

Mobility and habitat utilization of small mustelids in relation to cyclically fluctuating prey abundances

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We examined the winter season mobility and habitat utilization of two mustelid predators, the least weasel (*Mustela n. nivalis*) and the stoat (*M. erminea*) in western Finland. Cyclically fluctuating abundances of voles offered an opportunity to compare species-specific behavioral adjustments to the density of main prey. Daily lengths of small mustelid snowtracks in different habitats were recorded during six successive winters covering two three-year population cycles of voles (field vole *Microtus agrestis*, sibling vole *M. rossiaemeridionalis* and bank vole *Clethrionomys glareolus*). Tracks of least weasels were longest in the low phase of the vole cycle indicating that least weasels as *Microtus* vole specialists increased mobility in searching for prey at low densities of voles. The mobility of stoats was highest in the early decline phase. Both small mustelid species preferred farmland habitats typical for *Microtus* species, in particular at high densities of voles. Stoats as semi-generalist predators may shift to alternative prey leading to changes in habitat utilization, when voles are decreased to low densities. This was observed when stoats utilized woodland habitats more in the low than in other phases of the vole cycle.

1. Introduction

High amplitude fluctuations in population densities is characteristic of herbivorous small mammals (voles, lemmings and hares) in northern ecosystems (Elton 1942, Krebs & Myers 1974, Norrdahl 1995). In northern Europe, cyclic populations of microtine (= arvicoline) rodents show low

densities every three to five years and density differences may be 50 to 100-fold between the peak and the low phases of the population cycle (e.g., Hansson 1969, Henttonen *et al.* 1987, Korpimäki *et al.* 1991). Increasing experimental evidence suggests that predators may drive these cycles (e.g., Korpimäki & Norrdahl 1998), and predation has been shown to be the major cause of mor-

tality of voles during the decline phase of the cycle (Norrdahl & Korpimäki 1995, Steen 1995).

Predators of microtine rodents in northern Europe can be divided into three tentative categories according to their dietary width and movement patterns: resident generalists, resident specialists and nomadic or migratory specialists (Andersson & Erlinge 1977, Korpimäki 1992). Resident generalists (e.g., the red fox *Vulpes vulpes* and the eagle owl *Bubo bubo*) respond to changes in prey densities functionally, by increasing the proportion of small rodents in their diet when the density of microtines is increasing (Englund 1965, Korpimäki *et al.* 1990). Nomadic or migratory specialists (e.g., the kestrel *Falco tinnunculus* and Tengmalm's owl *Aegolius funereus*) mainly respond to changes in prey densities numerically, by immigration and emigration (Korpimäki & Norrdahl 1989a, 1991a, 1991b). Resident generalists or nomadic/migratory specialists are not considered to be the cause of the cyclicity in populations of microtine rodents, because their direct responses tend to stabilize fluctuations in prey density (Andersson & Erlinge 1977, Erlinge *et al.* 1983, Korpimäki 1993, 1994). The response of resident specialists (e.g., the least weasel *Mustela nivalis*) to changing prey density is mainly numerical, since increasing rodent density increases fecundity of specialist predators (e.g., Erlinge 1974, Tapper 1979). Resident specialist predators could drive the population cycles of microtine rodents, because their densities lag well behind prey abundances, thus destabilizing predator-prey dynamics (Korpimäki *et al.* 1991, Hanski *et al.* 1993).

Microtus voles (field vole *Microtus agrestis* and sibling vole *M. rossiaemeridionalis*, syn. *M. epiroticus*) are the main prey of small mustelids (least weasel, subspecies *nivalis*, and stoat *Mustela erminea*) in western Finland (Korpimäki *et al.* 1991). However, stoats are able to shift to alternative prey, such as mice (*Micromys minutus* and *Mus musculus*), bank voles (*Clethrionomys glareolus*), water voles (*Arvicola terrestris*), brown rats (*Rattus norvegicus*), muskrat (*Ondatra zibethica*), hares (*Lepus* spp.) and small birds, when densities of main prey are low (Korpimäki *et al.* 1991). Least weasels are residents specialized on *Microtus* voles; analysis of winter food have shown that *Microtus* always comprises greater than 50%

of the prey items of least weasels in winter (Korpimäki *et al.* 1991). Although densities of bank voles can be higher than densities of *Microtus* species in the low phase of the vole cycle (Korpimäki & Norrdahl 1991a), the proportion of bank voles remains low (mean 9%, max. 24%) in the diet of least weasels (Korpimäki *et al.* 1991).

