Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment

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We conducted a field experiment that manipulated landscapes by mowing so that the amount of unfavorable habitat (low cover) for prairie voles (*Microtus ochrogaster*) increased while the number and size of favorable patches (high cover) remained constant. Distance between favorable patches increased as the amount of unfavorable habitat increased, so we could test two current hypotheses concerning the effect of habitat fragmentation on local populations: 1) increased distance between favorable habitat patches reduces successful per capita dispersal (emigration and immigration) because dispersers suffer greater exposure to predators (the predation hypothesis); and 2) per capita dispersal is inversely density dependent in voles because increased aggression at higher density inhibits movements (the social fence hypothesis). As predicted by the predation hypothesis, increased distance between favorable habitat patches led to decreased successful dispersal among patches and increased per capita mortality, particularly among subadult and adult males (the categories of voles most likely to emigrate). As predicted by the social fence hypothesis, dispersal was inversely density dependent, and dispersing voles displayed a greater frequency of wounding (an indication of increased aggressive interactions) than did residents. The amount of wounding in general did not increase with density, however, and, as distance between patches increased to 60 m, successful dispersal became rare and erratic. Nevertheless, our overall results supported current hypotheses regarding the effects of increased habitat fragmentation on patterns of dispersal and mortality. Examining the impact of these effects on local population dynamics within different landscapes will require longer periods of observation.

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Rates of dispersal can strongly affect use of habitat patches by small mammals (Johnson and Gaines 1987, Morris 1996, Ims and Hhermann 2001, Andreassen et al. 2002, Lin and Batzli 2004), but their relationship to density remains controversial. Some research suggests that dispersal rates are independent of density (Gaines and McClenaghan 1980, Lidicker and Stenseth 1992), some research suggests that they are directly density dependent (Diffendorfer et al. 1998, Aars and Ims 2000, Gundersen et al. 2002), and some research, particularly on arvicoline (microtine) rodents, suggests that they are inversely density dependent (Diffendorfer et al. 1999, Andreassen and Ims 2001, Lin and Batzli 2001a).

In a fragmented landscape, successful dispersal between habitat patches occurs in three consecutive stages (Lidicker and Stenseth 1992): movement out of the home patch (emigration), transfer between patches and movement into a new patch (immigration). As the distance between patches increases with fragmentation, emigrants are less likely to succeed in moving between patches (Diffendorfer et al. 1999), presumably because reduced cover leads to increased predation during transfer between patches (Birney et al. 1976, Baker and Brooks 1981, Peles and Barrett 1996). We call this explanation the predation hypothesis. If increased exposure to predators reduces successful dispersal, as distance

between patches increases, per capita mortality should also increase for categories of animals most likely to disperse.

Rates of successful dispersal may also reflect intrinsic factors, such as social interactions and spacing behavior (Abramsky and Tracy 1980, Bondrup-Neilsen 1986, Brandt 1992). For example, the social fence hypothesis (Hestbeck 1982) asserts that emigration will be inversely density dependent because the number of aggressive encounters with unfamiliar voles increases with density. This hypothesis was first proposed as a mechanism to explain population cycles as a result of variable movement between habitats of differing quality. Its basic argument, however, should apply to dispersal between any habitat patches because increasing density of aggressive neighbors generally should inhibit movement. Assuming that incidence of wounding reflects levels of aggression within a population, the social fence hypothesis predicts: 1) emigration from a population will be inversely related to the density within the home patch, and 2) frequency of wounding, particularly among dispersers, should increase with density.

Here we report the results of a field experiment that tests both the predation hypothesis and the social fence hypothesis by examining the effects of increased fragmentation of a landscape on movement, mortality and wounding of prairie voles. We used prairie voles, *Microtus ochrogaster* (Wagner), because subadults and adults display high levels of aggression toward unfamiliar voles of both sexes but not towards their mates or other members of their social group (Getz et al. 1981, Harper 1996). Such behavior is a requirement for the operation of the social fence. In addition, a previous study indicated that dispersal by prairie voles appears to be inversely density dependent (Lin and Batzli 2001a).

Methods

Study site and experimental design

We conducted the experiment at the University of Illinois Ecological Research Area (Phillips Tract) located 5 km northeast of Urbana, Illinois. Perennial grasses (*Festuca elatior* L., *Bromus inermis* Leyss. and *Poa pratensis* L.) dominated the vegetation, but a variety of forbs and woody plants also occurred in these grasslands (Lin and Batzli 2001a). Tree saplings and invasive shrubs were periodically removed from unmowed areas to arrest succession. Mature vegetation reached a height of about 1 m and provided favorable habitat for voles (Cole and Batzli 1979, Desy et al. 1990, Lin and Batzli 2001a).

Our experimental design included two blocks (replicates) of three different treatments, each represented by a different type of landscape (Fig. 1). All landscapes provided three patches of favorable habitat (one 35 × 40 m or 0.14 ha and two 35 × 20 m or 0.07 ha) to
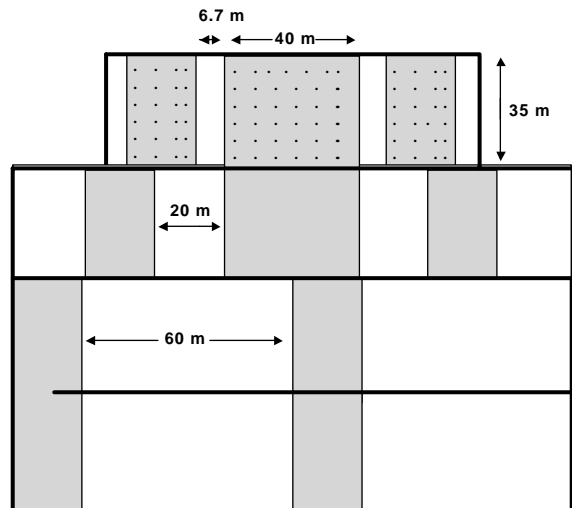

