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The effects of habitat manipulation on population distribution and foraging behavior in meadow voles

Jyrki Pusenius and Kenneth A. Schmidt

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Individuals, free to choose between different habitat patches, should settle among them such that fitness is equalized. Alternatives to this ideal free distribution result into fitness differences among the patches. The concordance between fitnesses and foraging costs among inhabitants of different quality patches, demonstrated in recent studies, suggests that the mode of habitat selection and the resulting fitness patterns may have important implications to the resource use of a forager and to the survival of its prey. We studied how coarse scale selection between habitat patches of different quality and quitting harvest rate in these patches are related to each other and to fine scale patch use in meadow voles (*Microtus pennsylvanicus*). To demonstrate these relationships, we manipulated habitat patches within large field enclosures by mowing vegetative cover and adding supplemental food according to a 2 × 2 factorial design. We tracked vole population densities, collected giving-up densities (GUDs, a measure of patch quitting harvest rate), and monitored the removal of seeds from lattice grids with 1.5 m intervals (an index of fine-scale space use) in the manipulated habitat patches. Changes in habitat quality induced changes in habitat use at different spatial scales. In preferred habitats with intact cover, voles were despotic and GUDs were low, but increased with the addition of food. In contrast, voles in less-preferred mowed habitats settled into an ideal free distribution, GUDs were high and uninfluenced by the addition of food. Seed removal was enhanced by the presence of cover but inhibited by supplemental food. Across all treatments, vole densities and GUDs were strongly correlated making it impossible to separate their effects on seed removal rates. However, this relationship broke down in unmowed habitats, where GUDs rather than vole density primarily influenced seed removal by voles. GUDs and seed removal correlated with predation on tree seedlings formerly planted into the enclosures, demonstrating the mechanisms between coarse-scale habitat manipulations and community level consequences on a forager's prey.

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Our understanding of habitat use has greatly profited from mechanistic approaches that experimentally manipulate habitat quality (e.g. predation risk, food availability) and monitor the subsequent movements of individuals and their resulting distributions (Bowers and Dooley 1993, Diffendorfer 1998, Basquill and Bondrup-Nielsen 1999a, b, Abramsky et al. 2000a, Pusenius et al. 2000). An alternative approach uses giving-up densities from artificial food patches (Brown 1988, Brown et al. 1992, Kotler 1997, Morris 1997, Morris and Davidson 2000) to measure foraging costs associated with a particular habitat type or habitat feature. These two approaches, population response and giving-up densities, should converge on similar explanations and results; all else equal, individuals should settle disproportionately in habitats with lower

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foraging costs. But despite their widespread usage, these two approaches have seldom been merged together (but see Morris and Davidson 2000).

Density-dependent habitat selection provides the conceptual framework for coarse-scale habitat selection (Rosenzweig 1981, 1991, Morris 1988, 1990, Brown 1998). Assuming competitors have free and equal access to all available habitat patches, individuals that experience declines in fitness with increased density should settle among available habitat types such that fitness is equalized (Milinski and Parker 1991, Abramsky et al. 2000b). The resulting stable distribution of individuals across multiple habitats is called an ideal free distribution (IFD; Fretwell et al. 1970). Various modifications and alternatives to the IFD result in fitness differences among habitats (for reviews, see Milinski and Parker 1991, Tregenza et al. 1996). The ideal despotic distribution (IDD, Fretwell 1972) applies under situations where habitat selection of subordinate individuals is constrained by territoriality of dominant individuals. Alternatively, the truncated phenotype distribution (TPD, Milinski and Parker 1991), predicts that phenotypes are split between patches, with the best competitors and highest fitness occurring in the patch where competitive differences are greatest.

At the microscale, habitat selection falls under the purview of patch use theory. A forager, which balances its time between foraging under predation risk and choosing alternative activities, should depart from a resource patch when its harvest rate falls to the sum of predation (P), missed opportunity (MOC) and metabolic (C) foraging costs (Brown 1988, 1992). The rate of resource harvest at which this relationship holds and the forager ceases foraging is called patch quitting harvest rate, i.e. $QHR = P + MOC + C$. A forager that can assess and respond to spatial heterogeneity in resource abundance should exploit only those resource patches that it considers profitable (Stephens and Krebs 1986, Schmidt and Brown 1996, Schmidt et al. 2001). Profitable patches contain resources in excess of a forager's QHR. The total area of patches that exceed the QHR determines the amount of available space an individual will use. The unused patches represent enemy-free space (sensu Schmidt et al. 2001) to the forager's prey, because of the absence of foraging activity in these patches. Total predation rates on prey should decline as the sum total of patches with resource densities below the QHR increases, i.e. for any prey individual the probability of encountering a forager should be inversely related with the forager's QHR. Besides forming by the existence of unprofitable patches within a forager's home range, enemy-free space may also form in gaps between home ranges of neighboring foragers.

Quitting harvest rates may fluctuate in time and space through various mechanisms. For example, the state of the individual forager, its perceived risk of predation, and its marginal valuation of food (i.e. energy) and time influence the QHR (Brown 1992, Brown et al. 1992). The QHR should vary in relation to factors affecting large-scale differences in predation risk and food availability that, in turn, affect the foraging costs of individual foragers (Morgan et al. 1997, Olsson and Holmgren 1999, Schmidt et al. 2001). Conversely examining patterns in QHRs and its component costs should reveal information about the forager and the environment it exploits (Brown et al. 1994a, Abramsky et al. 2000b).

