

Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles

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We used depletable food patches to determine the effect of microhabitat (mowed versus unmowed adjacent grasslands) and time (day versus night) on the foraging behavior of common voles (*Microtus arvalis*). The food remaining after 12-h periods (giving-up density, GUD) measured the vole's habitat selection under predation risk. In accord with several other rodent species and the effects of avian predators, voles had significantly lower GUDs in the unmowed than mowed portion of the grassland. GUDs in patches along the border between adjacent habitats were more similar to the risky mowed grassland than the safe unmowed grass. Time interacted strongly with microhabitat. In the mowed grass, voles had significantly higher GUDs at night than day. Whereas in the unmowed grass, GUDs were significantly higher during the day than night. Vole GUDs did not vary with time along the boundary. This suggests that predators are more abundant or effective in the mowed grass at night (owls?), and in the unmowed grass during the day (weasels?). In terms of predation risk, the voles perceived the mowed grass at night as the riskiest and the unmowed grass at night as the safest. Voles may have difficulties assessing resources under high predation risk: GUDs among patches were well equalized in the unmowed microhabitat whereas in the mowed grass only day GUDs did not vary significantly among patches. We linked these results to the vole's day-night-activity and life span. For the 533 voles live-trapped at the study area, the ratio of day versus night captures for each individual served as an activity index and the span between first and last capture measured minimum life span. In accord with higher GUDs at night, very few individuals behaved selectively towards the night, but individual life expectancy increased with temporal opportunism. Microhabitat differences in GUDs reflect short-term strategies of predator avoidance and the trapping data reflect long-term patterns of anti-predator behavior.

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Predators hunting voles kill (direct lethal effect) and frighten (indirect non-lethal effect) their prey. Predators, through their lethal effects, can influence population dynamics and might contribute to drive the flush-crash cycles of certain vole populations (Korpimäki and Krebs 1996, Korpimäki and Norrdahl 1998). Breeding suppression in female voles as a consequence of indirect effects of predation has been debated (Mappes et al. 1998) but recent studies show that it may

be one of the behavioral tactics of prey animals in response to predator abundance (Boonstra et al. 1998, Carlsen et al. 1999). Small mammals experience considerable temporal and spatial variability in predation risk, and these risks should be manifest in their feeding behavior (Price et al. 1984, Anderson 1986).

Predator avoidance influences the prey's behavior regarding activity times, foraging tactics, and microhabitat selection (e.g. Lima et al. 1985, Cowlshaw

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1997, Schmitz et al. 1997). The non-lethal effects lead to behavioral changes whereby voles should sacrifice food for safety. These effects can be measured by the animals' use of artificial food patches. The patches represent depletable food sources in a habitat that is characterized by food, intra- and interspecific contacts, and abiotic factors such as refuge and weather. The underlying model (Brown 1988, 1992), an extension of Charnov's (1976) marginal value theorem, predicts that a forager will stop depleting a patch when the benefits of the harvest rate no longer exceed the sum of energetic, predation and missed opportunity costs of foraging. Feeding therefore results in declining harvest rates until the forager reaches its giving-up density (GUD) and quits the patch (Brown 1988). This parameter reflects the harvest rate that is not acceptable to justify the predation risk and other costs of foraging.

