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PATCH SELECTION AND TREE-SEEDLING PREDATION BY RESIDENT VS. IMMIGRANT MEADOW VOLES

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Abstract. Many small mammal species may exhibit source–sink dynamics, in which some patches (sources) are occupied mainly by residents, while others (sinks) are occupied mainly by recent immigrants. Residents and immigrants are expected to differ in their degree of familiarity with their surroundings, which could affect resource use. Small mammals are known to inhibit the establishment of tree seedlings, especially when population densities are high, and habitat quality, especially the availability of cover and food, has been found to affect local densities. In addition, availability of food can affect the use of other food items, especially those of lower quality. Our goals were to study how population status (residents vs. immigrants) affects use of habitat patches differing in cover and food availability, and how the quality of habitats and individuals interact and affect tree-seedling predation by meadow voles (*Microtus pennsylvanicus*). We conducted a field experiment in six 40 m × 40 m enclosures in an old field. The enclosed populations were randomized into resident vs. immigrant treatments and exposed to a habitat manipulation treatment (cover vs. food) using a 2 × 2 factorial design within the enclosures. We planted seedlings of red maple (*Acer rubrum*) and black birch (*Betula lenta*) in each habitat patch and censused them for three weeks. Seedling predation was lower in food-supplemented than in non-supplemented patches. Voles were attracted by cover and killed more seedlings within it than in open patches. Immigrants moved more between habitat patches than residents. When controlling for the number of visitors to patches, the immigrants killed fewer seedlings than did the residents. This study demonstrates that spatial dynamics of animal consumers, such as source–sink movements between habitat patches, can influence community dynamics of plants, such as the invasion of old fields by trees, in ways beyond those predicted by simple numerical relationships between consumers and resources.

Key words: *foraging behavior; habitat selection; herbivory; meadow vole; Microtus pennsylvanicus; old-field succession; source–sink dynamics; tree-seedling predation.*

INTRODUCTION

Many populations of small mammals, including voles, occupy patchy landscapes (e.g., Lidicker 1975, Ostfeld 1992). Within such landscapes, small mammals readily disperse between patches (Ims et al. 1993, Diffendorfer et al. 1995, Bowers et al. 1996). Whether their patterns of dispersal conform to source–sink models (Holt 1985, Pulliam 1988) or an alternative model (e.g., the balanced-dispersal model of McPeck and Holt [1992]) is under debate (Diffendorfer 1998). According to source–sink models, habitat patches contain either source populations, which have positive in situ rates of population growth, or sink populations, which have

negative in situ rates of population growth. Because sink populations would decline to extinction without immigration, sinks must be net importers of dispersers, which originate in source populations. Source patches should be occupied predominantly by long-term residents, whereas sink patches should be occupied predominantly by recent immigrants. This dominance by either residents or immigrants applies at least qualitatively to other models of dispersal as well.

To our knowledge, no prior studies have determined the consequences of dispersal dynamics for the resources on which herbivorous small mammals depend. We expected residents and recent immigrants to show divergent foraging behaviors due to differing tenure in stable home ranges, and therefore differing degrees of familiarity with the habitat. Specifically, we expected recent immigrants to show less site tenacity and to be less effective at locating resources than residents, re-

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PLATE 1. The meadow vole (*Microtus pennsylvanicus*) is a wide-ranging species and ubiquitous member of grassland communities in North America. Its effects on these communities may be profound. Photograph by Robert H. Tamarin.

sulting in reduced impacts on their resources at equivalent vole densities. Because herbivory by voles is important in plant community dynamics (Huntly 1991), differences in foraging behavior of voles in populations consisting of residents vs. immigrants may generate divergent effects on the plant community.

The impact of voles on the plant community has been shown to be density dependent (Ostfeld 1994). This applies to both herbaceous plants, which are the voles' primary food, and seedlings of trees (Gill and Marks 1991, Ostfeld and Canham 1993). The highest densities of voles are found in habitats that provide superior cover and food (e.g., Morris 1984). Abundant cover reduces predation risk and is associated with greater time spent foraging by sciurids and various desert rodents (Brown 1992). Abundant food resources attract foragers but also affect the marginal value of additional food items, so that in a food-rich environment foragers may be less willing to take risks (Kotler 1997). Furthermore, the quality of food items should influence whether they are worth the risk. Tree seedlings are not considered preferred food items for voles (e.g., Ostfeld and Canham 1993), and their consumption should be especially sensitive to risk of predation and to the availability of alternative high-quality food items.