Recent studies have revealed that long-term foraging patterns are closely related to forager fitness (Olsson and Holmgren 1999, Morris and Davidson 2000). The relationship can be illustrated by analyzing individual fitness costs. For example, following Brown (1992) the equation for the predation cost is: $P = \mu F/(\partial F/\partial e)$. The predation cost increases with increasing the probability of predation, μ, the expected fitness potential of a surviving forager, F, or with decreasing marginal valuation of energy, $\partial F/\partial e$. Besides their relationship with P, the components μ and $\partial F/\partial e$ are also related to an individual's expected fitness given it survives to realize its fitness. Therefore we can explore, at least qualitatively, fitness differences between individuals or populations as detected by changes in their quitting harvest rates (Morris and Davidson 2000).

For instance, according to the asset protection principle (Clark 1994) a forager with high survivor's fitness, F, has more to lose from predation than a forager with low fitness. Hence both the forager's predation cost and QHR should increase concomitantly with fitness. Second, a forager in or near a state of negative energy balance puts a high premium on the value of energy, $\partial F/\partial e$, while devaluating safety from predators (Lima 1988, Brown 1992, Brown et al. 1992) and consequently decreases its QHR. Assuming fitness is positively related to an individual's energy balance (Stephens and Krebs 1986), there will again be a positive relationship between fitness and quitting harvest rates. In contrast, predation risk, μ, is inversely related to fitness but positively related to quitting harvest rates (Thorson et al. 1998). Thus, if fitness differences are due to differential predation risk, an inverse relationship between fitness and QHR should prevail (Morris and Davidson 2000). The preceding points suggest that the observed relationship between fitness and QHR can be used to infer which factor(s) (μ, $\partial F/\partial e$, survivor's fitness) are likely explaining most of the variation in P.

The relationships between QHRs and fitness make the collection of QHR data (often through a surrogate, such as giving-up densities; Brown 1988) a powerful technique for investigating the fitness consequences of variability in habitat quality, the distribution of individuals across habitats, and density-dependent decline in fitness. Recent studies (Olsson et al. 1999, Morris and Davidson 2000) have demonstrated that differences in giving-up densities from artificial resource patches matched differences in fitness between habitats. In our current study, we go a step further. We experimentally manipulated habitats and followed both the distribution of meadow voles (*Microtus pennsylvanicus*) across habitat patches and the foraging costs associated with each habitat. By measuring both the population responses at coarse scales and foraging responses at local scales, we can test for concordance of results between the two approaches with implications toward the efficacy of using behavioral measures to infer population characteristics, such as fitness and habitat distribution.

Furthermore we examined the relative roles of population density and foraging behavior that in turn determine patterns of space use by meadow voles. Finally, we quantified the amount of enemy-free space in each habitat and correlated the amount of enemy-free space and predation on tree seedlings planted in each habitat (see Pusenius et al. 2000). Thus the results we document below also have broader implications for multiple trophic levels.

Predictions

Our study system consists of replicate vole populations that redistribute themselves among four discrete habitats of different quality ($Q1 \neq Q2 \neq Q3 \neq Q4$) initially following habitat manipulations (i.e. mowing and food addition). If an IDD prevails, each dominant individual should take control of an economically defendable (Davies and Houston 1984) proportion of the resources in the best habitat. After all the resources in the best habitat have been acquisitioned, the fraction of the population that failed to gain access to resources there should occupy the less favorable habitats in order of decreasing quality. The proportion of subordinates forced into less favorable habitats should correlate positively with the total vole density, N (Messier et al. 1990, Tregenza et al. 1996). In contrast, if an IFD prevails, the fraction of population in each habitat should depend on the quality of the habitats, i.e. Q1,…, Q4 (Milinski and Parker 1991) but not N (Messier et al. 1990, Tregenza et al. 1996). TPD can be identified by different mean phenotypic values in traits (e.g. body mass) indicating competitive ability across habitat patches (Milinski and Parker 1991).

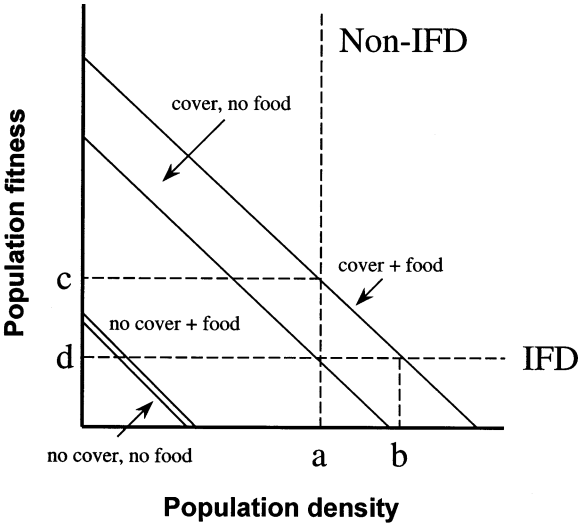

Fig. 1. Predicted relationships between population density, fitness and habitat quality (presence of cover and food supplementation), when populations conform to ideal free distribution (IFD) and when they do not (Non-IFD).

Depending on the distribution of voles (IFD vs IDD/TPD), the habitat manipulations may cause a change in fitness with a predicted concomitant change in the QHR according to the principles outlined above. We summarize predicted responses to changes in habitat quality in Fig. 1. We assume that fitness declines linearly with forager density. Increasing habitat quality through food addition increases the y-intercept, whereas decreasing habitat quality by increasing predation risk (mowing protective cover) decreases the intercept. If the foragers settle into a new IFD as indicated by the horizontal line in Fig. 1, fitness remains constant across habitats; higher quality habitats simply contain more individuals (point b vs a; Fig. 1). If the foragers do not settle into a new IFD following manipulation, densities remain the same as before manipulation (vertical line in Fig. 1), but fitness is higher under more favorable conditions (point c vs d; Fig. 1). We assume that QHR and fitness are qualitatively interchangeable if habitats do not differ in predation risk. Thus we predict QHRs will be similar for populations that are in an IFD. If voles do not settle into an IFD, QHRs will be higher in the plots with food addition. We expect the effect of food addition to be greater in safe habitats because the higher densities of individuals will make food limitation more likely (Fig. 1). In contrast, safety is more limiting in risky habitats, and thus food addition is unlikely to have a substantial effect on fitness. In response to predation risk manipulation, QHRs will increase relative to safe habitats, although fitness decreases because predation risk and fitness are inversely related. Finally, following the arguments of Schmidt et al. (2001) and above, we predict that the amount of space used (seed removal from lattice grids) would decrease with increasing QHR, but increase with population density. Surviving seeds indicate enemy-free space, at least during the duration of the experiment, and the rate of predation on experimental tree seedlings should correlate with this index of enemy-free space.

