THE INFLUENCE OF HABITAT QUALITY ON DISPERSAL, DEMOGRAPHY, AND POPULATION DYNAMICS OF VOLES

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Abstract. We compared the effects of habitat quality on dispersal, demography, dynamics, and fitness of prairie vole (*Microtus ochrogaster*) and meadow vole (*M. pennsylvanicus*) populations by manipulating habitat patches in experimental landscapes. Four habitat patches in each of four replicate landscapes differed in availability of high-quality food and amount of vegetative cover in a 2×2 factorial design. High cover had a strong positive effect on basic habitat quality, as reflected by the performance of founders early in the season, but supplemental food had only a small effect.

Population growth ceased for prairie voles after week 18 (mid-October) when densities had reached much higher levels in habitats with high cover (260 ± 27 voles/ha in high cover with either high or low food; mean ± 1 SE) than in habitats with low cover (115 ± 38 voles/ha in high food, low cover and 60 ± 15 voles/ha in low food, low cover). Population growth had ceased in three habitat types for meadow voles by week 20 at much higher densities than for prairie voles in high cover (636 ± 101 voles/ha with high food, high cover; 556 ± 117 voles/ha with low food, high cover; 110 ± 74 voles/ha with high food, low cover; and 51 ± 16 voles/ha with low food, low cover).

Correlates of fitness for prairie voles, particularly the number of young surviving to adulthood per female, indicated greater individual fitness in high cover than in low cover, which suggests ideal despotic habitat selection. The proportion of the total population found in habitat patches with high cover continued to increase until prairie vole populations stabilized late in the season. This result did not agree with expectations of either the ideal free model or the ideal despotic model of habitat selection. Fitness differed little for meadow voles in different habitat types, and the proportions of the populations in different habitats remained constant after the founders had settled and population growth began. Both of these patterns supported the ideal free model of habitat selection for meadow voles.

Because positive net recruitment occurred in all habitats for both species of voles, source–sink dynamics could not occur in our experimental system. Two subpopulations of meadow voles in low-food, low-cover habitats did go extinct temporarily, but this habitat type did not appear to be a population sink because the losses occurred primarily from emigration rather than mortality. Emigration rates for both species of voles were inversely related to carrying capacity of the habitat (estimated as the density at which populations stabilized). This relationship and ideal free habitat selection are required by the balanced dispersal model, which produces equal numbers of dispersers between a pair of habitat types. Dispersal of meadow voles was balanced throughout the growing season, but dispersal of prairie voles was unbalanced, with net movement of individuals from low-quality to high-quality habitats until late in the season when populations stabilized. Unbalanced dispersal early in the season may have reflected a delayed response to habitat quality by prairie voles.

Populations in high cover approached stable densities largely as a result of density-dependent in situ net recruitment, whereas populations in low cover stabilized more as a result of density-dependent net movement for both species of voles. Per capita emigration did not show a consistent positive relation to population growth in high cover, as would be expected if dispersal contributed to the tendency for prairie voles to display multiannual population cycles in such habitats. In fact, emigration generally declined as density increased (inversely density dependent), which should have fostered greater population growth as densities increased. Nevertheless, population growth declined late in the season, which implied that emigration (dispersal) did not strongly affect the pattern of population dynamics in high-quality habitats.

The overall results for the two species were remarkably similar, although prairie voles did differ from meadow voles in several respects. Meadow voles performed less well in low-cover habitats than did prairie voles, which probably reflected their greater sensitivity to predation risk. Prairie voles tended to move into habitats with supplemental food, and young prairie voles had greater body growth in habitats with supplemental food, whereas meadow voles showed neither response. Finally, although the results for meadow voles consistently indicated ideal free habitat selection throughout the growing season, those for prairie voles did not until late in the season. This difference between species likely reflected a more rapid response to habitat quality by the more vagile meadow voles.

Key words: balanced dispersal; demography; density-dependent dispersal; growth-dependent dispersal; ideal despotic habitat selection; ideal free habitat selection; meadow voles; Microtus ochrogaster; Microtus pennsylvanicus; *population dynamics; population regulation; prairie voles.*

INTRODUCTION

Landscapes are spatially heterogeneous, and different habitat patches vary in their suitability (quality) for a species. Habitat suitability varies with such factors as availability of high-quality food, risk of predation, interspecific competition, and population density (Fretwell and Lucas 1970). The effects of these factors on in situ demographic processes of small mammal populations have become clear in the last decade (Desy and Batzli 1989, Batzli 1992, Krebs et al. 1995). Their effects on the movement between habitat patches are less clear, however, even though many theoretical models point to the importance of movements between habitats for explanations of population dynamics (Fretwell and Lucas 1970, Levins 1970, Stenseth 1983, Pulliam 1988, Lidicker 1988, 1995, Pulliam and Danielson 1991, McPeek and Holt 1992, Lemel et al. 1997).