Fig. 1. Diagram of the experimental design showing one replicate of three fenced landscapes (fences indicated by heavy lines) with favorable habitat patches (gray) separated by 6.7, 20 or 60 m of unfavorable habitat (white). Black dots represent the location of trap stations at 6 m intervals within favorable habitat patches of one treatment (6.7 m). The same trap intervals were used in all treatments.

simulate a moderately complex landscape, but the proportion of unfavorable habitat within each treatment differed. Distance between favorable patches increased from 6.7 m to 20 m to 60 m, as the proportion of unfavorable habitat increased from 25% to 50% to 75% of the landscape, respectively. Landscapes within each replicate block were isolated from one another and surrounding habitat by corrugated steel roofing panels that extended 30–40 cm into and above the ground. Predators can cross such fences, but voles cannot when vegetation is kept low near the fence line (Lin and Batzli 2001b), as it was during our experiment.

Number and size of favorable patches can affect populations of small mammals (Stamps et al. 1987a, 1987b, Bowers and Dooley 1993, Andren 1994, Diffendorfer et al. 1995, Bowers and Matter 1997, Dooley and Bowers 1998), but the shape of a habitat (square versus rectangular) does not markedly affect dispersal rates or other demographic characteristics of vole populations (Harper et al. 1993). To avoid the effects of size and number of patches, we changed the distance between favorable habitats without changing the area or number of favorable patches. Although we needed to bend the largest landscape into a U-shape to fit into our study sites (Fig. 1), thereby changing the shape of the large patch, the length of coterminous edge between favorable and unfavorable habitat remained constant across treatments.

Frequent mowing reduced habitat quality and reduced movement of prairie voles between patches of favorable habitat in earlier experiments conducted at our study site (Cole 1978, Lin and Batzli 2001a), so we used mowing to

create and maintain unfavorable habitat between favorable habitat patches. As shown in a previous experiment, the process of mowing itself did not directly influence the survivorship of voles, but mortality of prairie voles was higher where height of vegetation was maintained at 10–20 cm (Lin and Batzli 2001b). In this experiment, height of vegetation in the unfavorable habitat was maintained at 5–15 cm to further inhibit voles from establishing residency.

We systematically searched mowed habitat every two weeks during the growing season for signs of vole activity (active burrows or runways), which rarely occurred. Preliminary trapping with 20% of traps in mowed areas indicated that activity there was less than 10% of that expected based upon trapping effort (only 5 of 344 animals were caught in mowed areas). Furthermore, all except one of the voles captured in mowed habitat were also captured in unmowed habitat. Although movement of voles appears to be primarily affected by cover (Lin and Batzli 2004), density of voles and amount of available food also can affect movements (Desy et al. 1990, Ostfeld and Canham 1995). In our study similar composition of vegetation among landscapes likely provided similar amounts of high quality food in favorable patches for all treatments within each replicate.

We started populations in all landscapes in May of 2002 by placing four pairs of adult voles in each large patch of favorable habitat (a moderate density of 57 voles per ha) using stock collected by removing animals left in the pens from a preliminary experiment. By combining individuals from different pens we ensured that populations began with unrelated adults.

Live trapping

We conducted live trapping in patches of favorable habitat at monthly intervals from May 2002 to May 2003, except for January and February when the voles did not reproduce because of severe winter conditions. We trapped for four successive days and checked traps just after dawn and just before dusk. All nine favorable habitat patches of the three landscapes within a replicate block were trapped simultaneously. Trapping of both replicates was always completed within a two-week period. One replicate could not be trapped in December because of cold weather (reproduction had ceased in the replicate that was trapped), so no data from this month were used for statistical analyses.

We set one Longworth trap at each station on a grid with 6 m intervals, a total of 42 traps per large patch and 24 traps per small patch (Fig. 1). Traps were placed in predator-proof cages to prevent raiding by raccoons (Getz and Batzli 1974) and provided with cracked corn

for food and non-absorbent artificial cotton for bedding, the latter only when predicted daily low temperatures fell below 5°C. We broke traps open and left them in place between trapping sessions to maintain familiarity of resident voles with traps. Upon capture all voles were marked with numbered Monel ear tags, sexed and weighed. We noted location, reproductive condition, molting, external parasites and wounds, then released the voles at the point of capture. Incidence of wounding provided a measure of aggression as in previous studies (Krebs 1964, Christian 1970, Batzli and Pitelka 1971, Lidicker 1973, 1979, Rose and Gaines 1976).

We defined successful dispersers as those animals that moved from one favorable patch to another during or between trapping sessions and called them emigrants when moving out of a patch and immigrants when moving into a patch. Previous work with the California vole (*Microtus californicus* (Peale), Ostfeld et al. 1985) and the prairie vole (Solomon and Jacquot 2002) suggested that some adult males become wanderers and disperse across habitats without becoming residents in a new patch. We classified voles moving between favorable patches multiple times within a single trapping session as wanderers and only counted the first movement to avoid biased estimates of per capita dispersal. Even so, our estimate of monthly dispersal only served as an index of emigration and immigration rates because undetected movements no doubt occurred between trapping sessions.