Materials and methods

Study site and habitat manipulations

We carried out our experiments in six adjoining 40 × 40 m enclosures in old field habitat on the property of the Institute of Ecosystem Studies in southeastern New York State, U.S.A. Enclosures were fenced with galvanized hardware cloth extending 1 m above and 0.5 m below ground and with a mesh size of 0.8 cm. Grasses (*Bromus inermis*, *Poa pratensis*, *Arrhenatherum elatius*, *Phleum pratense*) and forbs (*Galium mollugo*, *Solanum carolinense*, *Glechoma hederacea*, *Oxalis repens*, *Potentilla* spp., *Hieracium pratense*, *Solidago* spp.) dominated vegetation in the enclosures.

The present study utilized an experimental system designed to study the effects of the level of experience of voles within their neighborhood (residents vs immigrants) and habitat quality on the rate of tree seedling predation of meadow voles (see Pusenius et al. 2000 for details). We created three replicates of resident and immigrant populations and subjected each population to cover reduction and food augmentation. We conducted habitat manipulations using a 2 × 2 factorial design within the enclosures. Each enclosure was divided into four 20 × 20 m quadrats. Two diagonal quadrats were chosen for cover reduction treatment and were mown to a height of 5 cm. One quadrat of both reduced cover and intact vegetation treatments were randomly selected for food augmentation, which consisted of distributing commercial alfalfa cubes into the chosen quadrats. We mowed the diagonal quadrats between 1 and 2 October 1998. Due to the very modest regrowth of vegetation, no further mowing was required during the experiment. We augmented the alfalfa cubes on 6 October and thereafter repeated the procedure once each week to ensure a consistent amount and quality of supplemental food. One alfalfa cube weighed, on average, 20 g, and the cubes were sown randomly at 1 cube per 2 m^2 (10 g per m^2 per week). Based on the energetic value of alfalfa cubes (9 kJ/g) and the energy consumption of voles (60 kJ/day for a related species, *Microtus arvalis*; Ryszkowski et al. 1973), we estimate that the alfalfa cubes alone could supply enough energy to support 86 voles in each augmented 20 × 20 m quadrate between augmentation events.

Censuses and manipulations of vole populations

We created the experimental vole populations from individuals occurring naturally within the enclosures. Each enclosure had 25 trap points arranged in a grid with 7.5 m intervals. We used Ugglan multiple capture traps baited with whole oats and supplied with cotton bedding. We ear-tagged all captured voles during the first capture and subsequently checked tag number, body mass and sexual status. We established immigrant populations between 14 and 17 October by exchanging the vole populations among 3 randomly chosen enclosures. We assessed the distribution of voles among the habitat patches using live-trapping data obtained between 3 and 6 November. Thus immigrant voles should have had time to settle down and become accustomed to their new location (Pusenius et al. 2000). On each trapping day, we set traps in the evening before sunset and checked them the next morning. We estimated vole density within each enclosure and habitat using the Jackknife-estimate supplied in the software CAPTURE (Rexstad and Burnham 1998).

Assessing quitting harvest rates: giving-up densities

We assessed quitting harvest rates by collecting giving-up densities from artificial food patches (Brown 1988) composed of plastic trays (diameter 30 cm, depth 3 cm) containing 5 g of oats seeds thoroughly mixed into 1.0 l of sifted sand. Voles foraging in the artificial food patches should experience diminishing returns as their harvest rate declines with time spent in the patch. Given such diminishing returns, a vole should exploit a patch until its harvest rate declines to the sum of its foraging costs. The density of remaining food at which this relationship is satisfied and the forager ceases exploiting the patch is its giving-up density, GUD (Brown 1988, 1992). GUDs thus provide a surrogate for the quitting harvest rate in a resource patch. We collected GUDs between sunset and sunrise on the nights of 20 October and 1 November 1998. On each occasion, we placed a single tray at the midpoint of each 20 × 20 m habitat patch. In the morning, we sieved the trays to remove the uneaten food, cleaned them of debris, and weighed the seeds to determine the giving-up density. In most cases, we identified vole activity based on the presence of feces and urine in the patch.

Space use: seed grid experiment

We quantified fine-scale patch selection in each habitat type from the proportion of seeds removed from an experimental lattice grid (Thompson et al. 1991). On 12 November 1998, we established a 10 × 10 lattice grid (1.5 m intervals) within each 20 × 20 m habitat patch with 10 m buffer zones between grids situated in adjacent habitats. We marked the grid points with 20 cm long wooden skewer sticks and placed a single oat seed at the base of each skewer within the vegetation, which made detection by birds unlikely. We censused the grids 2 and 4 days after placing out the oats. During both census periods, we noted the presence or absence of a

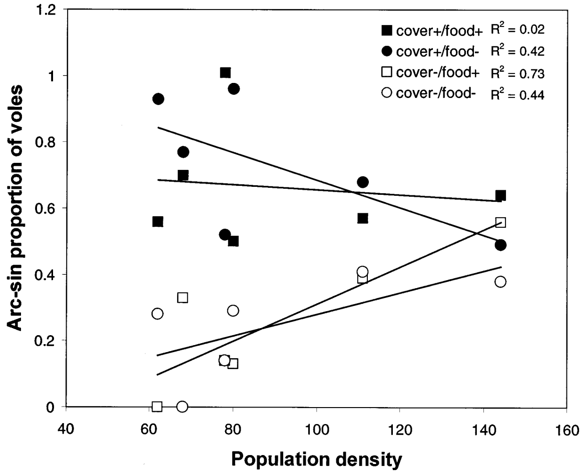

Fig. 2. Proportion (arcsin-transformation) of voles in the different manipulated habitat patches as a function of population density (voles per enclosure). Coefficient of determination (R^2) of the regression between the proportion of voles and population density is given for each habitat.

seed. We presumed missing seeds to be eaten by voles and did not replace them. Mice were not present in the plots and ant and bird activity was virtually nonexistent (pers. obs.).