The effects of environmental factors on movement between habitats remain unclear for several reasons. First, most studies of movements have focused on movement within habitats, either assessing size of home ranges or dispersal to a new home range within the same habitat. Second, documentation of movements between habitat patches and separation of mortality from dispersal have proved difficult (Stenseth and Lidicker 1992). Few experiments have altered the quality of neighboring patches of habitat to study dispersal, even though dispersal is likely to be influenced by the quality of both the resident and colonizing habitats (Fretwell and Lucas 1970). Third, those few studies that have investigated movements between different types of habitat patches had no replication, which made it difficult to separate site-specific from more general factors (Ostfeld and Klosterman 1986, Morris 1989, Halama and Dueser 1994). Finally, general patterns may be difficult to detect because different species, even though closely related, may respond to the same kind of habitat patchiness in different ways (Wiens 1989).

Comparative studies of habitat-specific demography among habitat patches (reviewed by Krohne 1997) and experimental manipulation of environmental factors (Batzli 1992, Krebs et al. 1995, Batzli et al. 1999) have shown that risk of predation, availability of high-quality food, and interspecific competition are important factors influencing the local population dynamics of small mammals. However, none of these studies examined the effect of movement among habitats on local population dynamics. Most studies of movement concentrate on dispersal from natal home ranges (reviewed by Stenseth and Lidicker 1992) and provide little information about dispersal between habitats with different qualities and population densities. As a result, empirical studies that put the local population in the context of a larger landscape and that consider the influence of landscape components are badly needed (Lidicker 1995, Barrett and Peles 1999).

The main objective of our research was to investigate the effects of habitat quality on demography, dispersal, and population dynamics of small mammals. Assessing habitat quality is not a simple matter, however. Basic habitat quality is a function of the characteristics of both the habitat and the focal species and, therefore, is best indicated by the fitness of individual members of the focal species (Van Horne 1983). The habitat quality actually experienced by individuals (realized habitat quality), however, will likely decline as density increases because of such things as declining food supply, increasing attraction of predators, and increasing transmission of disease. Assuming that quality of habitats relative to one another do not shift dramatically with season or some other factor independently of density, the best assessment of basic habitat quality is likely to be fitness of the target species measured at relatively low population densities (Fretwell and Lucas 1970, Hanski 1996). If animals only occupy one habitat type when densities are below a threshold level, then that behavior should indicate which habitat has the highest basic quality.

Several studies have shown that two environmental factors are strongly correlated with basic habitat quality for small mammals. Increased availability of high-quality food leads to increased reproductive success of small mammals (Desy and Batzli 1989, Boutin 1990), and greater vegetative cover leads to increased density, apparently because of protection from predation (Birney et al. 1976, Baker and Brooks 1981, Adler and Wilson 1989, Peles and Barrett 1996). Thus, the basic quality of grassland habitats for small mammals should increase with greater availability of high-quality food and with greater vegetative cover.

In east–central Illinois, USA two species of voles, prairie voles (*Microtus ochrogaster*) and meadow voles (*M. pennsylvanicus*), co-occur in a mosaic of habitat types: road sides, old fields in various stages of succession, agriculture fields with herbaceous cover, and restored tallgrass prairies that are maintained by fire. Both meadow voles and prairie voles prefer habitats with higher cover, but prairie voles show greater tolerance of low cover (Klatt 1986, Klatt and Getz 1987). Both species are herbivorous and show strong overlap in their diets, although meadow voles consistently eat more monocots (Haken and Batzli 1996). Meadow voles appear to be more active, have larger home ranges, have higher average daily metabolic rates, and therefore, eat more food (Young Owl and Batzli 1998). Prairie voles have territorial females, form monogamous (with territorial males) or communal nesting groups, and display periodic multi-annual fluctuations in density (population cycles) in high-quality habitat (Getz et al. 1987, 1993, Getz and Hofmann 1999). On the other hand, meadow voles have territorial females, a promiscuous breeding system, and seasonal changes in density with erratic year-to-year fluctuations (Madison 1985, Getz and Hofmann 1999).

To test hypotheses regarding the responses of voles we manipulated habitat quality for enclosed populations and followed movements among habitat patches and local dynamics within habitat patches. We conducted the same experiment on prairie voles and meadow voles to see if these two morphologically similar species would respond to the same manipulation in similar ways in spite of well-documented differences in their nutrition, behavior, and patterns of population dynamics. We used manipulated habitat patches within enclosures for several reasons. First, we could control factors in addition to habitat quality, such as patch size and juxtaposition, that may influence local population dynamics. Second, we could replicate an experimental landscape but not a natural one. Third, by using enclosures we could separate dispersal from in situ mortality. Our previous work indicated that nearly all disappearance from experimental enclosures at our study site can be attributed to predation (Lin and Batzli 1995). Although several experiments have been conducted to examine the effects of quantitative aspects of habitat patches (size, shape, and isolation) on small mammals (Barrett and Peles 1999), to our knowledge, this is the first report of an experiment that explores qualitative aspects of habitat patches (food availability and cover) on small mammal populations.