To examine age differences associated with dispersers, we classified voles into three age classes based upon body weight (Desy and Batzli 1989): juveniles (<22 g for both sexes), subadults and adults (>30 g for males and >28 g for females). The body weight of a disperser at the time of dispersal was estimated as the average of the last weight in its home patch and the first weight in the new patch. Voles with body weights near category boundaries sometimes lost weight, but they never reverted to a younger age class.

We used minimum number of voles known to be alive (MNKA) to calculate abundance for each landscape (number of voles/landscape) because trapping success was high (Boonstra 1985). We calculated trapping success as the proportion of voles known to be alive that were captured during a given trapping period. Voles weighing >35 g upon first capture were assumed to be in the trappable population (>15 g), but not captured, during the previous month. Because time between trapping sessions varied, we assumed constant survival between trapping sessions and adjusted survival to a 28 day period ($S_a = S_o^{(t/28)}$ where S_a is adjusted survival, S_o is observed survival, and t is the number of days between trapping). Because the predation hypothesis was cast in terms of mortality, we also calculated mortality over 28 day time periods as $1 - S_a$.

Statistical analyses

We used repeated measures (RM) ANOVA to compare the effect of increasing the distance between patches on the density of voles in different landscapes over time and two-way ANOVA to detect differences among treatments and seasons in monthly trapping success, per capita movement and per capita mortality. We divided trapping sessions into seasons as follows: summer (June–July–August 2002), fall (September–October–November 2002), and spring (March–April–May 2003) and used mean values per 28 days during each season for estimates of movement and mortality. Because we could not trap during cold winter months (December–February), and cumulative mortality during those three months would bias our estimates of trapping success and dispersal, we did not use winter data for these analyses. A valid estimate of per capita mortality could be calculated for winter, although only one observation (mid-November to mid-March) could be made per replicate and constant mortality had to be assumed for the period.

For post-hoc multiple comparisons of treatments of means we used Fisher's LSD. Differences among means were considered statistically significant at $\alpha < 0.10$ to decrease the likelihood of making type II errors with only two replicates of treatments (N = 2). Arcsine transformations helped to normalize proportional data prior to statistical analysis.

We used regression analysis to compare the effects of the abundance (number per landscape) on overall dispersal within a landscape, the effects of density (number per ha) in the home patch on per capita emigration and the effects of density in the new patch on per capita immigration. Although the total number of dispersers in a landscape equals the total number of emigrants or immigrants in that landscape, the number of emigrants, immigrants and density all vary at the patch-specific level within a landscape. As a result, per capita dispersal for a landscape and per capita emigration and immigration at the patch-specific level differed. Because responses did not appear to be consistent among treatments, we calculated separate regression equations to analyze the effect of density on per capita movement for each treatment. A variety of curvilinear models were evaluated for their fit to the data, but only a logarithmic model improved upon a linear model for emigration and immigration at the patch level, and none improved on a linear model for dispersal at the landscape level.

We calculated chi-square values to compare the frequencies of dispersers and residents in the background populations for each age class (juveniles, subadults and adults) and sex (male or female) and to compare the frequency of wounding for residents and dispersers. Because we detected few successful dispersers in some treatments, we lumped data across treatments

and replicates for these comparisons. We also regressed proportion of wounded emigrants against density in their home patch, proportion of wounded immigrants against density of their new habitat patch and proportion of wounded residents against density of their home patch. Because aggression rarely occurs against juveniles (Getz et al. 1981, Harper 1996), we only used data on wounding for subadults and adults.

Results

Trapping success and abundance

From May 2002 to May 2003, a total of 1420 prairie voles (683 and 737 voles in the two replicates) were captured 10 577 times (5239 and 5338 captures, respectively). Trapping success was 90% across the study (91% and 89% in the two replicates) and was consistent among treatments and among seasons (two-way ANOVA, $F_{2,9} = 0.37$, $p = 0.70$ for treatment; $F_{2,9} = 0.57$, $p = 0.59$ for season, and $F_{4,9} = 0.67$, $p = 0.63$ for interaction). These results support the consistency of our estimates for numbers of voles, dispersal and mortality.

As expected, the density of voles varied across monthly trapping sessions, increasing during the growing season when reproduction occurred and decreasing during winter when reproduction did not occur (RM-ANOVA, $F_{9,27} = 23.8$, $p < 0.01$, Fig. 2). The abundance of voles also differed among the three treatments, being consistently lower in patches separated by 20 and 60 m than those separated by only 6.7 m ($F_{2,3} = 28.7$, $p = 0.01$). Although densities for the 20 m treatment also remained lower than the 60 m treatment for most of the first growing season, by November these two treatments
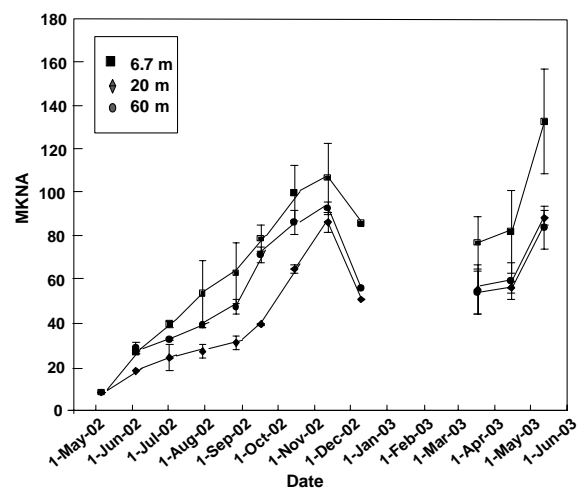

Fig. 2. Mean minimum known number alive (MKNA) for prairie voles in landscapes with favorable habitat patches separated by distances of 6.7, 20 and 60 m. Vertical lines indicate ± 1 SE (N = 2).

had similar densities. The temporal pattern was consistent across different treatments ($F_{18,27} = 0.81$, $p = 0.67$ for interaction). Although abundance did vary across seasons, mean (± 1 SE) density (number per landscape) across all landscapes during fall of 2002 (80.9 ± 4.9 voles, $N = 18$) did not differ significantly from the mean density for spring of 2003 (76.7 ± 6.4 voles, $N = 18$).