Consequences for prey: predation on tree seedlings

On 18 October 1998, we planted seedlings of red maple (*Acer rubrum*) and black birch (*Betula lenta*) in the enclosures. Each habitat manipulation received 2 seedling stations and each station received 8 seedlings for a total of 64 seedlings per enclosure ($2 \times 4 \times 8 = 64$). In each station, we arranged the 8 seedlings into 2 rows of 4 seedlings with a 25 cm-spacing between individual seedlings. We censused seedlings 9 times post-planting, and use the results of the last census (19 November) in the present study (for more details see Pusenius et al. 2000).

Statistical analyses

Our experimental units were enclosures each consisting of 4 habitat patches connected via habitat selection of voles. We took into account the dependency of measurements from the different habitat patches of each enclosure by using repeated measures analysis of variance (rmANOVA) to test for the effects of mowing, food addition, and their interactions on habitat preference, body mass, and GUDs. We included population status into the models as a between subject factor. Vole densities were transformed using the arcsine square-root proportion of voles in each habitat patch. GUDs were logarithimically transformed to normalize the data and to provide a more linear fit between GUDs and quitting harvest rates (Kotler and Brown 1990). Population density within each enclosure was added as a covariate into the model testing habitat preferences. The results of Pusenius et al. (2000) indicate that the rate of movement between habitat patches decreased with time elapsed from the experimental manipulations. Thus we considered the seed grids surrounded by buffer zones as independent replicates and applied standard ANOVA techniques for the analysis of seed removal.

We also performed an isodar analysis (Morris 1988, 1990) to determine if voles were distributed in an ideal free manner. Isodars plot the density of a population in one habitat versus its corresponding population density in a second habitat that is connected to the first via density-dependent habitat selection. Populations at an IFD can be detected by an isodar slope > 0, whereas the isodar intercept corresponds to differences in maximum fitness between the two habitats (Morris 1988, 1990). We examined isodars between food addition treatments for mowed and unmowed treatments separately. Isodars are likely to be nonlinear when predation risk varies between the habitats under comparison (Brown 1998) and not conducive to analysis given our low sample size.

We ran the statistical analyses using SPSS 10.1. software (SPSS 1992). We use univariate tests of rmANOVA whenever the criteria represented by Potvin et al. (1990) were met. We apply one-tailed P-values where one-way hypotheses had been set a priori. All data values we give are a mean ($\pm$ SE).

Results

Population distribution

Vole densities ranged from < 100 individuals/ha to > 800/ha in the different habitats. Prior to habitat manipulations, voles showed no preference between the habitat patches (rmANOVA, $P > 0.17$) slated for future manipulation of food and cover. The analysis of post-manipulation trapping data revealed a significant main effect of cover (Fig. 2, Table 1), and a significant cover by population density interaction. In the enclosures with the lowest densities, voles occupied primarily the unmowed patches (Fig. 2), indicating preference for cover. However, the proportion of voles in different patches was density-dependent. The proportion of voles in the mowed (low quality) habitat correlated positively with total vole density (Pearson's product moment correlation coefficient, $r_p = 0.89$, $N = 6$, $P = 0.017$), whereas the proportion of voles in the unmowed habitat correlated negatively with total vole density ($r_p = -0.87$, $N = 6$, $P = 0.024$). These results are consistent only with the IDD model.

We found a significant isodar regression between vole densities (with and without food addition) in the unmowed habitats, but with a negative slope ($B = -0.88$, $r^2 = 0.61$, one-tailed $P = 0.033$) and thus inconsistent with an IFD. However, the regression between densities of the mowed patches with and without food addition had a positive slope ($B = 1.39$, $r^2 = 0.60$, one-tailed $P = 0.036$) not significantly different from one and an intercept not significantly different from zero indicating an IFD. Thus, the type of distribution of voles across habitats appeared to be dependent on which habitats are compared.

Table 1. The effects of cover, food and population status (residents vs immigrants) manipulations and population density on the proportion of voles found in the different habitat patches. Cover and food are within-subject factors, population status and density (covariate) are between-subject factors in rmANCOVA model. Main effects of population status and density are dropped due to their irrelevance when testing proportions.

Source of variation	df	MS	F	Sig.
Cover (C)	1	0.35	85.07	0.003
C by Density (D)	1	0.11	27.87	0.013
C by Status (S)	1	0.01	1.41	0.32
Error	3	0.004		
Food (F)	1	0.01	0.07	0.81
F by D	1	0.004	0.05	0.84
F by S	1	0.03	0.34	0.60
Error	3	0.08		
C by F	1	0.03	0.94	0.40
C by F by D	1	0.02	0.77	0.44
C by F by S	1	0.04	1.31	0.34
Error	3	0.03		

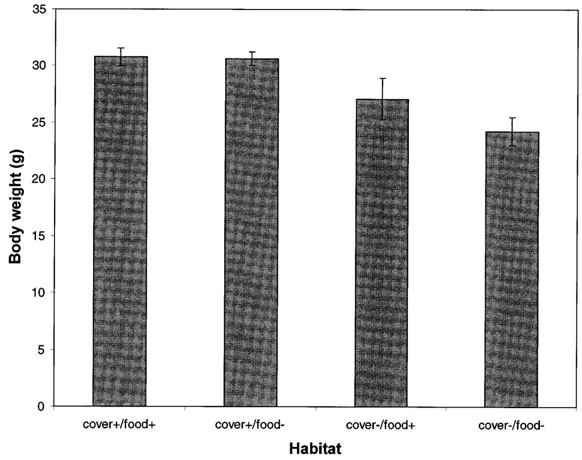

Fig. 3. Body weight of voles (± SE) in the different manipulated habitat patches.