Common voles (*Microtus arvalis* Pallas, 1779) are microtine rodents that typically inhabit fields and meadows. They can be active day and night (Erkinaro 1969). At high abundance they can cause crop damage (Hanak and Mazak 1979). Three features of voles motivate the present study. First, given their high mortality rate and prevalence in the diets of diverse predators (Stein 1958, Halle 1993), voles must experience severe predation risk, at least during certain times and in certain places. Second, while the grassland habitat of common voles is rather homogeneous, it does offer habitat variability with respect to magnitude of vegetation cover. In general rodent species as diverse as Negev desert gerbils (Brown et al. 1994a), North American desert rodents (Kotler 1984, Brown 1989), Indian crested porcupines (Brown and Alkon 1990), guinea pigs (Cassini 1991), and squirrels and chipmunks (Bowers et al. 1993, Brown and Morgan 1995) perceive greater risk in open (less vegetation cover or structure) than bush (more cover or structure) habitats. Voles may be expected to respond similarly. Third, voles are unusual with respect to the previously mentioned rodents in that they are active both night and day (Daan and Slopsema 1978, Halle 1995). Night and day vary in abiotic factors, numbers of predators, types of predators, and the appropriate senses and responses of prey to predators and vice versa for predators to prey. Just as these differences have promoted the evolution of owls versus hawks as temporally selective predators, the different challenges and opportunities of day versus night are thought to have encouraged most rodents to be selectively nocturnal or diurnal (Park 1940, Ashby 1972, Daan 1981). Why are common voles diel opportunists? Why are there not specialized nocturnal "mouse" voles and diurnal "squirrel" voles?

In the context of these three features of voles, we measured giving-up densities of free-living common voles to determine the effects of habitat (mowed grassland, unmowed grassland, and edge habitat) and night versus day on the voles' feeding behaviors and their

perceptions of foraging costs and opportunities. When cover is reduced by mowing without removing the grass, the mowed and unmowed areas should differ only in predation risk. Other factors should remain the same, especially given the short duration of the GUD experiments. Comparing GUDs of mowed and unmowed areas of the grassland should reveal if and how voles react to different numbers or aptitudes of predators. If the voles are able to assess patch quality including predation risk, one should find relatively equalized GUDs within habitats and lower GUDs in the safe, unmowed habitat (Valone and Brown 1989). Further, if predation risk differs from day to night due to night active predators such as owls and foxes, GUDs should be higher at night (Brown et al. 1994a).

Mark-recapture studies of animals yield information on population dynamics and demography as well as social, temporal, and spatial behavior (Delany 1974, Flowerdew 1976). Extensive live-trapping allowed us to separate individuals into three activity categories: selectively nocturnal, selectively diurnal, and opportunistic in their day/night activity schedules. Predator avoidance aims, in part, to extend the individual's life. The estimation of life spans of free ranging animals can be achieved by marking newborns followed by intense live-trapping until the animal disappears (Flowerdew 1976). However, this is extremely time consuming and it requires a large number of newborns. An easier approach is to calculate the span between first and last capture for each animal, irrespective of age or condition. While underestimating actual life span, this measure gives a relative approximation of life span. We can use this measure to test for the effect of day/night activity propensities on survivorship. If the seed tray experiments suggest that predation risk is not equally distributed over day and night, voles minimizing predatory risk should adjust their activity pattern accordingly.

Methods

Study area

The experiment was carried out on a five-year-old 8-ha grassland in the floodplain of the river Unstrut, 2 km north of Bad Langensalza, Thuringia, Germany (51°08'N, 10°38'E). Characteristic plant species included grasses such as *Festuca* spp. and *Dactylis glomerata* that are frequently eaten by voles (Myllymäki 1977, Leutert 1983). Before the feeding experiment the grassland was partially mowed without removal of the cut grass. This created an irregular mosaic of mowed and unmowed sections with a vegetation height of about 50 cm in the unmowed and 15 cm in the cut area at the time of the experiment. The unmowed stripes had an average size of 200 m², covered about 30% of the

grassland, and rarely exceeded a size of 30 m by 15 m. Neither fertilization nor grazing occurred.