We conducted a field experiment to determine the effects of population status (resident or immigrant), food supplementation, and cover reduction on patterns of tree-seedling predation by meadow voles (see Plate 1). We predicted that (1) immigrants would be less effective than residents as predators on tree seedlings; (2) if voles preferentially occupy patches with good vegetative cover and augmented food, more seedlings would be killed within these patches; (3) alternatively, if food supplementation decreases the marginal value of seedlings, fewer seedlings would be eaten in patches with than in those without supplemental food.

MATERIALS AND METHODS

The experiment used six adjoining 40 m × 40 m enclosures in an old field of the Institute of Ecosystem

Studies in southeastern New York State (USA). Fences of the enclosures were made of galvanized hardware cloth with mesh size of 1.3 cm; fences extended 1 m above- and 0.5 m belowground. Vegetation in the enclosures was dominated by 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.).

We randomly assigned three enclosures each as either resident or immigrant treatments. Populations of voles in each enclosure were further exposed to a habitat-manipulation treatment (cover reduction vs. food enhancement) using a 2 × 2 factorial design. The area within each enclosure was divided into four 20 × 20 m quadrats. Two diagonal quadrats were chosen for the cover-reduction treatment and were mowed to a height of 5 cm. Then one quadrat each of the reduced-cover and intact-vegetation treatments was randomly selected to receive food augmentation, which was carried out by distributing commercial alfalfa cubes into the chosen quadrats. The mowing was done 3 wk before, and the first food augmentation 2 wk before, the start of the experiment (18 October 1998) to give the voles time to acclimate to the new environment. Due to the modest regrowth of vegetation, no further mowing was needed during the experiment. The alfalfa cubes were augmented once each week throughout the experiment to ensure the amount and quality of the extra food. One alfalfa cube weighed on average 20 g, and the cubes were sown randomly, one cube per 2 m² per week. Based on the energy value of alfalfa cubes (9 kJ/g) and the energy consumption of voles (60 kJ/d, reported by Ryzkowski et al. [1973] for *Microtus arvalis*, a species slightly smaller than *M. pennsylvanicus* with a very similar diet; Ostfeld 1985) we calculated that the energy supplied by the alfalfa cubes alone would be enough to support 86 voles in each augmented 20 × 20 m quadrat.

The experiments used vole populations occurring naturally within the enclosures. Each enclosure had 25 trap stations arranged in a grid with 7.5-m intervals. We used Ugglan multiple-capture traps (Grahnb, Marieholm, Sweden) baited with whole oats and supplied with cotton bedding. Captured voles were eartagged at first capture and subsequently checked for tag number, sex, mass, and reproductive condition. During the study we performed three live-trapping periods at 1-wk intervals. The first period, during which the immigrant populations were formed, had seven trap checks, with the traps checked twice a day, in the morning and evening. The latter trapping periods had two checks on consecutive mornings.

The immigrant populations were established by exchanging the vole populations among enclosures. The exchanged voles were released at the midpoint of their new enclosure. To control for stress due to handling, we also live-trapped the voles in the resident populations at the same time, but released them at their capture sites. The live-trapping and population exchange ended when the voles from the original populations were only rarely caught in the enclosures subject to population exchange. The exchanged individuals constituted the majority of voles captured in the immigrant treatment during the later census periods (see *Results*, below).

The abundance of voles within each enclosure was estimated using the jackknife-estimate of CAPTURE (Rexstad and Burnham 1998). Capture data from the two last morning checks of the first period as well as data from the second and the third census periods were used in the population estimates.

We planted seedlings of red maple (*Acer rubrum*) and black birch (*Betula lenta*), both of which invade old fields in this region (Gill and Marks 1991), in the enclosures. Both species were grown in a greenhouse from cold-stratified seeds. The black birch seeds were taken into a greenhouse for germination in July; red maple seeds were germinated in September. Two weeks before the experiment, the seedlings were transplanted into plastic tubes (one seedling per tube) from which they were planted into the field on 18 October 1998. We established two seedling stations of eight seedlings each in each habitat-manipulation category in each enclosure. At each station, the eight seedlings were arranged into two rows of four seedlings so that the distance between seedlings was 25 cm. The two species of seedlings were intermingled in a regular pattern. Seedlings were censused on days 1, 9, and 20 after planting (day 0). Seedlings that were missing, clipped at the base, or debarked by gnawing were classified as depredated by voles (see Ostfeld and Canham 1993). We wore latex gloves when planting seedlings and conducting censuses to prevent odor contamination.