Table 2. The effects of cover, food, and population status (residents vs immigrants) manipulations on body size of voles. Cover and food are within-subject factors, population status is a between-subject factor in rmANOVA model.

Source of variation	df	MS	F	Sig.
Cover (C)	1	151.86	13.47	0.021
C by Status (S)	1	7.31	0.65	0.47
Error	4	11.27		
Food (F)	1	13.87	1.72	0.26
F by S	1	7.92	0.99	0.38
Error	4	8.04		
C by F	1	10.88	4.53	0.10
C by F by S	1	1.60	0.66	0.46
Error	4	2.40		
S	1	9.68	0.63	0.47
Error	4	15.24		

Vole body mass did not differ between the subplots prior to habitat manipulation (rmANOVA, $P > 0.59$ for the effects of cover, food and their interaction). However, post-manipulation voles within cover were heavier than those in the mowed patches (Fig. 3, Table 2). These differences may have arisen from differences in habitat quality (i.e. voles in high quality habitat put on more weight) or because larger voles had priority access to higher quality habitat (i.e. pre-existing large voles monopolized the higher quality habitat). To test these alternatives, we compared the pre-population exchange body mass of immigrant voles that settled in the unmowed vs mowed patches after the population exchange. Voles in unmowed patches were larger than voles in mowed patches (28.16 ± 5.98 g, $N = 32$; 23.38 ± 7.11 g, $N = 8$, respectively; $t = 1.95$, $df = 38$, one-tailed $P = 0.030$) supporting the mechanism of dominance by larger individuals.

Using the number of individuals captured per trap station, we calculated the metric: [(variance/mean) − 1], as a cue of the spatial distribution of voles in the different habitat patches. The results indicate that the voles of unmowed patches were more uniformly distributed than those of mowed patches (-0.21 ± 0.11, $N = 12$; 0.53 ± 0.30, $N = 12$, respectively, $t = -2.41$, $P = 0.025$). The negative mean in the unmowed patches indicate tendency towards territoriality.

Giving-up densities

Because our predictions concerning GUDs are contingent upon the population distribution, which in turn depends upon the habitats compared (see above), we reiterate our earlier predictions of GUDs under different distributions. If individuals are distributed in an IFD (as observed between food addition treatments in mowed habitats) we expect GUDs to be equalized across comparisons. In contrast, if individuals are distributed in a non-IFD (as observed between food addition treatments in unmowed habitats) we expect GUDs to be unequal across comparisons, and will be higher in the plots with food addition. Finally, we expect GUDs to decline with increasing vole density and to increase under higher predation risk (i.e. in mowed habitats).

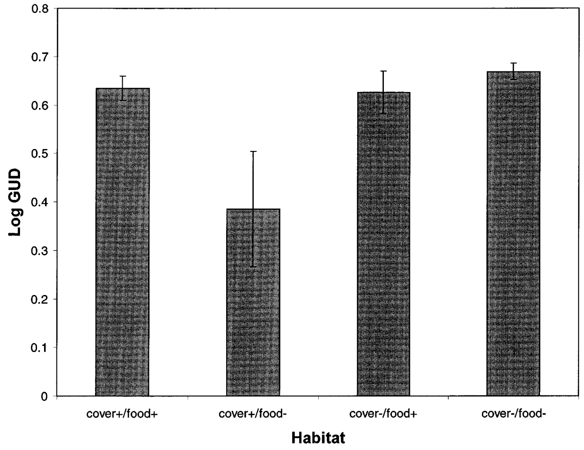

Fig. 4. Log giving-up densities (± SE) in the different manipulated habitat patches.

Table 3. The effects of cover, food, and population status (residents vs immigrants) manipulations on giving-up densities (log-transformed). Cover and food are within-subject factors, population status is a between-subject factor in rmANOVA model.

Source of variation	df	MS	F	Sig.
Cover (C)	1	0.11	5.02	0.089
C by Status (S)	1	0.01	0.50	0.52
Error	4	0.02		
Food (F)	1	0.06	1.64	0.27
F by S	1	0.01	0.25	0.64
Error	4	0.04		
C by F	1	0.13	11.74	0.027
C by F by S	1	0.03	2.63	0.18
Error	4	0.01		
S	1	0.07	3.00	0.16
Error	4	0.02		

Table 4. Results of ANCOVA using the proportion of seeds depredated (arcsine square-root transformed) as the dependent variable, population status, cover, and food addition as fully-crossed independent variables, and within habitat vole population density as a covariate.

Source of variation	df	MS	F	Sig.
Density	1	0.13	8.75	0.009
Population status	1	0.08	5.00	0.040
Cover	1	0.32	21.07	0.000
Food	1	0.01	0.83	0.38
Cover by Food	1	0.03	2.20	0.16
Cover by Density	1	0.05	3.58	0.077
Food by Density	1	0.09	6.22	0.024
Error	16	0.02		

GUDs were lowest in the habitat with intact cover and no extra food. Results of rmANOVA showed no significant main effect of vole density, status, cover manipulation or food addition on GUDs. However, there was a significant interaction between cover and food (Fig. 4, Table 3). GUDs were equalized across food addition treatment in mowed but not in unmowed treatments (Fig. 4). We detected a density-dependent decline in GUDs in the mowed habitat only ($r^2 = 0.76$, $P < 0.001$; unmowed habitat $r^2 = 0.07$, $P = 0.41$).