Experimental design

We established a regular grid of 18 food patches with 6 m spacing between patches (six trays in each of the two microhabitats and six trays on the boundary). Each food patch consisted of a plastic tray (20 × 30 × 5 cm) secured to the ground with tent pegs and covered with a plastic awning on stilts. This construction allowed the voles access to the trays, prevented access by birds, and protected the food patch from rain. The spacing between neighboring trays of a line ensured that individual voles had access to trays within each microhabitat (mowed, unmowed, and boundary). Each tray contained an initial food mass of 5 g millet seed, mixed into 1 l of commercially available sand. Preliminary trials showed that crushed pumpkin and sunflower seed resulted in near total food depletion, often leaving a GUD of zero remaining food. In contrast, millet seeds yielded sufficiently high GUDs to allow for the appropriate resolution of factors influencing voles' foraging costs. Following pre-baiting and preliminary trials to develop a successful protocol, we collected data for 8 d in October 1997. Twice daily, at sunrise and again at sunset, the sand was sieved and remaining seeds retrieved and cleaned of sand and debris. After weighing the recovered seeds to determine the GUDs, all trays were restocked to repeat the procedure at the following sunset, yielding a total of 16 GUDs per tray. GUDs collected at sunrise and sunset represented the consequences of nocturnal and diurnal activity, respectively.

In a mark-recapture study on that grassland about 100 m away from the seed trays, 60 Ugglan multiple capture live traps were placed as a 10 × 6 grid with 10 m spacing covering 0.60 ha of partially mowed habitat. In this area, two stripes of 20 m length and 8 m width remained unmowed. Trapping sessions took place in July and October 1997, and monthly from April 1998 to March 1999. After 48 h of pre-baiting, trapping was carried out for 3–5 d. In the traps, oats, rodent chow pellets, pieces of apple, and wood wool were provided for food and shelter. The traps were checked at sunrise and sunset, and individuals caught for the first time were marked individually.

The ambient temperature was recorded automatically every 5 min (Stow-Away data loggers, Onset Instruments, Pacasset, MA, USA) with two replicates in the mowed and unmowed microhabitat.

Data analysis

We analyzed GUD data using a partially hierarchical ANOVA. We tested for the effects of microhabitat

(mowed, unmowed and border), time (day versus night), the interaction between microhabitat and time, and station (the 18 patch locations) on GUDs. In this analysis, patch is nested within microhabitat, and time is fully crossed with habitat and patch.

We used the trapping data to calculate an index of diurnality (Hoogenboom et al. 1984, Halle and Lehmann 1992) for 533 voles present during the period from July 1997 until March 1999 and trapped over the course of at least two different months:

$$I_D = \frac{(\text{sum of daycatches} - \text{sum of nightcatches})}{(\text{sum of daycatches} + \text{sum of nightcatches})}$$

where I_D measures selectivity for daytime. This measure can vary between $I_D = 1$ (complete selectivity for daylight) and $I_D = -1$ (complete selectivity for night). We also estimated the minimum life span as the time between first and last catch.

Data were analyzed by routines supplied by the programs JOLLY (Hines 1990), SPSS 9.0 and Excel 5.0 for Windows.

Results

Tracks in the sand, trapping data, and droppings found in the food patches demonstrated that trays were visited exclusively by common voles. With the exception of a single capture of *Apodemus sylvaticus* in October 1998, *M. arvalis* was the only rodent species found in 4680 trap nights. At the time of the experiment, density was estimated to be high at 348 individuals per ha (Jacob and Halle 1999).

Habitat significantly influenced GUDs (Table 1). GUDs were significantly lower in the unmowed habitat (0.69 g, s.e. = 0.11) than in either the border (2.34 g, s.e. = 0.17) or mowed (2.55 g, s.e. = 0.19) habitats. Our food patches should have differed little in missed opportunity or metabolic costs of foraging across habitats as individuals had access to trays in all three microhabitats and missed opportunity costs are an environment-wide measure of the marginal value of time to the foraging animal (Brown et al. 1992). Based on GUDs, we conclude that the unmowed habitat was perceived as less risky than either the mowed or border habitats.