Traits of dispersers

Comparing the two replicates, similar percentages of individuals dispersed within each age class (10–12% for juveniles, 22–27% for subadults, 8–9% for adults; $\chi^2 = 0.62$, 0.42, 0.38, respectively; 1 df, $p > 0.37$ in all cases), so we combined data for the replicates. The frequency of juvenile dispersers reflected their abundance in the background populations, but subadults were over represented and adults were under represented among dispersers (Fig. 3A; $\chi^2 = 46.1$, 2 d.f., $p < 0.001$). Nevertheless, because of their greater overall abundance, adults contributed half of the total number of dispersers.
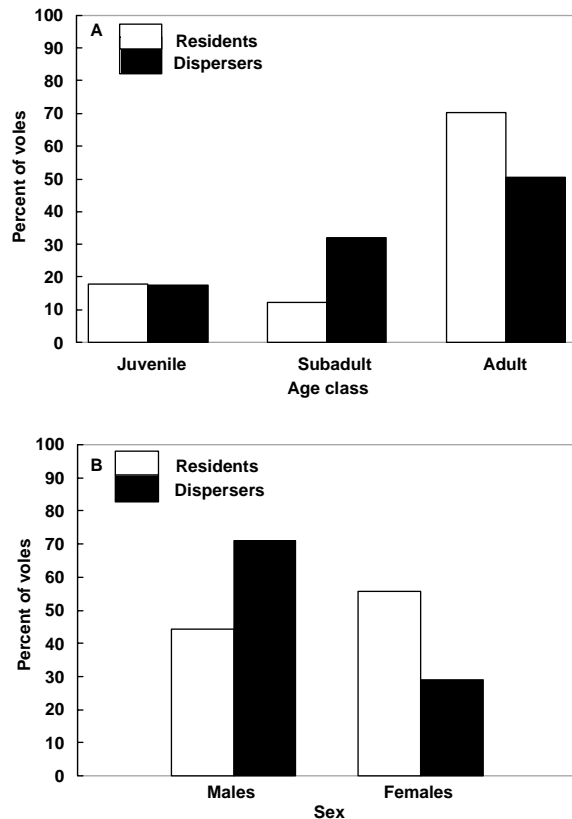
Again, for the two replicates, similar percentages of each sex dispersed, so data were combined across replicates (15–17% for males, 6% for females; $\chi^2 = 0.69$, 0.00, respectively, $df = 1$, $p > 0.40$ in both cases). Compared to the background populations, males (73% of dispersers) were heavily over represented and females (27% of dispersers) were heavily under represented ($\chi^2 = 39.6$, 1 df, $p < 0.001$, Fig. 3B).

Summing across all landscapes and replicates, only a total of 6 females (14% of female dispersers) moved between patches more than once within a trapping session and were considered wanderers, whereas 24 adult males (22% of male dispersers) did so. Trends for males were similar between replicates in all treatments, so replicates were lumped ($\chi^2 < 1.9$, $df = 1$, $p > 0.17$ in all cases). A much higher percentage of dispersing adult males wandered in landscapes with patches close together (79% at 6.7 m, but only 8% and 12% at 20 m and 60 m, respectively) than expected from the overall distribution of male dispersers among landscapes (43% at 6.7 m, 29% at 20 m and 28% at 60 m; $\chi^2 = 12.8$, $df = 2$, $p < 0.001$).

Dispersal and mortality at the landscape scale

Per capita dispersal within a landscape for adult and subadult males, the demographic categories most likely to disperse, decreased as distance between patches increased (two-way ANOVA, $F_{2,9} = 9.20$, $p = 0.01$, Fig. 4). Differences between landscapes with patches at 6.7 m or 60 m and with patches at 20 m or 60 m were significant ($p = 0.002$ and $p = 0.02$, respectively), but the difference between landscapes with patches at 6.7 or 20 m was not ($p = 0.23$).

Fig. 3. Percent of resident ($N = 1267$) and dispersing ($N = 153$) prairie voles categorized by age (A) – juveniles (< 22 g), subadults or adults (females > 28 g and males > 30 g) or by sex (B) – male or female.
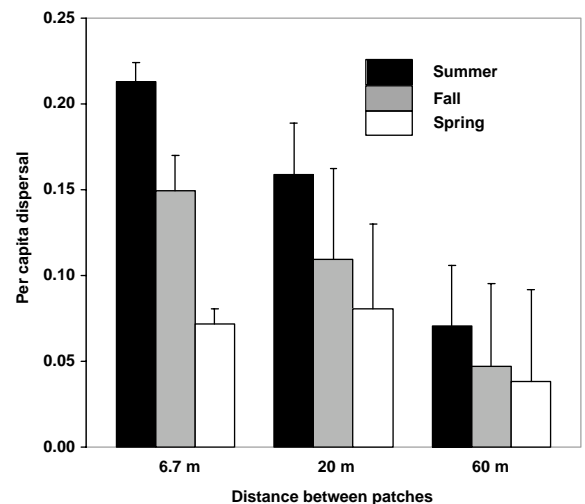

Fig. 4. Mean monthly (28 d) per capita dispersal of subadult and adult male prairie voles between habitat patches separated by 6.7, 20 or 60 m. Vertical lines indicate $+1$ SE ($N = 2$).

