sexually immature) voles ($R^2 = 52\%$, $p = 0.018$) than in the population as a whole. The combined density of all rodents jointly inhabiting the meadow had no demonstrable effect on activity patterns in root voles.

Predator pressure exerted by weasels did impact negatively upon the diurnal activity of root voles. However, the effect only achieved significance in years of low/medium vole population densities (of < 50 ind. per ha). It accounted for 73% of the variability in activity noted in those years. Taken together, the two factors: the population density of voles and the abundance of weasels — as independent variables in a multiple regression/correlation model — proved highly statistically significant, and explained over 75% of the variability to the diurnal activity of voles observed over the whole study period (Table 1).

The analysis of the 10-year data on other rodent species revealed that *Myodes glareolus* — another vole species present in the study area consistently (in 8 of the 10 years) — was slightly less diurnal (at 39% of captures) than *Microtus oeconomus*. This difference was non-significant (two-sample proportion test: $z = 1.81$, $p = 0.070$). The activity of bank voles during daylight hours correlated significantly with the density of *Microtus oeconomus* ($r = 0.78$, $R^2 = 60.8\%$, $p = 0.038$), but not with the density of their own species. Weasel abundance did not affect the temporal behavior of bank voles significantly.

Two mouse species *A. flavicollis* and *A. agrarius* were evidently nocturnal. In the former

Table 1. Changes in diurnal activity of *Microtus oeconomus* as estimated in the 10-year live-trapping study, with major inter-annual variability in vole population densities and predation by *Mustela nivalis*. All data for mid-summer (July).

Year	Vole density		Predation risk index	Diurnal activity		Correlation density/ day activity	Correlation predation/ day activity	Multiple regression[a]
	n	mean (SD)		%	mean (SD)			
"Low"								
1998	3		0	43			$r = -0.855$	
1997	26		7	34			$R^2 = 73.1\%$	
2003	28	28.3[b]	2	42	39.6[c]		$p = 0.030$	
2004	32	(14.84)	1	43	(3.61)		$n = 6$[d]	
1999	32		1	38		$r = 0.635$		
2006	49		4	38		$R^2 = 40.3\%$		$R^2 = 75.6\%$
"High"						$p = 0.049$		$p = 0.007$
2000	68		0	49		$n = 10$		$n = 10$
2001	68	75.8[b]	4	44	47.0[c]			
2005	79	(9.67)	2	47	(2.16)			
2002	88		5	48				

[a] diurnal activity (%) = 39.42 + 0.137**density – 1.27*predation (** $p = 0.005$; *$p = 0.015$).

[b] *t*-test: $t = 5.58$, $p < 0.001$.

[c] *t*-test: $t = 3.60$, $p = 0.007$.

[d] correlation significant only for years of low density.

species, diurnal activity was no more than incidental (with 9% of captures during daytime hours), whereas in the latter it was somewhat greater (at 26%). In both species, a majority of the day-active individuals were lactating females, which accounted for 8% out of the 9% in the case of *A. flavicollis* and 14% out of the 26% in *A. agrarius*. Low population densities and a relatively small number of captures precluded more detailed analyses.

Discussion

The results of the short term study confirmed well known differences in activity patterns of voles and mice. The similarities in activity patterns found between two microtines were less expected. The established facts that the diet of the bank vole is more caloric than that of the root vole (Grodzinski 1962, Hansson 1971), and that the former species naturally tends towards nocturnal activity, if not disturbed by *Apodemus* (Greenwood 1978, Wójcik & Wolk 1985) inclined us to expect less polyphasic activity and more nocturnal activity in the bank vole than in the root vole. Our results seem to indicate that at the time of the study, bank vole diet included much of green plant material and therefore they were as polyphasic as root voles. The aboveground activity of the two vole species was evenly distributed between the dark and light phases of the 24 h cycle, leaving our results in contradiction to earlier findings (reviewed by Madison 1985) on the prevailingly nocturnal behaviour of voles in summer. Evidently, vole activity patterns are flexible, and they respond to local conditions.

Ten-year data on the diel distribution of captures of voles and mice were used here to examine the effects of changing local conditions on rodent activity. Although the long-term trapping provided for nothing more than a crude estimate of daily activity, the general patterns were in fact very similar to those observed in our 72-hour trapping as well as in the other studies cited above. Therefore, to suppose that our long-term results reflected the true relative variability in activity between species and from year to year is reasonable. We were able to track, at the population level, changes in temporal behavior of voles affected by two important ecological factors: changing density and predation risk (Halle & Stenseth 2000). We found that root voles became less diurnal under increased risk of weasel predation and more diurnal when their own density increased. These two factors taken together explained over 75% of the variation in vole activity patterns.

On the sedge meadows at Białowieża, the weasel is the most important, most numerous and most specialized predator of voles. Raptors, owls and other mammalian carnivores are seen only infrequently in the area (Jedrzejewska & Jedrzejewski 1998, Zub 2004). Therefore, with weasel numbers strongly fluctuating from year to year, predation risk also varied greatly. Moreover, as weasels in the study area clearly display diurnal activity (Zub 2004), the reason for decreased daytime activity of voles in periods of high weasel abundance is clear. What is not obvious, however, is whether the observed decrease in diurnal activity at times of increased predation risk was in fact the direct response of local voles to prevailing activity patterns of local predators, as proposed by Halle (1993). It could result from an ancient antipredatory adaptation among mammals which makes them feel more secure in the darkness. The relative importance of these two (proximate and ultimate) factors in shaping vole diel activity under increased predation risk could be further clarified, if their reactions to a high risk of predation by typically diurnal and nocturnal predators (weasels and, for example, barn owls) are studied.

The observed increase in diurnal activity of voles at high population density was also reported by other authors (*see* Halle 2000 and references therein). This increase could reflect changes in social behavior in a crowded population that affect the feeding rhythms of individuals; especially the socially subordinate which try to avoid harmful interactions with dominants, as Reynolds and Gorman (1994) believe. This explanation is consistent with our finding that increased diurnal activity was most common in young (immature) voles. This shift in temporal behavior of voles in the crowded population was sufficient to counteract the tendency of voles to avoid daytime activity at times of high predation risk. The latter effect ceased to be significant in years of high population density.

Despite many obvious limitations, long-term live-trapping data might be of value in evaluation of changes in temporal behaviour of rodents in response to a range of ecological factors, whose variability was assessed in the course of a study. The approach can effectively supplement experimental studies, whose greater precision is offset by major temporal and spatial limitations, and hence limitations in two dimensions of great importance to ecological interactions.

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