Table 1. Effect of microhabitat (mowed, un-mowed, border) and darkness on giving-up densities. **: $p < 0.01$, ***: $p < 0.001$.

variables	d.f.	mean squares	F-ratio
Microhabitat	2	98.9	8.2**
Day/night	1	30.1	19.3***
Microhabitat × day/night	2	38.3	24.6***
Patch	15	12.0	7.7***
Error	253	1.34	

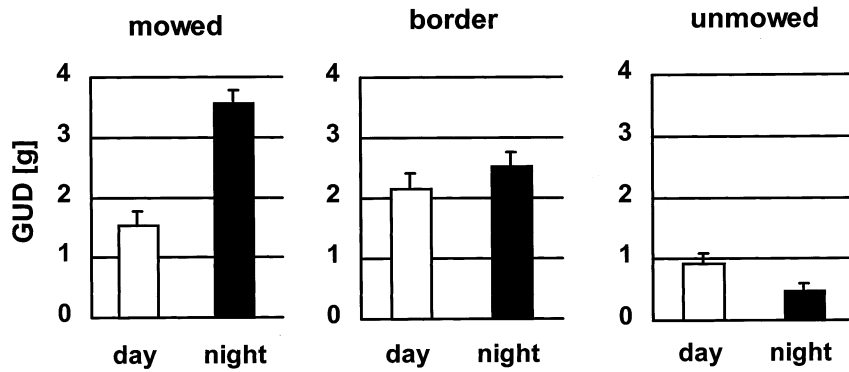


Fig. 1. Effect of darkness on GUDs for mowed and unmowed microhabitats and the border between them, error bars represent +1 SE.

Comparison of the day and night values for GUDs revealed significantly lower GUDs during the day (1.54 g, s.e. = 0.22) than for night (2.18 g, s.e. = 0.20).

The interaction between habitat and day/night was significant (Table 1). For the mowed grass, GUDs were significantly lower during the day than during the night. In contrast, for the unmowed grass habitat, GUDs were strikingly lower during the night than day (Fig. 1) but, in any case, lower than in the mowed section. For the border habitat, GUDs did not vary significantly with time. The voles' preference for day or night depends strongly on habitat. The nighttime was perceived as more favorable when foraging in the unmowed habitat while daytime was perceived as more favorable when foraging in the mowed habitat. These differences were also reflected in the numbers of trays skipped during exposure. In the mowed habitat two trays during the day and 13 trays during the night remained unforaged. At the border, two trays at night and one during the day remained unused. In the unmowed habitat no tray was ever left unvisited. The subsequent run of a Tukey HSD comparison showed that only two out of 15 possible combinations of GUD means of the microhabitats at day and night did not differ significantly. For the combinations of day- and night-GUDs for the border no difference was detected. Further, day-GUD means of mowed and border proved to be equal. The rank ordering of GUDs (the inverse of favorable) is: mowed night > border night = border day > mowed day > unmowed day > unmowed night. With respect to GUDs and predation risk, microhabitat matters most at night and least during the day.

The significant variation in GUDs among patches measures the ability of the voles to equalize GUDs among patches. A poor equalization of GUDs among patches within a microhabitat indicates either poor assessment, low mobility of the voles within a habitat, or microspatial variation in foraging costs (likely to be predation risk) at a scale smaller than habitat. To test for microspatial variation (effect of patch on GUD) we ran a Tukey HSD post hoc comparison. There were no detectable microspatial effects within the unmowed mi-

crohabitat and significant effects along the border and within the mowed microhabitat at night only.

Fig. 2 shows the relationship between selectivity for day and minimum life span. Inconsistent with the lower GUDs during the day, life span was not positively correlated with selectivity for the day. Rather a quadratic relation of minimum life span and I_D was found ($p = 0.004$). If we separate voles between those selective on the night ($I_D < -0.33$), selective on the day ($I_D > 0.33$) and temporally opportunistic ($-0.33 < I_D < 0.33$), we find 4%, 19%, 77% in each behavioral category, respectively. Most voles were temporally opportunistic, and very few behaved selectively towards the night. Interestingly, the longest minimum life spans emerged from temporal opportunists. The same pattern holds if we consider just those voles known to be alive