Seasonal differences in movement also occurred (Fig. 4, $F_{2,9} = 7.16$, p = 0.01) with per capita dispersal greater in summer than in either fall (p = 0.07) or spring (p = 0.004). Dispersal appeared to be greater at 6.7 m during fall than in spring, but neither the overall difference between fall and spring (p = 0.12) nor the effect of season among treatments ($F_{4,9} = 1.05$, p = 0.43 for interaction) was statistically significant.

Estimates of per capita mortality of subadult and adult male voles within a landscape were highly variable so that two-way ANOVA revealed no significant trends (treatment effect, $F_{2,12} = 0.44$, p = 0.65; seasonal effect, $F_{3,12} = 1.01$, p = 0.42; interaction, $F_{6,12} = 0.15$, p = 0.99). However, a reduced model (one-way ANOVA for treatment using a single, mean value for each landscape within a replicate) indicated that mortality increased as distance between patches increased ($F_{2,3} = 8.26$, p = 0.06; Fig. 5). This response appeared to be continuous as distance increased. Per capita mortality of juveniles, few of which dispersed, did not differ among landscapes (0.45 ± 0.02, 0.42 ± 0.15, and 0.66 ± 0.10 in patches separated by 6.7 m, 20 m, and 60 m, respectively ($F_{2,3} = 1.68$, p = 0.32).

Local emigration and immigration

Local emigration of adults and subadults from patches decreased as density increased (Fig. 6). The negative relationship between density at the home patch and emigration was highly significant for both replicates of patches separated by 6.7 m ($R^2 = 0.54$, p < 0.001 and $R^2 = 0.36$, p = 0.001; Fig. 6A) and 20 m ($R^2 = 0.15$, p = 0.04 and $R^2 = 0.36$, p < 0.001; Fig. 6B). Emigration rates from patches separated by 60 m, however, showed no
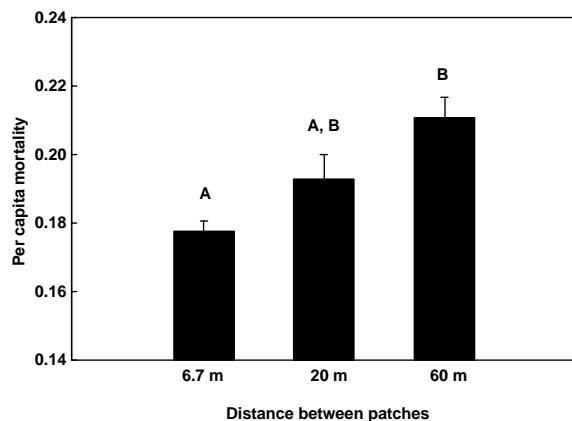

Fig. 5. Mean monthly (28 d) per capita mortality for subadult and adult male prairie voles in landscapes with habitat patches separated by 6.7, 20 or 60 m. Different letters indicate a statistical difference between treatments (Fisher's LSD, p < 0.10). Vertical lines indicate +1 SE (N = 2).
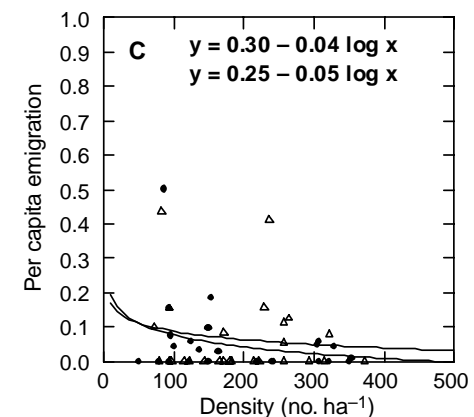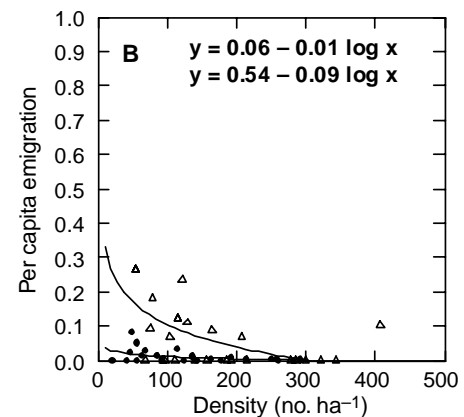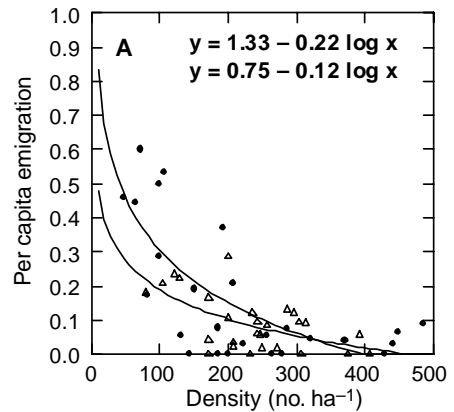

Fig. 6. Monthly (28 d) per capita emigration of subadult and adult prairie voles between habitat patches separated by (A) 6.7 m, (B) 20.0 m or (C) 60.0 m in relation to density in their home patch. Circles and top equation for replicate 1, triangles and bottom equation for replicate 2 (N = 27 in all cases).

significant relationship with density ($R^2 = 0.07$, p = 0.18 and $R^2 = 0.02$, p = 0.46; Fig. 6C). None of the slopes and intercepts of the transformed (linear) curves differed significantly within or among treatments (p > 0.10 in all cases).