Seed removal and enemy-free space

We used ANCOVA ($r^2 = 0.90$) to test for the main effects of vole density, population status (immigrant versus resident), mowing, and food addition on the proportion (arcsine square-root transformed) of seeds removed from the lattice grids by the second census. In addition, we included all pairwise interactions between density, mowing, and food addition. Vole density, population status, and mowing all had significant effects on the proportion of seeds removed from the lattice grids (Table 4). The proportion of seeds removed was smaller in mowed patches (0.24 ± 0.05) versus unmowed patches (0.72 ± 0.04), and resident voles removed more seeds than did immigrants (0.84 ± 0.08; 0.67 ± 0.10; respectively). Despite fewer seeds consumed in patches that received additional food (0.42 ± 0.07 versus 0.54 ± 0.09), food addition did not have a significant main effect. However, the interaction between food augmentation and density indicates that relatively fewer seeds were consumed as vole density increased in patches to which we added food (Table 4, Fig. 5).

Both vole density and GUDs were correlated with seed removal (Fig. 6 and 7). Ideally, we would like to separate the effects of vole density and giving-up densities on the proportion of seeds removed, but these measures were strongly and negatively correlated with

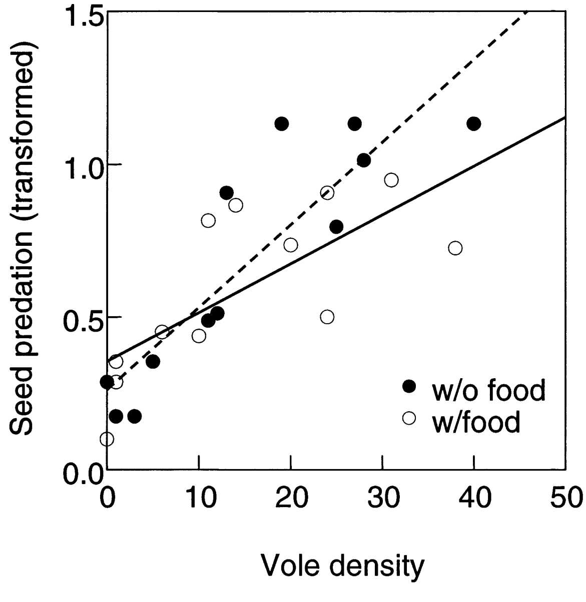

Fig. 5. Seed removal plotted against vole density for the two different food addition treatments. Seed removal is given as the proportion (arcsine square-root transformed) of seeds removed from the lattice grids by the second census.

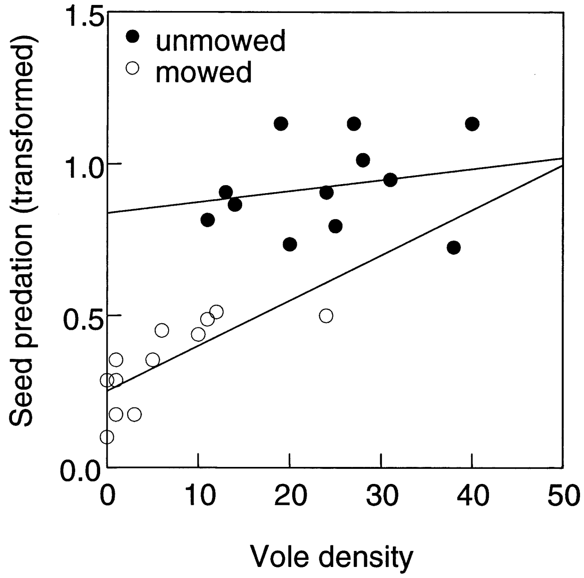

Fig. 6. Seed removal plotted against vole density for the two different mowing treatments. Seed removal is given as the proportion (arcsine square-root transformed) of seeds removed from the lattice grids by the second census.

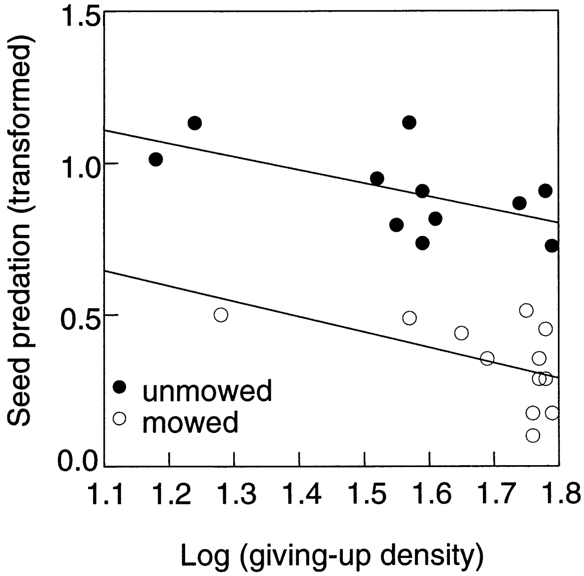

Fig. 7. Seed removal plotted against giving-up density. An outlier was removed from the unmowed data, which represented a data point > 5 standard deviations from the mean. Seed removal is given as the proportion (arcsine square-root transformed) of seeds removed from the lattice grids by the second census.