Here we report the effects of fluctuating vole abundances on the winter season mobility and habitat utilization of small mustelids. The mobility recorded may reflect several functional responses of predators to declining or low vole densities: e.g., habitat shift because use of alternative prey, increased mobility because searching for new vole patches or because low patch residency times. In general, predators are assumed to choose habitats in which their net energy intake and survival are maximized (e.g., Stephens & Krebs 1986, Sih 1993). Therefore, under conditions of widely fluctuating prey abundances, following specific questions raise: (i) do small mustelids adjust their mobility and habitat utilization to the prevailing phase of the population cycle of voles? (ii) Do least weasels and stoats differ in their pattern of habitat utilization? (iii) What are the possible consequences behavioral adjustments of small mustelids bring to the population dynamics of voles?

2. Material and methods

The study was carried out at Alajoki in western Finland (63°00'–63°05' N, 22°55'–23°00' E). The study area covers 28 km² and consists of farmland (74%), pine forest (17%), spruce forest (7%), river (1%) and inhabited area (1%). In the Alajoki study area, population dynamics of voles show cyclic fluctuations in densities with low phases every three years (Fig. 1). Population densities of *Microtus* and bank voles fluctuate synchronously, although the species mainly occupy different habitat types. Field and sibling voles mainly occupy farmlands and open-country grasslands, whereas bank voles also use woodlands and bushes (Myllymäki 1977, Norrdahl & Korpimäki 1993). The densities of least weasels track vole abundances with a 0.5–1-year lag, whereas the densities of stoats fluctuate according to vole dynamics without an obvious time lag (Korpimäki *et al.* 1991).

The study covered two vole cycles starting at a low phase in 1983 and ending at a decline phase in 1989 (Fig. 1). E. Korpimäki and K. Norrdahl followed and measured snowtracks of least weasels and stoats during six winters (Fig. 1). This was done once or twice a month from late November

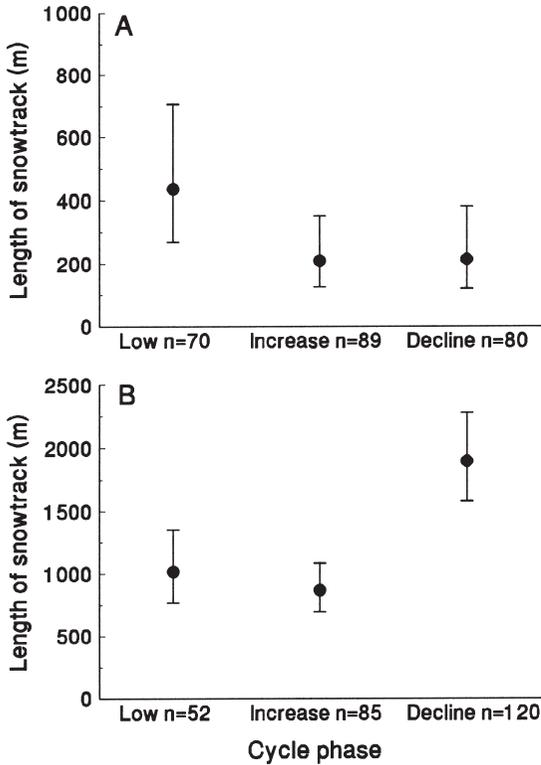


Fig. 2. Means and 95% confidence intervals for daily track length of (A) least weasels and (B) stoats in the different phases of the vole cycle presented in back-transformed scale.

nificant results for the cycle phase, *a posteriori* Tukey’s tests were conducted to find out which phases of the vole cycle differed from each other. When species × phase interaction was statistically significant, individual ANOVAs were carried out for each species.