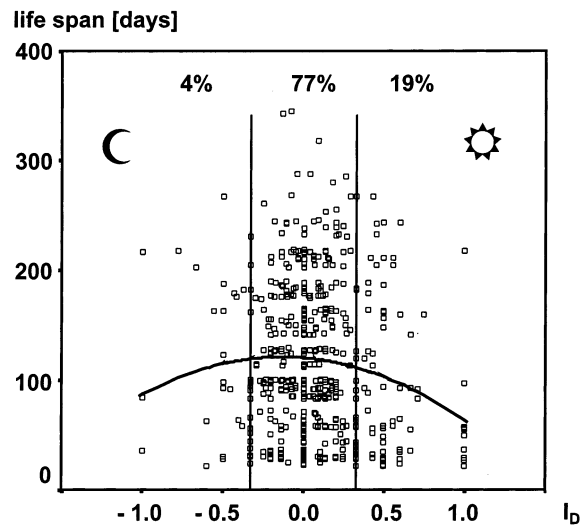


Fig. 2. Quadratic curve fit for the correlation of minimum life span and diurnality index I_D . The time between first and last catch was assumed to represent individual minimum life spans. The lower the I_D the more selective is an individual for the night. Percentages of the number of individuals are given according to equal ranges of I_D , separated by vertical lines. Equation: $y = 240.38 - 23.53x - 89.99x^2$, $n = 533$, $p = 0.004$; linear term $p = 0.297$; quadratic term $p = 0.014$.

during the feeding experiment and captured for at least two months ($n = 90$).

In terms of possible temperature effects on GUDs and foraging behavior, mean temperature for the mowed microhabitat was just 0.56°C higher than for the unmowed. Days were warmer than nights by 7.7°C for the mowed section and 6.9°C for the unmowed section. The largest temperature changes (up to 4.9°C) observed across 5-min intervals occurred around noon. Differences within and between habitats proved to be significant (one-way ANOVA, $p < 0.001$).

Discussion

We used giving-up densities to quantify the 'landscape of fear' (sensu John Laundre) experienced in time and space by common voles inhabiting a relatively homogeneous grassland habitat. As in many other rodent species with varying perceptions of predation risk depend on vegetation cover or structure (Brown and Alkon 1990, Hughes and Ward 1993, Kotler and Blaustein 1995, Holtcamp et al. 1997, Morris 1997, Thorson et al. 1998), voles behaved as though the unmowed grass was safer than the mowed grass. This pattern held for both night and day, although it was least extreme during the day and most extreme at night. Fear levels in the mowed habitat increased with night and fear levels in the unmowed habitat and along the border between mowed and unmowed grass did not change with time. Spatial variation in risk and giving-up densities for voles were least extreme during the day in the unmowed microhabitat and most extreme at night in the mowed one and at the border. Greatest variance occurs when GUDs are highest and it may well be that risky combinations of time and space create greater microspatial variation in risk. On the other hand we cannot exclude that voles are poorer assessors of patch quality when under high predation risk (Schmidt and Brown 1996).

For many terrestrial taxa examples of a daily interaction between time and space mediated through predation have been shown (Schaller 1972, Brown 1989, Altendorf 1997). Similar findings occur in totally different systems such as aquatic systems, where predation risk encourages some planktonic organisms to migrate vertically on a daily basis (Ohman et al. 1983, Atkinson et al. 1992).