each other. However, when diagnosing the residuals of the regression between density and GUDs, the absolute values of residuals increased with density ($r_p = 0.51$, $N = 24$, $P = 0.011$). The large absolute values of residuals were clearly associated with the unmowed habitats; in other words, the relationship between GUDs and density is habitat dependent (absolute values of standardized residuals; mowed, 0.22 ± 0.07, $N = 12$; unmowed, 0.84 ± 0.31, $N = 12$; Mann-Whitney U-test, $Z = -2.19$, $P = 0.028$). To examine these relationships further, we ran pairwise correlations between GUDs and density separately in the mowed and unmowed habitats. The correlation was strong in the mowed habitats ($r_p = -0.87$, $N = 12$, $P < 0.001$) but nonexistent in the unmowed ones ($r_p = -0.26$, $N = 12$, $P = 0.41$). Thus we regressed seed removal against vole density and GUDs in the unmowed habitats and found that GUDs were a significant predictor of the rate of seed removal in the multiple regression model ($B = -0.31 \pm 0.11$, $t = -2.83$, $P = 0.02$) while density was not ($B = 0.002 \pm 0.004$, $t = 0.49$, $P = 0.64$). We conclude that the effects of density and GUDs are inseparable in the mowed habitat, but that only GUD had a significant effect on seed removal in the unmowed habitat.

Finally, the proportion of depredated tree seedlings correlated significantly with the proportion of seeds removed ($r_p = 0.54$, $N = 24$, one-tailed $P = 0.003$) and GUDs ($r_p = -0.38$, $N = 24$, one-tailed $P = 0.034$).

Discussion

Meadow voles responded to large-scale manipulations of predation risk (mowing) and food availability at two different spatial scales. At the coarse-scale, voles redistributed themselves following manipulations among the habitat types of different quality. At the fine-scale, patch use (i.e. quitting harvest rate) was influenced by foraging costs set by the coarse-scale habitat manipulations and modified by the consequential distribution of individuals among habitats. Together, density and quitting harvest rate determined the amount of available space voles used in the different habitat patches. We interpret the amount of space used as an index of enemy-free space and found it to have a significant relationship with predation rates on experimental tree seedlings. Below, we provide a detailed discussion of these patterns.

Population distribution

After our habitat and population exchange manipulations, voles could (re)settle into either an ideal-free, ideal-despotic or truncated-phenotype distribution as they adjusted their densities to our manipulations. Interestingly, the type of population distribution depended on the habitats we compared. The greatest differences arose between mowed and unmowed patches. In this case our observations argue against an IFD. First, the positive correlation between population density and the proportion of voles in the less preferred mowed patches indicates IDD. Second, individuals inhabiting the unmowed habitats were larger than those of the mowed patches. Although this latter pattern could also indicate a TPD, territoriality of large individuals in the unmowed patches would explain both of these patterns. When all the space available in the unmowed patches was pre-empted, many young, as well as some old individuals weakened by age (pers. obs.), were forced to occupy the lower quality mowed patches. As a result, the distribution of body size diverged between the unmowed and mowed patches. This conclusion is further supported by the association between pre-exchange body mass and habitat occupancy following manipulation; larger voles occupied the best habitat.

Our live-trapping data do not allow a detailed assessment of social interactions between individuals, but our observations are consistent with the existing knowledge of spacing behavior of voles. Spacing behavior is known to change with age, sex and habitat quality (e.g. Viitala and Pusenius 1990). According to radio-tracking results of Madison (1980) the social system of meadow voles is based on territoriality of breeding females. Thus, spatial distribution approaching territoriality and the presence of large females still completing their reproductive season in the unmowed patches is consistent with the former knowledge. Breeding males form a small proportion of a meadow vole population (Cockburn 1988) and do not contribute much to the overall spatial pattern. Young individuals usually tolerate each other well, as the positive mean of spatial index in mowed habitats also suggests.

In addition, habitat characteristics may modify the spacing behavior of voles. The most important of these characteristics are the availability and distribution of limiting resources, such as food, potential mates, and protective cover (e.g. Ostfeld 1985). The studies of Koivunen et al. (1996, 1998) suggest that in patchy landscapes large field voles (*Microtus agrestis*) pre-empt sites with protective cover to guard against owl predation. We suggest that similar behavior occurs in populations of meadow voles, a close ecological and taxonomical relative of the field vole (Anderson 1985), inhabiting patchy grassland habitats where avian predators are likewise a considerable threat to voles.

Isodar analysis revealed effects of food augmentation consistent with an IFD in the mowed habitat. The observed isodar slope (not significantly different from 1) and intercept (not significantly different from 0) indicate no qualitative or quantitative effects due to food addition (Morris 1994). In other words, in mowed habitats predation risk was probably the overriding factor in determining population density, whereas food addition did not appreciably influence habitat quality. In unmowed habitats, isodar analyses were inconsistent with an IFD, and thus match our earlier conclusions of territoriality by dominant individuals in these patches. In contrast to the mowed habitats, where vole densities remained low, food addition in the unmowed habitats, where vole densities remained high, is more likely to have an appreciable impact on fitness of the inhabitants.

Giving-up densities and population fitness

Our results validate the use of giving-up densities as an index of population fitness (Olsson and Holmgren 1999, Olsson et al. 1999, Morris and Davidson 2000). First, we observed that GUDs declined with increasing vole population density as expected under negative density-dependence, although we observed this pattern only in mowed treatments. However, if territoriality sets a limit on the density of individuals within unmowed habitats as suggested above, this may eliminate a density-dependent relationship in those habitats. Second, voles were distributed in an IFD in the mowed habitats implying equal fitness across food addition treatments. In accordance, we demonstrated that GUDs were equal between treatments (compare GUDs between food and no food in mowed treatments; Fig. 4) as predicted for an IFD. Third, the non-IFD situation present in the unmowed habitats implies fitness differences, with fitness higher in the food addition treatment. In this case, we demonstrated that GUDs were higher in the food addition treatment (compare GUDs between food and no food in unmowed treatments; Fig. 4) as predicted under non-IFD conditions. Fourth, because mowing increases predation risk, but decreases fitness, we expected GUDs to increase in mowed versus unmowed treatments. The cover by food interaction supported this prediction (compare GUDs between unmowed and mowed treatments without food; Fig. 4). Apparently the main effect of mowing was obscured by the addition of food, since these two effects act in opposite directions.