Total track lengths were log_e-transformed to normalize the residual distributions of ANOVAs. The results are reported in back-transformed scale in tables and figures with 95% confidence intervals. All statistical analysis were carried out using procedure GLM in SAS statistical software, version 6.12.

3. Results

3.1. Mobility

Three-way ANOVA yielded statistically significant results for species, sex, phase, species × sex and species × phase effects on the total length of the snowtrack. Because of the significant interactions, the main effects are not reported here. Significant species × sex ($F_{1,484} = 30.27, p = 0.0001$) interaction resulted from stoats having longer tracks than least weasels, and female least weasels having shorter tracks than male least weasels (Table 1). Individual ANOVAs for each species showed statistically significant phase effect for least weasel ($F_{2,233} = 4.39, p = 0.0135$) and for stoats ($F_{2,251} = 16.03, p = 0.0001$). Tukey’s tests were conducted to see which cycle phases differed from each other. For least weasel, the difference was found between the low phase and the other two phases, as least weasels ranged over a wider area during the low phase of the population cycle of voles (Fig. 2). For stoat, a significant difference was found between the decline phase of the cycle and the other two phases, indicating that mobility of stoats was highest during the decline phase (Fig. 2).

Table 1. Mean (95% confidence intervals in parentheses) daily total track length (presented in back-transformed scale) and the mean difference in logratios (utilized–available) in habitat utilization of least weasels and stoats between farmland and woodland habitats. Positive values represent preference of farmland habitats. Values denoted by different supercript letters are significantly different (adjusted for multiple comparisons with Tukey’s test).

Species	Sex	Track length (m)		Difference in logratio	
		Mean (95% CI)		Mean (95% CI)	
Least weasel	Males	660.7 ^a	(570.8, 764.8)	4.35 ^a	(3.90, 4.81)
	Females	109.8 ^b	(72.6, 166.1)	4.06 ^a	(2.78, 5.35)
Stoat	Males	1394.7 ^c	(1172.7, 1658.7)	1.80 ^b	(1.26, 2.34)
	Females	1015.2 ^c	(801.8, 1285.4)	3.36 ^a	(2.62, 4.09)

3.2. Habitat utilization

Small mustelids preferred farmland habitats (Table 2). Three-way ANOVA showed significant species and phase main effects, and significant species \times sex interaction on the difference in logratios between utilized and available habitat categories. The species main effect ($F_{1,484} = 15.23$, $p = 0.0001$) and species \times sex interaction ($F_{1,484} = 4.90$, $p = 0.0273$) was due to least weasels and female stoats having proportionally longer tracks than male stoats on farmland compared to the lengths of tracks on woodland (Table 1). For the phase effect ($F_{2,484} = 7.09$, $p = 0.0009$) a significant difference was found between the low and the decline phase (Table 3), which was due to a lower farmland/woodland ratio at the low phase of the cycle than at the decline phase. When comparing the ratio between low and increase phases, the ratio was marginally lower in the former than in the latter phase ($p = 0.06$ in Tukey's pairwise comparison, Table 3). In the increase and decline phases, farmland habitats were preferred by both species of small mustelids, but in the low phase, only least weasel males utilized farmland more than expected by random (Table 2). These results indicate that in general small mustelids used woodland habitats in the low phase more than in the two other phases.