We are quite confident that the giving-up densities reflected spatial and temporal differences in perceived predation risk rather than habitat or day/night variation in background food availability or metabolic costs of foraging. Background food availability does influence GUDs (e.g. fox squirrels, Brown et al. 1992), but the forager responds to its environment-wide food availability, not local availability within one of its microhabitats. In our short-term seed-tray experiment,

the mowed and unmowed habitats probably offered similar productivities and feeding opportunities as the mowed grass was left in situ. Possible differences such as enhanced plant growth because of reduced self shading and lower levels of secondary compounds (Hartley et al. 1995) may have improved conditions in the mowed microhabitat. Even so, the unmowed habitat was clearly preferred. Furthermore, a single vole individual had ready access to food patches within all habitats and so habitat differences in food availability should not influence habitat-specific differences in GUDs (see Appendix of Brown and Alkon 1990). The metabolic cost of foraging also influences GUDs. In gerbils, giving-up densities increase with declining ambient temperature (Kotler et al. 1993). Such effects are relatively small if the range of temperatures is not extreme, and these effects in desert rodents are small compared to variation in the cost of predation (Brown et al. 1994b). This may contribute to lower GUDs during day versus nights. However, the effect of predation risk seems necessary to explain the reverse effect in the unmowed grass (GUDs lower during the night) and the large magnitude of the effect in the mowed grass (1.53 g during day and 3.56 g at night).

Although we worked at the population level, it is worth speculating on the possible impacts on GUDs of the social system and differences among voles in their state. Subordinates may be forced into the mowed habitat. But the dominants' motive for occupying the unmowed habitat would still be habitat-specific differences in predation risk. In this case, dominants may enjoy safety while subordinates must endure risk. Furthermore, given the high densities in October, all space should be filled by territorial females. Before mowing, there should not have been major differences in habitat quality concerning predation risk or female territories. Telemetry studies on common voles on that plot in fall 1998 showed clearly that size and position of home ranges of adult residents did not differ before and after mowing and neither did density and survival (Jacob and Halle 2000). They did not move to the unmowed sections and it is rather unlikely that feeding of subadults would have been tolerated better by the adults living in the mowed than unmowed habitats. Therefore adults and subadults probably differed little in their distribution of feeding activities among the three habitats and among the feeding trays.

Presumably the diverse suite and tactics of potential predators contribute to the spatial and temporal lability of the fear landscape. Many effective and specialized predators of common voles are nocturnal or most active at twilight such as common weasel and stoat (*Mustela nivalis* and *M. erminea*), red fox (*Vulpes vulpes*), barn owl (*Tyto alba*), and long-eared owl (*Asio otus*) (Stein 1958). Sightings, droppings, and spit pellets indicated the presence of weasel, stoat, fox, and long-eared owl at the study site. Main diurnal predators at

the site during the study period included common buzzard (*Buteo buteo*), common European kite (*Milvus milvus*), and some diurnal activity by weasel and fox was observed. For rodents, cover provides protection from avian predators and foxes (Kotler et al. 1988, 1991, Cassini 1991), and this probably explains the higher perceived predation risk in the mowed than unmowed microhabitats. Furthermore, the large number of effective nocturnal predators may explain why GUDs were highest under the combination of night and mowed microhabitat.

That lowest GUDs occurred under the combination of night and unmowed habitat suggests two hypotheses. Predators may be selecting the unmowed microhabitat as their favorable hunting habitat during the day. Or, the attractiveness of the mowed microhabitat for nocturnal predators may reduce their activity levels in the unmowed habitat during the night. Either way the spatial and temporal patterns of predation risk probably incorporate a foraging game (Halle 1988, van Balan and Sabelis 1993, Hugie and Dill 1994, Brown et al. 1999) between the predators and the activity patterns of the vole.

Why are common voles active both night and day? Possibilities include the need for a small herbivorous rodent to regularly consume food throughout the day and night. Or, daily changes in the growth, germination or weathering of vegetation may create a regular renewal of feeding opportunities that encourage temporally opportunistic foraging patterns. We feel that our results implicate a strong role of predation risk. The interaction of time with foraging microhabitat on GUDs shows how voles should be facultatively nocturnal and diurnal. When harvesting resources from the mowed microhabitat, the daytime was safest. When harvesting from the unmowed habitat, nighttime was safest.