We considered 3 wk to be a sufficient time period for this study for two primary reasons. First, prior similar studies at these sites (Ostfeld and Canham 1993, Ostfeld et al. 1997) showed that most seedlings clipped

by voles are attacked within the first 1–3 wk after planting. Second, our principal interests were the behavioral differences between resident voles and recent immigrants. Continuing the study for longer periods would have allowed immigrant voles to establish residency, and therefore would have compromised our ability to distinguish differences.

The main dependent variables of the experiment were (1) the proportion of tree seedlings depredated in the different habitat patches, and (2) the estimate of the abundance of voles in the different habitat patches. Independent variables due to the treatments were population status, a between-subject factor, and habitat quality, composed of two fully crossed within-subject factors, cover and food. The measurements obtained in the different habitat patches within each enclosure are clearly not independent of each other due to the expected movements of voles between the habitat patches. Because the census results were also interdependent through time, we analyzed the data with a repeated-measures analysis of variance (rmANOVA). As population density may affect the way the voles settle among habitat patches (Fretwell and Lucas 1970), we used density as a constant covariate in the analysis of habitat selection. In addition, as vole densities affect the rate of seedling predation (Ostfeld and Canham 1993), the number of voles encountered within each patch was included as a covariate in the model explaining variation in seedling predation. To reflect the total number of voles experienced by the seedlings over time, we used the cumulative number of individual voles encountered as the covariates for the later census periods, including the animals caught during the trapping period in question as well as those caught earlier. When comparing the overall rate of seedling predation between the resident and immigrant populations, we controlled for the number of visitors in the different habitat patches during the study (i.e., the number of potential seedling predators captured in trap stations adjacent to the seedling stations). We began the analyses by comparing the overall rates of predation on the different species of seedlings by resident vs. immigrant populations of voles. The number of potential seedling predators was included as a covariate in the analysis. There were no differences in predation rates on the two seedling species (rmANCOVA, species: $F_{1,4} = 2.79$, $P = 0.17$). Therefore, the data from the two seedling species and two stations within each habitat patch were pooled for the subsequent analysis of spatial and temporal patterns of seedling predation. Vole densities were square-root transformed, and the proportion of seedlings killed were arc-sine square-root transformed. Statistical analyses were performed using SPSS for Windows 5.0 (Norusis 1992).

RESULTS

Population densities of voles did not differ between the population status treatments (residents: 646 ± 95.3

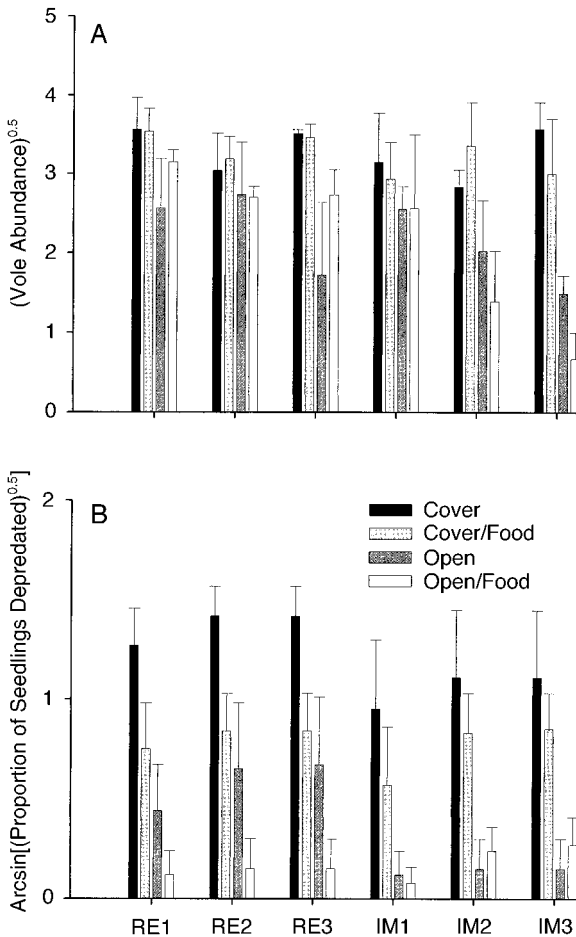


FIG. 1. Results of vole and tree-seedling censuses in the different habitat patches. Transformed data are means \pm 1 SE. (A) Number of resident and immigrant voles (square-root transformed) in the different habitat patches during the successive trapping periods. RE1, RE2, and RE3 denote residents during the three successive trapping periods; IM1, IM2, and IM3 denote immigrants during the three successive trapping periods. (B) Proportion of seedlings killed (arcsine square-root transformed) by residents and immigrants until the censuses on days 1, 9, and 20. RE1, RE2, and RE3 denote resident enclosures during the three successive censuses; IM1, IM2, and IM3 denote immigrant enclosures during the three successive censuses.

voles/ha; immigrants: 518 ± 70.8 voles/ha [mean \pm 1 SE], $t_4 = 1.06$, $P = 0.35$). Populations in the immigrant treatment consisted of $86.7 \pm 1.4\%$ immigrants. Within enclosures, the densities of voles were higher in quadrats with cover intact than in those with cover removed (Fig. 1A, Table 1). The rmANOVA suggested a non-significant trend where the effect of cover increased through time. Supplemental food had no significant main effect on local abundance of voles (Fig. 1A, Table 1), but was involved in the significant time \times cover \times food interaction.