HYPOTHESES AND PREDICTIONS

Habitat selection

The ideal free distribution (IFD) of Fretwell and Lucas (1970) is the most widely known model of habitat selection. It states that if animals have complete information (ideal) and movement is unconstrained (free), individuals should move to those habitats in which their fitness is maximized. The model predicts that as densities increase, fitness within each habitat will decline, but the fitness of resident individuals in different habitats will remain equal to one another. An alternative model, the ideal despotic distribution (IDD) of Fretwell and Lucas (1970), assumes that movement is constrained by agonistic behavior. It states that the territorial behavior of dominant individuals reduces the ability of subordinate individuals to settle in habitats with greater basic quality. Again, as overall population size increases, individual fitness will decline within each habitat, but residents in habitats with greater basic quality (dominant individuals) maintain higher fitness.

Both the IFD and IDD predict changes of habitat use as population density changes because only habitats with high basic quality will be occupied when overall population density is very low. IDD predicts a threshold at which high-quality habitat is saturated by territorial dominants, and surplus individuals (subordinates) start to use low-quality habitats. Then, as total population size increases, an increasing proportion of population should occur in low-quality habitats (Fretwell and Lucas 1970: Fig. 4). In contrast the IFD predicts that, after all habitats are occupied, the proportion of the population in high- and low-quality habitats should remain constant as total population size increases, so long as their relative quality remains constant (Pulliam and Caraco 1984, Morris 1988).

Because both species of voles have territorial females, we expected IDD for both species, which led to our predictions of unequal fitness among habitats and increasing use of low-quality habitats as overall population size increased.

Dispersal patterns

Pulliam (1988) categorized habitats into two basic types, sources and sinks. In source habitats, the number of births exceeds the number of deaths, and surplus individuals emigrate (disperse). In sink habitats, the number of deaths exceeds the number of births, so the subpopulation declines to extinction in the absence of immigration. At demographic equilibrium (recruitment = losses) the source habitat will be a net exporter of individuals, and the sink habitat will be a net importer of individuals.

Differences in habitat quality may not be as extreme as those in a source–sink relationship. A two-patch model of McPeek and Holt (1992) suggested that, under such circumstance, animals that are free to move will maximize their fitness when the ratio of their per capita emigration rates from each habitat patch is inversely proportional to the carrying capacities of the patches. Note that the conditions for ideal free habitat selection are assumed for this balanced dispersal model. If densities within habitats remain proportional to their carrying capacities, as expected by IFD habitat selection, this should lead to equal numbers of individuals dispersing between habitats (balanced dispersal; Lemel et al. 1997). Brown (1969) developed similar ideas involving the ratio of the number of individuals moving in each direction between two habitats, which he called the exchange ratio.

Net movement from lower quality habitats to higher quality habitats could occur when lower quality habitats maintain positive in situ recruitment but individuals still prefer higher quality habitat. This phenomenon, which we call unbalanced dispersal, seems likely when fitness remains higher in higher quality habitats and social dominants cannot expel most subordinates. Of course, source–sink dispersal between habitats is also unequal, but in that case the higher quality habitat has a net loss rather than a net gain as in unbalanced dispersal. At least one empirical study suggests that unbalanced dispersal can occur in populations of voles (Paradis 1995). Halama and Dueser (1994) also reported data that indicated movement of white-footed mice (*Peromyscus leucopus*) from lower to higher quality habitats.

These three patterns of dispersal can be distinguished by comparing net in situ recruitment (births − deaths) and net movement for each habitat (immigration −

emigration). The source–sink model predicts that low-quality habitats have negative net in situ recruitment and positive net immigration; the balanced dispersal model predicts that low- and high-quality habitats both have positive net in situ recruitment, but lower quality habitats maintain higher per capita emigration rates so that equal numbers of individuals move between pairs of habitats at equilibrium; and the unbalanced dispersal model predicts that positive net in situ recruitment occurs in low- and high-quality habitats but that net movement from lower to higher quality habitats still occurs.

Because meadow voles have low tolerance of low-cover habitats (Klatt 1986), these habitats seemed likely to be sink habitats for them, and we expected them to show source–sink dynamics. Prairie voles, however, tolerate low-cover habitats better, and these habitats seemed unlikely to be sinks. However, assuming that prairie voles are imperfectly despotic, we thought they might display unbalanced dispersal.

Dispersal and population dynamics

Habitat patchiness could stabilize population densities in high-quality habitats if low-quality habitats provide dispersal sinks. This would only occur, however, when per capita emigration in high-quality habitats is directly density dependent (increasing per capita emigration with increasing densities) and sufficient to balance net recruitment. Lidicker (1975) pointed out that density-dependent dispersal, which should have the highest per capita emigration at carrying capacity, may not always occur. Presaturation dispersal (highest dispersal rates before reaching carrying capacity) could occur, which would tend to destabilize populations. Stenseth (1983) and Stenseth and Lidicker (1992) argued that if dispersal is an important causal agent of cyclic fluctuations in density of populations, per capita emigration should be positively correlated with per capita population growth rather than with population density. This conclusion was based upon the arguments that (1) selection for optimal dispersal for voles should result in low dispersal at low densities (limited mates) and high densities (high predation risk) and greatest per capita dispersal during rapid population growth (greater reproductive opportunities elsewhere) and that (2) per capita population growth should be greatest during the phase of the most intense increase. However, in traditional models of population growth per capita population growth is either constant (exponential model) or greatest as populations begin to grow (logistic model), so we would expect correlation of per capita emigration at maximum absolute rate, not per capita rate, of population growth.