The pattern of immigration of adults and subadults in relation to density in the new patch mimicked that for emigration from home patches ($R^2 = 0.36$, p = 0.001 and $R^2 = 0.35$, p = 0.001 for replicates at 6.7 m; $R^2 = 0.34$, p = 0.001 and $R^2 = 0.45$, p < 0.001 for replicates at 20 m; $R^2 = 0.01$, p = 0.35 and $R^2 = 0.06$, p = 0.23 for replicates at 60 m; N = 27 in all cases), so those results are not shown. The patterns for overall dispersal at the landscape scale resembled those for movement for emigrants and immigrants at the local scale, except that the relationships were linear in the former and curvilinear in the latter ($R^2 = 0.70$, p = 0.005 and $R^2 = 0.46$, p = 0.05 for replicates at 6.7 m; $R^2 = 0.71$, p = 0.004 and $R^2 = 0.53$, p = 0.03 for replicates at 20 m; $R^2 = 0.40$, p = 0.07 and $R^2 = 0.04$, p = 0.61 for replicates at 60 m; N = 9 in all cases). In all cases, the intercepts and slopes (effect of density) tended to decrease as distance between patches increased and successful dispersal decreased.

Incidence of wounding

The frequency of wounding of subadults and adults did not differ between the two replicates (21–23% for nondispersing residents, 17–21% for dispersers before movement and 41–44% for dispersers after movement; $\chi^2 < 0.36$, df = 1, p > 0.55 in all cases), and we combined data across replicates. Comparison of residents and dispersers in their home patch before dispersal indicated similar levels of wounding ($\chi^2 = 0.64$, 1 df, p = 0.42, Fig. 7). The incidence of wounding for dispersers after moving to a new patch, however, was greater than either for residents ($\chi^2 = 26.1$, 1 df, p < 0.001) or for dispersers before moving ($\chi^2 = 16.7$, 1 df, p < 0.001).
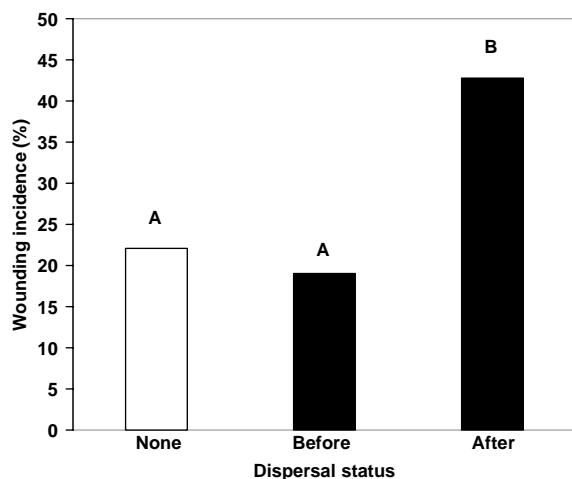

Fig. 7. Frequency of wounding for subadult and adult prairie voles when non-dispersing residents (N = 1042) and when dispersers, either before or after moving from one habitat patch to another (N = 126). Different letters indicate a statistically significant difference between frequencies.

The proportion of wounded emigrants was not significantly related to density in their home patches in any of the landscapes (p > 0.13 in all six cases). Similarly, no significant relationships occurred between the proportion of wounded immigrants and density in their new habitat patches in any of the landscapes (p > 0.38 in all six cases). Finally, the incidence of wounding among residents was not significantly related to density in their home patches in any of the landscapes (p > 0.10 in all six cases). Data were not pooled across treatments or replicates for these relationships with density because the direction of trends sometimes differed among landscapes.

Discussion

Distance effects on dispersal and mortality

Results from our experiment supported the predation hypothesis. As expected, successful per capita dispersal decreased as distance between favorable habitat patches increased (Fig. 4). Furthermore, the categories of voles most likely to disperse (subadult and adult males) showed greater mortality as distance between favorable patches increased (Fig. 5), whereas the category of voles least likely to disperse (juveniles) did not. Previous work has shown a decrease in successful dispersal as the distance separating patches for voles increased (Diffendorfer et al. 1995, Andreassen and Ims 2001), but those experiments did not manipulate distance between patches independently of other landscape features nor could they examine per capita mortality in relation to dispersal distance.

Both males and females dispersed, but a substantial majority of movements (70%) were by adult and subadult males, and subadults dispersed in greater numbers than expected based on the background populations. These findings were not surprising because male-biased dispersal is typical among mammals (Greenwood 1980), and Lin and Batzli (2004) found a similar propensity for subadult prairie voles to move between adjacent habitats. Among dispersers, we detected most nomadic wanderers to be adult males, a result consistent with previous work that showed subadult males more likely than adult males to become residents in new habitat (Ostfeld et al. 1985, Solomon and Jacquot 2002).

Dispersal, aggression and density

As expected by the social fence hypothesis, movements (emigration and immigration) by adults and subadults were inversely density dependent in landscapes with patches separated by 6.7 or 20 m (Fig. 6). Because population densities tend to increase during the course

of a growing season, one might argue that our results confound seasonal and density effects. Recall, however, that our data were gathered over two growing seasons and the fall densities during the first season did not differ significantly from the spring densities during the second (Fig. 2).