Immigrants were more mobile than residents within trapping periods. During the first trapping period, none

of the 27 residents that were captured at least twice moved between habitat patches, whereas 5 of the 24 immigrants captured at least twice did (Fisher's exact test, $P = 0.018$). In subsequent trapping periods, movements among patches were rare; only one vole (a resident) was observed to change habitat patches during the third trapping period. Immigrants also were more mobile between trapping periods. Between the first and second trapping period, 5 of 44 residents vs. 25 of 30 immigrants changed patches (likelihood ratio = 41.7, $df = 1$, $P < 0.001$). Between the second and third trapping sessions, 3 of 38 residents and 10 of 25 immigrants changed patches (likelihood ratio = 9.50, $df = 1$, $P = 0.002$).

Altogether, 97 of 192 (50.5%) tree seedlings planted into the enclosures with resident voles were predated, compared to 69 of 192 seedlings (35.9%) of those planted into the enclosures with immigrants. The ANCOVA model ($F_{2,3} = 14.7$, $P = 0.026$, $R^2 = 0.85$) revealed that both local vole abundance ($F_{1,3} = 24.38$, $P = 0.016$) and population status ($F_{1,3} = 14.5$, $P = 0.032$) had significant effects on seedling predation

TABLE 1. Results of repeated-measures ANOVA for the effects of population status (between-subject factor), time, cover, and food augmentation (within-subject factors) on abundance of voles (square-root transformed, jackknife estimates from CAPTURE [Rexstad and Burnham 1999]) during three census periods.

Source of variation	SS	df	MS	F	P
Within + Residual	0.42	3	0.14		
Regression	7.27	1	7.27	51.85	0.006
Population status	0.43	1	0.43	3.06	0.179
Within + Residual	0.50	8	0.06		
Time	3.23	2	1.62	26.09	0.000
Population \times Time	0.42	2	0.21	0.38	0.086
Within + Residual	6.46	4	1.61		
Cover	16.37	1	16.37	10.15	0.033
Population \times Cover	0.92	1	0.92	0.57	0.493
Within + Residual	4.18	4	1.04		
Food	0.00	1	0.00	0.00	0.956
Population \times Food	0.87	1	0.87	0.84	0.412
Within + Residual	3.37	8	0.42		
Time \times Cover	3.49	2	1.75	4.15	0.058
Population \times Time \times Cover	0.92	2	0.46	1.10	0.379
Within + Residual	6.12	8	0.76		
Time \times Food	0.12	2	0.06	0.08	0.924
Population \times Time \times Food	0.70	2	0.35	0.46	0.649
Within + Residual	1.64	4	0.41		
Cover \times Food	0.01	1	0.01	0.02	0.901
Population \times Cover \times Food	0.66	1	0.66	1.61	0.274
Within + Residual	1.17	8	0.15		
Time \times Cover \times Food	1.41	2	0.70	4.81	0.042
Population \times Time \times Cover \times Food	0.16	2	0.08	0.54	0.600

Note: Jackknife estimates of abundance of voles, calculated from data pooled over all three census periods for each enclosure, are used as covariates in the analysis.

TABLE 2. Results of repeated-measures ANOVA for the effects of population status (between-subject factor), time, cover, and food augmentation (within-subject factors) on tree-seedling predation (arcsine square-root transformed) during three census periods.