The potential foraging game between voles and their predators (e.g., predator facilitation, Korpimäki and Norrdahl 1998) may encourage activity throughout the day and night. If all voles were active just at night (or during the day), the predators may aggregate accordingly and create a scenario where the daytime (or nighttime) is now the preferable feeding time. Hence, in the long run, there is no escape from the great variety of diurnal and nocturnal vole predators by selectively choosing the day or night (Halle 1993). The ESS distribution of feeding times between predators and voles may require both nighttime and daytime activity (Halle and Lehmann 1987).

The voles differ substantially from gerbils of the Negev Desert where presumably intense pressure from diurnal predators and harsher physical conditions preclude daytime activity (Kotler et al. 1994). At some Negev Desert sites, jirds (*Meriones* sp.) do exhibit some daytime activity while remaining primarily nocturnal. In North American deserts it is common to have strictly

nocturnal rodents (pocket mice and kangaroo rats of the Heteromyidae) coexisting with strictly diurnal rodents (ground squirrels and chipmunks of *Spermophilus*, *Ammospermophilus* and *Eutamias*) (Brown 1989). Among well-studied rodents, voles seem to be the exception in exhibiting high levels of day and night activity.

Once day and night activity by voles is favored the question arises as to whether an individual should be temporally opportunistic or whether the population should split into individuals that feed selectively at night ("mouse" voles) and individuals that feed selectively during the day ("squirrel" voles). The data on activity patterns and minimum life span show that most voles were temporal opportunists with just a few selectively using the day and even fewer selectively using the night. Perhaps in accord with social rank, subordinate animals may be forced to be "mouse" voles or "squirrel" voles. The results of our GUD experiment may reflect short-term effects of predation risk while the trapping data may reflect longer term effects of temporal and spatial patterns of predation risk.

We do not have GUD measurements spanning the long-term live-trapping. It is quite likely that GUDs varied seasonally as shown for desert rodents in the Sonoran (Brown 1989) and Negev deserts (Brown et al. 1994a). With seasonal changes in predation risk, temporal and spatial habitat preferences may also change. Therefore, while intriguing and interesting, the link between GUD and life span in this study is merely a first step towards better understanding the relationship between foraging strategies and life span as a fitness parameter.

The ESS strategy of the voles seems to be a population of individuals using a mixed strategy (temporal opportunism) rather than a mixture of individuals using pure strategies (selectively nocturnal and selectively diurnal). Both the complementary nature of food and safety (Brown 1992, Houston et al. 1993) and advantages such as safety in numbers and exchanges of warning signals (Gerkema and Verhulst 1990) may explain the mixed strategy ESS of temporal opportunism. When spatial and/or temporal habitats vary in food and safety, the ESS encourages a forager to use a mix of high risk-high food and low risk-low food habitats (Brown 1998). As a consequence, a forager in a high energy state craves safety, and a forager in a state of high safety craves food (asset protection principle of Clark 1994). Furthermore the short-term synchronous activity of microtine rodents (Daan and Slopsema 1978, Halle 1995, Halle and Halle 1999) may also discourage the development of exclusively day-active or night-active subpopulations.

For voles, as probably occurs for many taxa and systems, predation risk promotes habitat heterogeneity in space and time. The interaction of space and time with predation risk creates an even richer degree of

heterogeneity and may create varied feeding opportunities. Animals, by switching activity among feeding in spatio-temporal habitats may be able to more finely balance the conflicting demands for food and safety. Individuals in dire need of energy can exploit rich but risky windows of feeding opportunity (nighttime in the mowed microhabitat) while individuals with excellent prospects because of social status or energy state can exploit poorer but safe windows of opportunity (nighttime in the unmowed microhabitat). These behavioral opportunities indubitably influence the foragers' population dynamics (Fryxell and Lundberg 1997), that of their predators (Schwinning and Rosenzweig 1990) and ultimately the composition of prey and predators within the community (Persson 1999). Being able to use food patches to measure these spatio-temporal habitats and the associated landscape of fear is an important first step in thinking about and making these links.

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