Although the trends for patches separated by 60 m were similar to the others, significant relationships between density and movement did not consistently occur at this distance. These data suggest that, as distance between patches increased, successful dispersal became rare and more erratic so that social factors had a less detectable effect. Thus, our results for shorter distances between patches were consistent with previous work that found decreased movement of prairie voles as density increased (Abramsky and Tracy 1980, Gaines and Johnson 1982, Desy et al. 1990, Lin and Batzli 2001a), but our results for longer distance between patches were equivocal. Decreased movement (not necessarily dispersal) at higher density has also been observed for other arvicoline rodents, including field voles (*Microtus agrestis* L., Sandell et al. 1991), meadow voles (*Microtus pennsylvanicus* (Ord), Ostfeld and Canham 1995) and root voles (*Microtus oeconomus* (Pallas), Gundersen et al. 2002), which suggests that movement of arvicoline rodents generally is inversely density dependent.

Finally, our data indicated that increased wounding was associated with the act of dispersal, which also agrees with the expectations of the social fence hypothesis. Specifically, incidence of wounding among subadults and adults did not differ between residents and dispersers when captured in their home patch (prior to emigration) but increased for dispersers captured in their new habitat patch after immigration (Fig. 7). We were unable to determine the exact timing of wounding during dispersal events, but because residents are territorial (Getz and Hoffman 1986) and aggression is more likely to occur among unfamiliar voles (Getz et al. 1981), we suspect that additional wounding occurred after dispersers entered a new habitat patch.

Contrary to the predictions of the social fence hypothesis, we did not find a relationship between density within a patch and wounding. Our findings were consistent with those of Rose and Gaines (1976), who found no correlation of incidence of wounding with density for either sex of prairie vole. Krebs (1964) did report increased wounding for male collared lemmings (*Dicrosontyx groenlandicus* (Trail)) and brown lemmings (*Lemmus trimucronatus* (Richardson)) during early summer in years of high density, however, and Christian (1970) found increased wounding for meadow voles during the breeding season and at higher density. For California voles Lidicker (1973, 1979) also observed an increase in wounding during the breeding season and at high densities, but Batzli and Pitelka (1971) only found increased wounding during the breeding season and not at higher densities. We were unable to make meaningful comparisons between rates of wounding between the breeding and non-breeding season because we only had data for one month (November) when pregnant females were not common.

Future work

The relationships of increased distance between patches in a landscape to successful dispersal (negative), to mortality (positive) and to overall abundance (negative) suggest that population dynamics within favorable patches may be affected by the relative amount of unfavorable habitat within a landscape. This possibility raises additional questions that may be answered by our experimental protocol. Do populations in small patches go extinct more frequently, particularly when at greater distances from larger patches, as predicted by metapopulation theory (Hanksi 1999)? Do the patterns of population dynamics differ in landscapes with different relative amounts of unfavorable habitat, as predicted by Lidicker (1988)? Longer observations of our experimental populations (at least five years) will be required to answer these questions.

References

Aars, J. and Ims, R. A. 2000. Population dynamics and genetic consequences of spatial density-dependent dispersal in patchy populations. – Am. Nat. 155: 252–265.

Abramsky, Z. and Tracy, C. R. 1980. Relation between home range size and regulation of population size in *Microtus ochrogaster*. – Oikos 34: 347–355.

Andreassen, H. P. and Ims, R. A. 2001. Dispersal movements in patchy vole populations: the role of patch configuration, density-dependence and demography. – Ecology 82: 2911–2926.

Andreassen, H. P., Stenseth, N. C. and Ims, R. A. 2002. Dispersal behaviour and population dynamics of vertebrates. – In: Bullock, J. M., Kenward, R. E. and Hails, R. S. (eds), Dispersal ecology. Symp. Ser. Brit. Ecol. Soc. Blackwell, pp. 65–95.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Batzli, G. O. and Pitelka, F. A. 1971. Condition and diet of cycling populations of the California vole, *Microtus californicus*. – J. Mammal. 52: 141–163.

Baker, J. A. and Brooks, R. J. 1981. Distribution patterns of raptors in relation to density of meadow voles. – Condor 83: 42–47.

Birney, E. C., Grant, W. E. and Baird, D. D. 1976. Importance of vegetative cover to cycles of *Microtus*. – Ecology 60: 349–361.

Bondrup-Neilsen, S. 1986. Investigation of spacing behavior of *Clethrionomys gapperi* by experimentation. – J. Anim. Ecol. 55: 269–279.

Boonstra, R. 1985. Demography of *Microtus pennsylvanicus* in Southern Ontario: enumeration versus Jolly–Seber estimation compared. – Can. J. Zool. 55: 1166–1175.

Bowers, M. A. and Dooley, J. L. Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. – Oecologia 94: 247–254.

Bowers, M. A. and Matter, S. F. 1997. Landscape ecology of mammals: relationships between density and patch size. – J. Mammal. 78: 999–1013.

Brandt, C. A. 1992. Social factors in immigration and emigration. – In: Stenseth, N. C. and Lidicker, W. Z., Jr. (eds), Animal dispersal, small mammals as a model. Chapman and Hall, pp. 96–141.

Christian, J. J. 1970. Social subordination, population density, and mammalian evolution. – Science 168: 84–89.

Cole, F. R. 1978. A movement barrier useful in population studies of small mammals. – Am. Midl. Nat. 100: 480–482.

Cole, F. R. and Batzli, G. O. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. – J. Anim. Ecol. 48: 455–470.

Desy, E. A. and Batzli, G. O. 1989. Effects of food and predation on behavior of prairie vole demography: a field experiment. – Ecology 70: 411–421.

Desy, E. A., Batzli, G. O. and Liu, J. 1990. Effects of food and predation on prairie voles: a field experiment. – Oikos 58: 159–168.

Diffendorfer, J. E., Gaines, M. S. and Holt, R. D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Microtus*, and *Peromyscus*). – Ecology 76: 827–839.