4. Discussion

4.1. Mobility and habitat utilization in relation to the prevailing phase of the vole cycle

Because of their larger body size, stoats have larger home ranges and longer daily moving distances than common weasels (*M. n. vulgaris*) or least weasels (*M. n. nivalis*, the smallest subspecies of *M. nivalis* with northern distribution) (for stoats Erlinge 1977, Simms 1979, Debrot & Mermod 1983; for common weasels Erlinge 1974, King 1975, Jedrzejewski *et al.* 1995; for least weasels Simms 1979, Oksanen *et al.* 1992, Oksanen & Henttonen 1996). Longer snowtracks of stoats compared to tracks of least weasels in our study agree with previous studies, and can be explained by smaller home ranges of least weasels, although due to subnivian hunting we may have underestimated the total mobility of least weasels. Caution is especially needed when interpreting the results of least weasel females. Higher mobility of males (particularly in least weasels) compared with females, however, might be also the result of the increasing activity of males during the reproductive season in late March, when males are seeking for females (Erlinge 1974, 1977).

Tracks of least weasels were longest in the low phase of the vole cycle. Increased mobility of

Table 2. Mean (\pm S.E.) difference in logratios (utilized–available) in habitat utilization of least weasels and stoats between farmland and woodland habitats in different phases of the vole cycle (the number of individual tracks followed equals to degrees of freedom + 1 in statistical tests below). Positive values represent preference of farmland habitats. Differences in logratios, which do not differ significantly (t -test^a) from zero, indicate random habitat utilization.

Species	Sex	Low	Increase	Decline
Least weasel	Males	3.8 \pm 0.4 $t_{58} = 9.3^{***}$	4.3 \pm 0.3 $t_{79} = 12.2^{***}$	5.0 \pm 0.2 $t_{72} = 21.3^{***}$
	Females	2.6 \pm 1.4 $t_{10} = 1.8$ NS	3.8 \pm 0.9 $t_8 = 4.4^{**}$	5.8 \pm 0 ^b
Stoat	Males	0.7 \pm 0.7 $t_{33} = 1.0$ NS	1.7 \pm 0.5 $t_{55} = 3.6^{**}$	3.0 \pm 0.4 $t_{74} = 7.2^{***}$
	Females	2.3 \pm 1.2 $t_{17} = 1.9$ NS	4.2 \pm 0.5 $t_{28} = 7.9^{***}$	3.5 \pm 0.6 $t_{44} = 6.2^{***}$

^a Significance levels adjusted by the table-wide sequential Bonferroni method (Rice 1989) are given as follows: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

^b All tracks ($n = 7$) recorded in farmland.

least weasels during food declines has also been observed in the tundra of northern Norway (Oksanen *et al.* 1992) and in the taiga of Finnish Lapland (Oksanen & Henttonen 1996). In parts of these northern landscapes, where small *Microtus* species are absent, *Clethrionomys* voles (*C. glareolus*; grey-sided vole, *C. rufocanus* and red vole, *C. rutilus*) appear to be more profitable prey than large *Microtus* species (root vole, *M. oeconomus*) to subnivean hunting technique of least weasels. In our study area, however, least weasels are dependent on *Microtus* in winter (Korpimäki *et al.* 1991). Therefore, they have to put more effort in searching for prey at low densities. Concurrently, the densities of least weasels are still relatively high, because of the delayed numerical response to changes in vole abundances (Korpimäki *et al.* 1991), making it even more difficult to catch enough *Microtus* voles.

The mobility of stoats was highest during the decline phase of the cycle. At this time, the densities of voles are declining from peak densities (Fig. 1), but are still relatively high. During declines, the percentage of *Microtus* in the diet of stoats is high (ca. 73% (Korpimäki *et al.* 1991)), whereas during low and increase phases, the proportion of *Microtus* is below 25% and 40%, respectively. Higher daily mobility of stoats during declines could be due to stoats increasing consumption of *Microtus* by active hunting and storing of voles. Surplus killing and storing of prey by small mustelids is earlier documented (e.g., Erlinge *et al.* 1974, Simms 1979, Oksanen *et al.* 1985 with references). On the other hand, hunting alternative prey during low and increase phases seems to result in shorter moving distances of stoats. A possible rea-

son for this is the large body size of alternative prey, such as water voles, rats, and muskrats, which may facilitate the daily energy requirements without continuous hunting. When vole densities are lowest, stoats may also occupy and utilize the last vole patches longer than smaller least weasels (Erlinge & Sandell 1988), resulting in a decreased mobility and energy expenditure of stoats. Accordingly, the obvious difference in the mobility of least weasels and stoats in relation to the prevailing cycle phase may result from least weasels being specialists and stoats being semi-generalist predators of voles.