In east–central Illinois, prairie voles tend to display multi-annual population cycles, but meadow voles do not (Getz et al. 1987, Getz and Hofmann 1999). The causes of population cycles in prairie voles have not been established, but if dispersal contributes strongly to population cycling, we would expect per capita emigration generally to be positively correlated with population growth rather than with population density. Per capita emigration of meadow voles, which display erratic population dynamics in east–central Illinois, should not be positively correlated with either density or population growth rates.

METHODS

Study area

We conducted field work with prairie voles from May to March of 1995–1996 and with meadow voles from May to March 1996–1997 at the Ecological Research Area of the University of Illinois, which is located 5 km northeast of Urbana, Illinois, USA. The study area was an old pasture with vegetation dominated by perennial grasses with patches of forbs, shrubs, vines, and tree seedlings. Invading woody plants had been periodically removed over the past 10 yr and were reduced during the course of our experiment by mowing, which was one of our experimental treatments. A detailed description of the vegetation in our experimental enclosures is given in Table 1 and in the *Results* section.

Major predators observed in the area included feral cats (*Felis catus*), red foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), least weasels (*Mustela nivalis*), long-tailed weasels (*Mustela frenata*), fox snakes (*Elaphe vulpina*), Red-tailed Hawks (*Buteo jamaicensis*), and Great Horned Owls (*Bubo virginianus*). More detailed information on the local predators can be found in Lin and Batzli (1995).

Experimental design

To manipulate the quality of habitats available to voles, we constructed four 0.52-ha vole-proof enclosures. These were subdivided into four different habitat types, two of which were provided with supplemental food and two of which were mowed. This 2 × 2 factorial design gave four treatment combinations (Fig. 1): (1) high food, high cover (HH); (2) high food, low cover (HL); (3) low food, high cover (LH); and (4) low food, low cover (LL). Throughout this paper we refer to the four habitat types by the abbreviated notation for their treatment. Manipulation of food and cover were randomly assigned to habitat patches within a replicate, except that the same cover treatments were never adjacent to one another. We kept the relative positions of cover treatments constant because juxtaposition of adjacent habitats may have substantial influence on local movements. Our design meant that dispersers from the high-cover habitats (HH and LH) had equal access to both of the low-cover habitats (HL and LL), and vice versa.

Habitats with high food contained commercial rabbit chow ad libitum in 250-mL bottles lying on their sides in a checkerboard pattern (Fig. 1). Rabbit chow is a high-quality food on which voles grow and reproduce

TABLE 1. Mean abundance and palatability to voles of species of plants that occurred in half or more of 16 habitat patches at the Ecological Research Area of the University of Illinois in east–central Illinois, USA, based on vegetative samples taken early (June) and late (October) in the growing seasons of 1995 and 1996.

| Plant taxa | Growth form | June | | | | October | | | |
| | | Abundance (g/m^2) | | Palatability | | Abundance (g/m^2) | | Palatability | |
		1995	1996	MO	MP	1995	1996	MO	MP
Monocotyledons									
Poa pratensis	G	86.2 (16)	71.2 (16)	+	+	48.4 (16)	56.0 (16)	−	+
Festuca elatior	G	59.0 (16)	67.0 (16)	+ +	+ +	76.7 (16)	65.8 (16)	−	+
Bromus inermis	G	65.2 (16)	41.3 (16)	+	+	21.0 (16)	23.8 (16)	−	−
Carex spp.	G	2.0 (11)	4.0 (13)	+	+	2.3 (10)	1.6 (14)	+/−	+
Dactylis glomerata	G	0.3 (4)	6.6 (9)	+	+ +	1.1 (7)	1.0 (7)	?	?
Bromus japonicus	G	1.3 (10)	0.6 (8)	+ +	+ +	0.0 (0)	0.0 (1)	+	+
Total live monocots	G	218 ± 21	194 ± 36			152 ± 21	149 ± 18		
Dicotyledons									
Solidago altissima	F	74.3 (16)	6.8 (15)	−	− −	50.4 (16)	8.6 (16)	− −	− −
Trifolium pratense	F	4.5 (10)	16.1 (10)	+ +	+ +	3.8 (8)	1.5 (10)	+ +	+ +
Daucus carota	F	2.3 (16)	5.6 (12)	+	+/−	0.9 (13)	2.6 (14)	+	+/−
Rubus alleghenensis	S	7.1 (11)	1.0 (10)	−	− −	8.1 (11)	1.3 (12)	?	?
Rosa multiflora	S	6.5 (9)	1.3 (9)	− −	− −	3.8 (10)	1.1 (5)	−	?
Rhus radicans	S/V	5.7 (9)	0.0 (0)	?	?	0.5 (4)	0.0 (0)	?	?
Convolvulus americanus	F/V	3.3 (14)	1.4 (12)	?	?	0.0 (7)	0.3 (9)	?	?
Campsis radicans	S/V	2.1 (12)	1.1 (7)	?	?	0.0 (3)	4.2 (9)	−	+
Achillea millefolium	F	1.7 (8)	4.1 (9)	−	−	0.3 (10)	0.2 (8)	?	?
Cirsium discolor	F	0.3 (11)	5.1 (14)	− −	−	0.6 (10)	1.5 (12)	?	?
Erigeron annuus	F	0.6 (7)	2.9 (9)	+	− −	0.1 (4)	1.0 (9)	?	?
Crataegus mollis	T	1.3 (9)	1.0 (11)	?	?	0.5 (7)	2.5 (9)	?	?
Prunus serotina	T	1.2 (7)	0.6 (9)	?	?	1.1 (10)	1.2 (7)	?	?
Pastinaca sativa	F	1.5 (15)	0.1 (13)	−	−	0.4 (13)	0.6 (11)	− −	− −
Geum verum	F	0.4 (7)	0.2 (9)	−	−	0.3 (8)	0.1 (4)	?	?
Taraxacum officinale	F	0.3 (12)	0.3 (11)	+	+	0.2 (7)	0.1 (7)	+ +	+ +
Ambrosia trifida	F	0.4 (12)	0.1 (13)	+/−	−	0.0 (2)	0.6 (11)	−	− −
Dipsacus sylvestris	F	0.1 (4)	0.3 (5)	?	?	0.1 (7)	1.3 (8)	?	?
Stellaria aquatica	F	0.1 (12)	0.2 (10)	+	+	0.0 (3)	0.0 (2)	+	−
Aster ericoides	F	0.0 (0)	0.0 (1)	+	+	0.1 (6)	5.3 (9)	−	−
Total live dicots		118 ± 32	57 ± 22			103 ± 38	37 ± 11		
Litter (dead biomass)		287 ± 22	279 ± 36			569 ± 42	417 ± 26		
Total biomass		625 ± 43	534 ± 23			813 ± 77	610 ± 42		