Thus, our conclusions, that meadow voles have flexible distribution patterns, contingent upon the causes of fitness differences between habitats were upheld when we analyzed giving-up densities. GUDs, as a behavioral indicator of fitness, may be substituted for other types of habitat use data, e.g., based on population estimates from trapping. While these conclusions are encouraging, very few studies (Abramsky et al. 2000b, Morris and Davidson 2000, Olsson et al. 2001), have examined the extent to which behavioral measures may substitute for alternative forms of data collection, and general conclusions regarding their appropriate use are lacking.

Space use and predation

We used the rate of seed removal in lattice grids as a measure of the amount of space used by voles in each habitat. As predicted, space use decreased in response to mowing and to food addition. The effect of the latter was expressed as an interaction between food augmentation and vole density; i.e. a shallower increase in the rate of seed removal with density in the augmented versus non-augmented habitat patches (Fig. 5). These patterns demonstrate qualitative changes in seed removal/space use in response to habitat manipulations.

An interesting question is whether the amount of space used reflects only the number of individual foragers or whether there is also a behavioral component reflecting the prevailing foraging costs, i.e. quitting harvest rates. Thus we examined the quantitative relationships between vole density, giving-up density (as a surrogate for the QHR), and seed removal. Although collinearity prevented us from using the entire dataset simultaneously, separate analyses relative to the presence of cover were instructive. Vole density in unmowed patches did not correlate significantly with GUDs, and multiple regression revealed that of these factors only GUD was a statistically significant predictor of seed removal (Fig. 7). Vole densities were high enough (>275 voles/ha), such that low foraging activity cannot be attributed to a lack of foragers. Thus, in unmowed treatments, GUDs, i.e. the behavioral component took primacy over vole densities, and seed removal increased with decreasing GUD (Fig. 7). In contrast, in mowed patches, both GUDs and density were strongly and significantly correlated, and the effects of these factors on the rate of seed removal were inseparable. Nevertheless, visual inspection of the relationship between seed removal and GUDs was identical in either habitat type (Fig. 7) and may suggest it is our ability detect a primary effect of GUDs in mowed patches rather than changes in the ecology that differs between habitat types.

The strong relationship between vole density and GUDs seen in at least one of the habitat types (i.e. mowed habitat) suggests population density has a strong impact on the foraging costs of individuals. This is predicted by foraging theory (e.g. Mitchell and Valone 1990) and is supported empirically (Morris 1997, Davidson and Morris 2001). Moreover, a relationship between enemy-free space and population density is expected if enemy-free space forms primarily through gaps between predator home ranges (Lewis and Murray 1993, Schauber et al. in review) or territories, although this issue needs further theoretical consideration. Interestingly, population density influenced enemy-free space on mowed patches which had the lowest densities of voles and possibly larger and/or more frequent gaps between territories. The two mechanisms of creating enemy-free space discussed earlier (between versus within territories/home ranges) are not mutually exclusive and both may have been present in our study, although possibly at different relative magnitudes between treatments. Our methods were insufficient to tease apart these two mechanisms and they warrant future study.

Schmidt et al. (2001) suggested that quitting harvest rates, through their relationship to the proportion of space utilized, would be related to the magnitude of predation rates on alternative prey items. They demonstrated that predation by mice on artificial songbird nests was negatively related to quitting harvest rates of the nest predator, the white-footed mouse, *Peromyscus leucopus*. Similarly, we have documented that predation by meadow voles on red maple and black birch seedlings was negatively related to quitting harvest rates and positively related to the amount of space voles utilized. Thus, we have replicated the results of Schmidt et al. (2001) in a unique system. Furthermore, we have clearly demonstrated the relationship between quitting harvest rates and space use in meadow voles, one of two mechanisms suggested by Schmidt et al. (2001) by which quitting harvests rates influence predation rates.

Finally, the level of experience of individuals within their neighborhood (residents vs immigrants) also had an effect on the rate of seed removal. This result is in accordance with that of Pusenius et al. (2000) who found that residents were more likely to depredate tree seedlings than immigrants during a 3-week period following the population manipulation. Likewise, the 4-week interim between population manipulation and the seed removal experiment did not equalize the foraging efficiency of resident versus immigrant voles. Thus, it seems greater enemy-free space among immigrants compared to residents is at least partly the reason behind the finding of Pusenius et al. (2000). Interestingly, this "immigrant effect" may indicate a possible relationship between the value of information (assumed to by greater in residents) and activity level (Burt Kotler, pers. comm.).

In conclusion, vole densities, the prevailing foraging costs, and the experience of the voles with their environment each contributed to patterns of habitat use, foraging activity, and resulting predation rates on tree seedlings. Our results emphasize the importance of including consumer behavior when interpreting community level processes (Fryxell and Lundberg 1997). The next step is to expand these combinations of techniques to systems with multiple species. Desert rodent communities, particularly in Israel, represent some of the best examples of melding together behavioral, population, and community approaches. Giving-up densities (Brown et al. 1994b, Kotler 1997), habitat exclosures (Abramsky et al. 1990, 2000a), and isodar (Ovadia and Abramsky 1995, Abramsky et al. 2000a) approaches have been developed and/or tested extensively within these systems. While these studies have had a somewhat different emphasis (e.g. mechanisms of coexistence, habitat preferences, and the strength of interspecific competition) they compliment and preceded ours by developing an approach that examines how the naturally-selected behavior of foragers can be used to reveal species interactions and patterns of density-dependent variation (Rosenzweig and Abramsky 1997).

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