Diffendorfer, J. E., Gaines, M. S. and Holt, R. D. 1998. Testing models of source–sink dynamics and balanced dispersal. – Oikos 81: 417–433.

Diffendorfer, J. E., Gaines, M. S. and Holt, R. D. 1999. Patterns and impacts of movements at different scales in small mammals. – In: Barrett, G. W. and Peles, J. D. (eds), Landscape ecology of small mammals. Springer-Verlag, pp. 63–88.

Dooley, J. L., Jr. and Bowers, M. A. 1998. Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. – Ecology 79: 969–980.

Gaines, M. S. and McClenaghan, L. R., Jr. 1980. Dispersal in small mammals. – Annu. Rev. Ecol. Syst. 11: 163–196.

Gaines, M. S. and Johnson, M. L. 1982. Home range size and population dynamics in the prairie vole, *Microtus ochrogaster*. – Oikos 39: 63–70.

Getz, L. L. and Batzli, G. O. 1974. A device for preventing disturbance of small mammal live-traps. – J. Mammal. 55: 447–448.

Getz, L. L. and Hofmann, J. E. 1986. Social organization in free-living prairie voles, *Microtus ochrogaster*. – Behav. Ecol. Sociobiol. 18: 175–282.

Getz, L. L., Carter, C. S. and Gavish, L. 1981. The mating system of the prairie vole, *Microtus ochrogaster*: field and laboratory evidence for pair-bonding. – Behav. Ecol. Sociobiol. 8: 189–194.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140–1162.

Gundersen, G., Andraessen, H. P. and Ims, R. A. 2002. Individual and population level determinants of immigration success on local habitat patches: an experimental approach. – Ecol. Lett. 5: 294–301.

Hanski, I. 1999. Metapopulation ecology. – Oxford Univ. Press.

Harper, S. J. 1996. Behavioral responses of prairie voles to extrinsic factors and their effects on population dynamics. – PhD thesis, Univ. of Illinois at Urbana-Champaign.

Harper, S. J., Bollinger, E. K. and Barrett, G. A. 1993. Effects of habitat patch shape on population dynamics of meadow voles (*Microtus pennsylvanicus*). – J. Mammal. 74: 1045–1055.

Hestbeck, J. B. 1982. Population regulation of cyclic mammals: the social fence hypothesis. – Oikos 39: 157–163.

Ims, R. A. and Hhermann, D. Ø. 2001. Condition-dependent dispersal. – In: Clobert, J., Danchin, E., Dhondt, A. A. et al. (eds), Dispersal. Oxford Univ. Press, pp. 203–216.

Johnson, M. L. and Gaines, M. S. 1987. The selective basis for dispersal of prairie voles, *Microtus ochrogaster*. – Ecology 68: 684–694.

Krebs, C. J. 1964. The lemmings cycle at Baker Lake, Northwest Territories. – during 1959–1962. Arct. Inst. N. Am. Tech. Paper No. 15: 1–104.

Lidicker, W. Z., Jr. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. – Ecol. Monogr. 43: 271–302.

Lidicker, W. Z., Jr. 1979. Analysis of two freely-growing enclosed populations of the California vole. – J. Mammal. 60: 447–466.

Lidicker, W. Z., Jr. 1988. Solving the enigma of microtine "cycles". – J. Mammal. 69: 225–235.

Lidicker, W. Z. and Stenseth, N. C. 1992. To disperse or not to disperse: who does it and why. – In: Stenseth, N. C. and Lidicker, W. Z., Jr. (eds), Animal dispersal: small mammals as a model. Chapman and Hall, pp. 21–26.

Lin, Y. K. and Batzli, G. O. 2001a. The influence of habitat quality on dispersal, demography, and population dynamics of voles. – Ecol. Monogr. 71: 245–275.

Lin, Y. K. and Batzli, G. O. 2001b. The effect of interspecific competition on habitat selection by voles: an experimental approach. – Can. J. Zool. 79: 110–120.

Lin, Y. K. and Batzli, G. O. 2004. Movements of voles across habitat boundaries: effects of food and cover. – J. Mammal. 85: 216–224.

Morris, D. W. 1996. Temporal and spatial population dynamics among patches connected by habitat selection. – Oikos 75: 207–219.

Ostfeld, R. S. and Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. – Ecology 76: 521–532.

Ostfeld, R. S., Lidicker, W. Z., Jr. and Heske, E. J. 1985. The relationship between habitat heterogeneity, space use, and demography in a population of California voles (*Microtus californicus*). – Oikos 45: 433–442.

Peles, J. D. and Barrett, G. W. 1996. Effects of vegetative cover on the population dynamics of meadow voles. – J. Mammal. 77: 857–869.

Rose, R. K. and Gaines, M. S. 1976. Levels of aggression in fluctuating populations of the prairie vole, *Microtus ochrogaster*, in eastern Kansas. – J. Mammal. 57: 43–57.

Sandell, M., Agrell, J., Erlinge, S. et al. 1991. Adult philopatry and dispersal in the field vole *Microtus agrestis*. – Oecologia 86: 153–158.

Solomon, N. G. and Jacquot, J. J. 2002. Characteristics of resident and wandering prairie voles, *Microtus ochrogaster*. – Can. J. Zool. 80: 951–955.

Stamps, J. A., Buechner, M. and Krishnan, V. V. 1987a. The effects of edge permeability and habitat geometry on emigration from patches of habitat. – Am. Nat. 129: 533–552.

Stamps, J. A., Buechner, M. and Krishnan, V. V. 1987b. The effects of habitat geometry on territorial defense costs: intruder pressure in bounded habitats. – Am. Zool. 27: 307–325.

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