Notes: Totals for major categories are given as means ± 1 SE. The number of habitat patches in which each plant species occurred is given in parentheses. Palatability is given as preferred (+) or avoided (−) based on laboratory feeding trials and food habits in the field. MO = prairie voles (*Microtus ochrogaster*), and MP = meadow voles (*Microtus pennsylvanicus*). F = forb, F/V = forb/vine, G = graminoid, S = shrub, S/V = shrub/vine, and T = tree seedling.

well (Cole and Batzli 1979, Desy and Batzli 1989). Habitats with low cover were mowed as needed (roughly once every 2 wk) to keep vegetation 10–20 cm high. Mowing itself did not seem to affect movement patterns of voles because we found most individuals in the same home ranges before and after mowing and detected no unusual movements among pens associated with a mowing event.

All four enclosures were fenced by corrugated, galvanized steel panels that reached 0.5 m below ground and 1 m above ground. Predators could access pens through panels cut to 0.3 m above ground at 5 m intervals (at least 10 short panels on each wall). Habitat patches within the enclosures were also separated by steel panel walls, but each wall had three gates for voles (5 × 10-cm holes at ground level) that allowed movement between habitats (Fig. 1). The gates were placed at 0.5-m intervals near outside walls so that voles entering a new habitat had to traverse it completely (at least 50 m) before moving to still another habitat patch.

We used a design with reduced access between habitats for two reasons. First, voles probably do not have immediate access to all habitat types in nature and often need to traverse one habitat before entering another. Second, home ranges that encompass more than one habitat would be more likely if there were no barriers between habitats, which would complicate data analyses. We kept vegetation very low (3–5 cm) along a 30 cm wide strip along both sides of all panels to prevent escape of the voles and to discourage digging next to the panels.

We removed all small mammals from enclosures by live trapping for 2 wk before the experiment was initiated. Three pair of adult voles were released in the center of each habitat patch in early June for a density of 46 voles/ha, which is moderate for natural populations of voles in east–central Illinois (Getz and Hofmann 1999). Each territorial pair of prairie voles or territorial female meadow vole could exclusively use an average space of 430 m^2 when released (each habitat
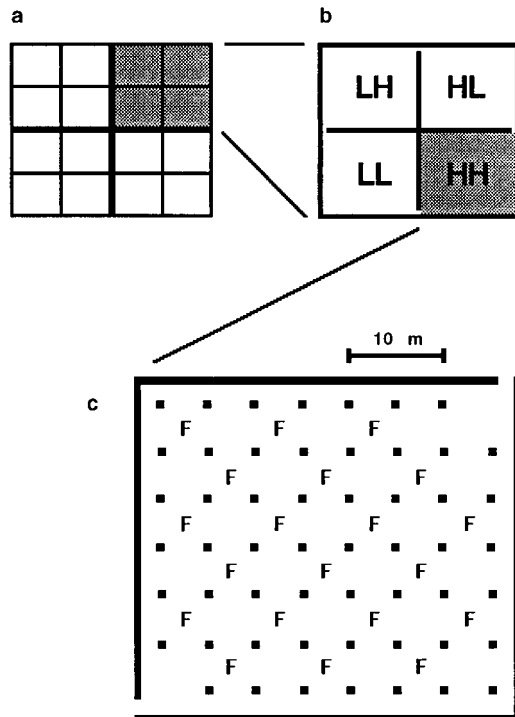
FIG. 1. Layout of replicated enclosures (separated by heavy lines) and habitat patches (33 × 39 m or 0.13 ha) within each enclosure at the Ecological Research Area of the University of Illinois in east–central Illinois, USA. Location of habitat types within an enclosure varied among replicates. The four habitat types are coded as follows: HH, high food, high cover; HL, high food, low cover; LH, low food, high cover; and LL, low food, low cover. Locations of trapping stations and feeding stations within a habitat patch are shown by squares and F's, respectively.