Small mustelids choose their habitats mainly according to prey abundances (Nyholm 1959, Erlinge 1974, 1975, 1977, King 1975, Debrot & Mermod 1983), but social relationships also affect their habitat use (Lockie 1966). The risk of intraguild predation may modify spacing pattern of least weasels in order to avoid stoats and birds of prey (King & Moors 1979, Erlinge & Sandell 1988, Korpimäki & Norrdahl 1989b). In particular at high vole densities, both mustelid species preferred farmland habitats typical for *Microtus*. During the low phase of the vole cycle, stoats utilized different habitats randomly, whereas least weasel males preferred farmlands also at low vole densities. Male stoats used woodlands more than female stoats or least weasels. Larger body size of male stoats may allow catching larger prey species outside the *Microtus* habitats (Erlinge 1981). Furthermore we suggest that the outcome obtained is a relevant estimate of the winter season habitat use of small mustelids, because we probably succeeded to record the habitat use of most individuals in our small mustelid populations by conducting snowtracking several times per year with half-month intervals. However, pseudoreplication cannot be avoided where individual snowtracks were used as independent observations in statistical analyses and tracks of same individuals could have been followed in consecutive trackings.

Table 3. Mean (95% confidence intervals in parentheses) difference in logratios (utilized–available) of habitat utilization by small mustelids in the different phases of the vole cycle. Differences in logratios denoted by different superscript letters are significantly different (adjusted for multiple comparisons with Tukey's test).

Phase	Mean	95% CI
Low	2.36 ^a	(1.64, 3.08)
Increase	3.51 ^{ab}	(2.82, 4.20)
Decline	4.31 ^b	(3.59, 5.03)

4.2. Patterns and causes of density fluctuations in *Microtus* voles

That specialist predators are the key factor in driving the microtine rodent cycle has recently been

emphasized in many empirical and theoretical studies (e.g., Henttonen 1987, Henttonen *et al.* 1987, Hanski *et al.* 1991, 1993, Korpimäki *et al.* 1991, Hanski & Korpimäki 1995, Hanski & Henttonen 1996, Korpimäki & Krebs 1996, Oksanen & Henttonen 1996). In the vicinity of the Alajoki study area, the large-scale experimental reduction of small mustelids showed significant positive effects on the population growth and reproduction of *Microtus* voles (Klemola *et al.* 1997, Korpimäki & Norrdahl 1998). However, our current study together with an earlier study on the diet of small mustelids (Korpimäki *et al.* 1991) indicates that least weasels and stoats have partly separate mechanisms in modifying vole population dynamics. As larger predators, stoats can increase the proportion of alternative prey in their diet when voles are scarce, and this is reflected in changes their habitat utilization pattern away from typical *Microtus* habitats in farmland. Because stoats can survive past periods of low vole density by using alternative prey, they are present and may hunt voles also in low vole densities. Thus stoats may deepen and extend the low phase of the vole cycle. The consumption of voles by stoats is highest concurrently during declining vole densities (Korpimäki *et al.* 1991), indicating that stoats can strongly contribute to an abrupt decline of vole densities. Least weasels are true vole specialists; their winter diet is always mostly composed of *Microtus* voles (Korpimäki *et al.* 1991). Due to delayed numerical response of least weasels to changes in vole densities, they have a potential to induce a crash of *Microtus* vole populations, and in particular, to deepen and extend the low phase. Solving the problem of extended low phase seems to be the key to more thorough understanding of population cycles of voles (Boonstra *et al.* 1998, Korpimäki & Norrdahl 1998). Long-term field experiments with density manipulations of small mustelid predators may result in plausible answers to open questions (Korpimäki & Krebs 1996).

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