Source of variation	SS	df	MS	F	P
Within + Residual	0.81	3	0.27		
Regression	3.63	1	3.63	13.50	0.035
Population status	0.49	1	0.49	1.83	0.269
Within + Residual	0.06	7	0.01		
Regression	0.00	1	0.00	0.02	0.899
Time	0.07	2	0.03	3.88	0.074
Population × Time	0.00	2	0.00	0.14	0.868
Within + Residual	0.90	3	0.30		
Regression	0.08	1	0.08	0.26	0.646
Cover	5.83	1	5.83	19.48	0.022
Population × Cover	0.00	1	0.00	0.00	0.977
Within + Residual	0.50	3	0.17		
Regression	0.01	1	0.01	0.09	0.784
Food	1.78	1	1.78	10.79	0.046
Population × Food	0.58	1	0.58	3.53	0.157
Within + Residual	0.06	7	0.01		
Regression	0.03	1	0.03	3.15	0.119
Time × Cover	0.02	2	0.01	1.27	0.338
Population × Time × Cover	0.01	2	0.00	0.37	0.704
Within + Residual	0.02	7	0.00		
Regression	0.03	1	0.03	10.24	0.015
Time × Food	0.01	2	0.00	1.14	0.372
Population × Time × Food	0.08	2	0.04	12.97	0.004
Within + Residual	0.28	3	0.09		
Regression	0.37	1	0.37	3.98	0.140
Cover × Food	0.38	1	0.38	4.19	0.133
Population × Cover × Food	0.00	1	0.00	0.00	0.971
Within + Residual	0.06	7	0.01		
Regression	0.02	1	0.02	2.49	0.159
Time × Cover × Food	0.00	2	0.00	0.16	0.855
Population × Time × Cover × Food	0.02	2	0.01	1.11	0.381

Note: Jackknife estimates (CAPTURE) of cumulative vole abundance (square-root transformed) in the different habitat patches just before each seedling census are used as covariates in the analysis.

(Table 2, Fig. 1B). Both cover and food augmentation had significant main effects (Table 2). Seedling predation was higher in high-cover than in low-cover patches, and lower in food-supplemented than non-supplemented patches (Table 2, Fig. 1B). Much of the seedling predation occurred within a few days after seedling introduction. The highly significant three-way interaction among population status, time, and food augmentation can be interpreted as indicating that food augmentation decreased seedling predation among the residents but not among the immigrants, and this difference increased with time (Table 2). Density was a significant covariate when analyzing the effects of population status and population status × time × food augmentation interaction. Seedling predation increased with increasing density of voles in each enclosure.

DISCUSSION

Although the rate of seedling predation in a patch is associated with the density of voles within it (Ostfeld and Canham 1993, Ostfeld et al. 1997), much variation can be accounted for by characteristics of the foragers, their habitat, and the interaction of these factors. Our experiment revealed strong differences between resident and immigrant meadow voles. The higher mobility of immigrants translated into more voles visiting areas with seedling stations, but when controlling for the number of visitors, the immigrants depredated fewer seedlings than did the residents. We interpret the greater mobility of immigrants than of residents as being caused by a lack of familiarity by immigrants with both their new physical surroundings and many of their new neighbors. Seedlings also may have gone undetected or were unattractive to voles less familiar with their surroundings. Extra food did not seem to attract voles. Food supplementation decreased the number of seedlings depredated by residents but did not affect the number of seedlings depredated by immigrants. The differential response to food supplementation associated with population status suggests that residents and immigrants evaluated seedlings differently in relation to the energy available in their neighborhood and also in relation to risk factors (cf. Brown 1992, Kotler 1997). The immigrants, unfamiliar with the best feeding patches and moving readily, may have had less favorable energy balances than the residents, and consequently may not have been sensitive to features of the habitat other than those indicating acute danger.

Ostfeld and Canham (1993) conducted a study of seedling predation in the same enclosure system eight years before our study, using density manipulations as the between-enclosure treatment and small mowed clearings as a within-enclosure treatment. In their high-density treatment, where the densities were comparable to those in our study, 91.1% of red maple seedlings introduced in November 1990 were depredated within 10 d. This is almost the same seedling predation rate (93.8%) recorded in our quadrats with residents, intact cover, and no extra food. Under the same conditions, but with immigrants, the predation rate was 70.8%. Food addition decreased the seedling predation rate in the treatments with residents and intact cover to 54.2%, which is comparable to the 60% reported by Ostfeld and Canham (1993) for their low-density populations, where densities were less than one third of those in our study. In our mowed patches where local densities were of the same magnitude as those in the low-density treatment of Ostfeld and Canham, the seedling predation rates were 48% (residents, without extra food) and 7% (residents, with extra food).

Our study suggests that populations consisting predominantly of residents or immigrants will differ in the total impact of consumers on seedlings and the spatial pattern of seedling predation. This difference appears

to be caused by differences between residents and immigrants in their mobility, the amount of information they have about their neighborhoods, and their perceptions of the marginal value of food. Thus, spatial dynamics of animal consumers, such as source-sink relationships between habitat patches, can be linked to community dynamics of plants, such as tree invasion of old fields, in ways beyond those predicted from simple numerical relationships between consumers and resources.

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