patch was ~33 × 39 m). Given that home ranges of female prairie voles and meadow voles are usually smaller than that (Madison 1985, Desy et al. 1990), each habitat patch should have had space available for additional voles at the beginning of the experiment. Thus, the early performance of the founding voles should reflect the basic quality of the habitats.

Live trapping

Each habitat patch had trapping stations at 5-m intervals in a 7 × 8 grid with one trap in each station, except that stations adjacent to dispersal gates had no trap, for a total of 54 trapping stations per habitat and 216 per enclosure (Fig. 1). Four alternate rows contained Longworth traps (B. N. Bolton, Vernon, British Columbia, Canada) and three contained large Sherman traps (H. B. Sherman Trap, Tallahassee, Florida, USA). Traps were protected by raccoon-proof cages (Getz and Batzli 1974) to prevent disturbance of traps after capture of voles. We also set a Sherman live trap every 10 m along the exterior of the enclosures to catch any escaping voles. We never caught any marked voles out-

side the enclosures, nor did we capture any marked voles that had moved between enclosures.

Live trapping began 2 wk after founders had been placed in the enclosures and continued for 3 d every 2 wk until mid-November (22 wk). A final trapping was conducted by live-trapping for a week and snap-trapping for a week during the following March to estimate overwinter survival. Live traps contained cracked corn (maize) for bait and cotton for bedding. Corn is a low-quality food that will not support growth or reproduction of the prairie vole in the laboratory (Desy and Batzli 1989). Traps were serviced at dawn, mid-morning, and dusk each day, but were closed at midday during hot weather. Traps remained in place, locked open, between trapping sessions.

Upon first capture each vole was marked with a numbered ear tag. The date, location, ear tag number, body mass (to the nearest gram), gender, reproductive condition, and general condition of each vole were recorded when captured. Voles were then released at the point of capture. Females in late pregnancy (with palpable embryos) or with nursing young (enlarged teats with hair removed) were tracked to their nests using fluorescent powder (Getz and Hofmann 1986). We intensively live trapped (2–3 live traps 3 d/wk) around each burrow or surface nest that contained reproductive females in an effort to capture young when they emerged.

Vegetation sampling

To estimate the effects of mowing on cover and composition of vegetation, we collected vegetation samples by clipping 0.2 × 0.5-m (0.1-m²) quadrats at ground level at 16 randomly chosen sites within each habitat patch. Samples were collected twice during the experiment, early in the season (late June) and late in the season (early October). All samples in the low cover habitats were collected 1–2 wk after mowing. Vegetation samples were air dried, then live material was sorted to species following the nomenclature of Jones (1963). All dead material was combined as litter. All components were dried at 60°C to constant mass.

DATA ANALYSES

Habitat characteristics

To compare the vegetation in different habitat patches, we categorized plant samples into five groups: total live monocots, total live dicots (woody stems excluded), litter (dead material), total biomass (all live and dead material), and high-quality forage for voles (highly palatable monocots and dicots). Palatabilities of plants were determined by examining food habits in relation to availability in the field (Cole and Batzli 1978, Lindroth and Batzli 1984, Haken and Batzli 1996) and by feeding trials in the laboratory (Marquis and Batzli 1989; M. Corse and G. O. Batzli, *unpublished manuscript*). In the early season, palatable spe-

cies for both species of voles included all live monocots (voles do not consume dead plant material) and a variety of herbaceous dicots (forbs), particularly legumes, although meadow voles favored fewer dicots than did prairie voles. Late in the growing season, the only palatable monocots for prairie voles were live annual grasses, whereas meadow voles also found several species of perennial grasses still palatable. Prairie voles preferred the same dicots as earlier, except for species that had dried, but again meadow voles preferred fewer dicot species.

Response of founders

To assess basic habitat quality, we compared demographic performance of founders released in different habitat types. We analyzed the cumulative per capita mortality and per capita movement using data from weeks 0–4 because new recruits began to appear in our traps in week 6. We compared per capita in situ recruitment of new young recruited from weeks 6–12 for founder females that had settled in different habitats. Because it usually takes at least 6 wk for a newly weaned female to wean her own young (time to first mating plus 3 wk for pregnancy plus 2 wk nursing young), nearly all young animals recruited before week 12 likely were born to founder females. Finally, we assessed changes in body mass of founders that settled in different habitat patches.

Demographic variables

Some animals were captured in more than one habitat in a given trapping session (percentages ranged from 0.6% to 6.9% among trapping sessions and replicates). We corrected our estimates of demographic variables for each habitat type by calculating residency values for each individual in each habitat type. Proportional residency in a given habitat patch was calculated as number of captures of an individual in that habitat divided by total number of captures of the individual in all habitats during the trapping session. We summed the residency values of all individuals in a given habitat to calculate size of the subpopulation in each habitat patch.

Dispersers sometimes moved from one habitat to another in stages. Partial dispersers were defined as individuals that changed residency values from one trapping session to the next. If an individual's residency value increased in a given habitat between two consecutive trapping sessions, then it was defined as a partial immigrant, and the increase in residency value was the immigration value of that individual. We summed the immigration values of all individuals in a given habitat to calculate immigration frequency in each habitat type. On the other hand, if, in a given habitat, an individual's residency value decreased from a trapping session to the next, then it was defined as a partial emigrant. Again we summed all emigration values to calculate emigration frequencies. With this meth-od, the total amounts of immigration and emigration for all habitat types within in a replicate were equal, as they should be.

We intensively trapped around nesting sites, captured nearly all recruits (>90%) at <25 g, and recorded few voles <25 g moving between habitat patches (11% of those that moved). We therefore assumed that all recruits were born in the habitat in which they were first captured. Juvenile voles captured at <15 g were considered recent weanlings. The weaning dates for young voles captured at ≥15 g, which we needed to calculate in situ recruitment during 2-wk intervals, were calculated by using the habitat-specific body growth rates that were based on repeated capture of individuals <25 g in each habitat type (see *Results: Fitness correlates*). In situ recruitment combines birth and survival to weaning. We could not estimate actual birth rates because we had no estimates of litter sizes in different habitats.

Because voles could not leave an enclosure, animals that disappeared were assumed to die midway between their last capture and the next trapping session. We assigned a habitat-specific death value to an individual equal to its residency value when it was last captured. We summed the death values of all individuals to calculate mortality in each habitat type. With these methods, the absolute biweekly change in density of the subpopulation in each habitat type could be reconciled with demographic change using a BIDE model: $\Delta N = B$ (in situ recruitment) $+ I$ (immigration) $- D$ (deaths) $- E$ (emigration). Similarly, per capita population growth rates ($N_t - N_{t-2}/N_{t-2}$) over each 2-wk period equaled the sum of per capita demographic variables.

To compare habitat-specific demography over the breeding season after recruitment had begun, we calculated mean values for the early season (weeks 8–14) and the late season (weeks 16–22). Data for each week were based upon changes that occurred since the last trapping period 2 wk earlier. For instance, recruitment of young or mortality for week 8 represented gains of unmarked animals or losses of marked animals from week 6 to week 8. Similarly, per capita demographic rates of change for week 8 represented changes from week 6 to week 8 divided by the density at week 6. The first recruits did not begin to appear in our traps until week 6, so we took that as the beginning of population growth.

To examine age differences we classified voles into three age classes based upon mean weekly body mass (Desy and Batzli 1989): juveniles (<22 g for both sexes), subadults (22–30 g for males and 22–28 g for females), and adults (>30 g for males and >28 g for females). Even though animals near borderlines sometimes lost mass, they never reverted to a younger class. Sex ratios of subpopulations in different habitat types and of total populations within each replicate were calculated for adults, subadults, and juveniles for the early

season (weeks 8–14) and the late season (weeks 16–22) in the growing season for each replicate.

To test the predictions of the three dispersal hypotheses, we first calculated means for the net movement of individuals into and out of each habitat type during weeks 8–22. We then compared the number of animals moving between pairs of habitat types over weeks 8–22 with paired t tests, six pairs of habitats with four replicates each. We also calculated net movement between habitats for prairie voles after the population growth had slowed or stopped (weeks 20–22). Finally, we examined the relationship between per capita emigration (dispersal) rate and carrying capacity by regressing the mean per capita emigration for weeks 8–22 on the average densities for each habitat patch during the last two trapping periods (weeks 20–22). The balanced dispersal hypothesis assumes that these variables are inversely related. Most populations had stabilized during the last weeks, so density at this time represented our best estimate of carrying capacity near the end of the growing season.

Individual fitness

To compare the fitness of individuals in different habitat patches, we utilized the body mass of juvenile voles when first captured, body growth rates of juvenile voles, number of young recruited per adult female, and the number of young per adult female that survived to adulthood. We could only assess survival to adulthood for juveniles born before week 14 because some young born after week 14 had not matured by mid-November. Body growth rates (in grams per week) were estimated for each habitat type from individuals first caught as juveniles (<22 g) and recaptured within 2 wk. Each individual was used only once. We used fixed-factor, two-way analysis of variance with repeated measures to assess the effects of food, cover, and season on the fitness correlates, except for survival to adulthood which we could assess only for the season as a whole (no repeated measure).

Density-dependent effects

Detection of direct density dependence from a time series over short intervals can be problematic because of biased results owing to autocorrelation. However, experimental manipulation of density has shown that direct density dependence for measures of performance does occur in populations of voles over relatively short time spans (Ostfeld and Canham 1995). Furthermore, time series analyses of long-term annual data have shown strong density dependence of population growth in a variety of small mammals using the Ricker model of logistic growth, which is equivalent to regressing per capita rate of population growth against population density (Fryxell et al. 1998, Stenseth 1999). Mindful of the possible bias in probability estimates, we used simple linear regressions to evaluate the relationship of density (independent variable) to per capita demo-

graphic parameters and population growth (dependent variables) for all habitat types with values calculated from trapping sessions from weeks 8–22. We also used linear regression to examine the relationship of per capita dispersal (emigration) to population density and to finite rate of population growth (calculated as $\lambda = N_t/N_{t-2}$).

Statistical analysis

We based our estimates of demographic variables and population densities on numbers of voles that were trapped (minimum number known to be alive). Because trappability of our animals was consistently high (see *Results*), estimates based upon statistical models for mark-and-recapture estimates would have improved the accuracy of minimal estimates little, if at all (Boonstra 1985). Confidence limits for estimates of demographic variables are provided by statistical mark-and-recapture models, but we used estimated variables themselves as the observations for each replicate in our ANOVAs. Thus, confidence intervals for our estimates were of little use.

Because we noted that vegetation in two of our replicate enclosures on higher ground (upslope) appeared to have more monocots and fewer dicots than replicates on lower ground (downslope), we used elevation as a main factor to detect significant differences in vegetation with position on the gentle slope. Thus, we conducted fixed-factor, three-way ANOVAs (with and without supplemental food, with and without reduced cover, and upslope and downslope) with repeated measures (early and late season) using biomasses of the five vegetational categories as dependent variables and the four enclosures as replicates. Mean values, calculated from the 16 samples of biomass per habitat patch per season, were used as the observed values for each replicate.

The vegetational analysis revealed differences between upslope and downslope replicates, so we also used elevation as a third main factor (in addition to food and cover) for three-way ANOVAs throughout our subsequent analyses where appropriate. If the main effects and interactions of elevation did not approach statistical significance ($P \leq 0.10$), we eliminated it as a factor and only reported results from two-way ANOVAs to simplify the analysis. We used repeated measures ANOVA throughout the paper to assess seasonal trends because we repeatedly sampled populations and habitat patches. Transformations of data were performed before statistical analysis as needed to address substantial violations of assumptions. We consistently applied a logarithmic transformation to densities and ratios and a modified Freeman and Tukey transformation to proportions, such as per capita mortality rates and per capita emigration rates, before analysis (Zar 1996).

Rather than presenting ANOVA tables for our many analyses in the text, we have placed them in ESA's

Electronic Data Archive. In the text, tables, and figures we report mean values (± 1 SE) together with probability levels associated with the statistical tests. We used sequential Bonferroni corrections for significance levels when doing multiple comparisons of data in a table. Nevertheless, we reported differences that reached significance levels of $P \leq 0.10$ to compensate for the relatively low power achieved with four replicates of a variable system.

<center>RESULTS</center>

<center>*Trapping success*</center>

A total of 656 prairie voles were captured 8657 times and a total of 1381 meadow voles were captured 10 963 times between early June and mid-November, 1995 and 1996, respectively. Overall trappability (number of individuals caught divided by the total number of individual known to be alive in a given trapping period) was 87% for prairie voles and 76% for meadow voles. Because trappability of animals remained relatively high under all conditions, our estimates for density and other demographic variables in the different habitat types should be quite accurate.

<center>*Vegetation*</center>

A cumulative total of at least 13 species of monocots (species of *Carex* could not be always be identified) and at least 49 species of dicots (some seedlings could not be identified) occurred in the 16 vegetation samples for each of the 16 habitat patches (256 samples in late June and 256 samples in early October of each year). Three species of perennial grasses, bluegrass (*Poa pratensis*), brome grass (*Bromus inermis*), and fescue (*Festuca elatior*), and one perennial forb, goldenrod (*Solidago altissima*), occurred in samples from all the habitat patches during at least one season of both years and dominated the vegetation (Table 1). These grasses had mean live biomasses >40 g/m^2 in June and >20 g/m^2 in October of both years, whereas goldenrod had live biomass comparable to the grasses in 1995 but <10 g/m^2 in 1996.

Although the production and species composition of monocots remained similar during the two years, production of dicots declined and relative importance of species shifted during 1996 (Table 1). In 1995 the most common group of plants, other than the dominants, were the shrubs multiflora rose (*Rosa multiflora*), wild blackberry (*Rubus alleghenensis*), and poison ivy (*Rhus radicans*), whose live biomass varied from 5.7 to 7.1 g/m^2 in June. In 1996, however, the live biomass of these shrubs declined to 0.0–1.3 g/m^2 in June, less than the live biomass of several forbs, including red clover (*Trifolium pratense*) with 16.1 g/m^2, wild carrot (*Daucus carota*) with 5.6 g/m^2, and field thistle (*Cirsium discolor*) with 5.1 g/m^2. Heath aster (*Aster ericoides*) was the only forb besides goldenrod to reach 5 g/m^2 in October. Red clover was the most abundant
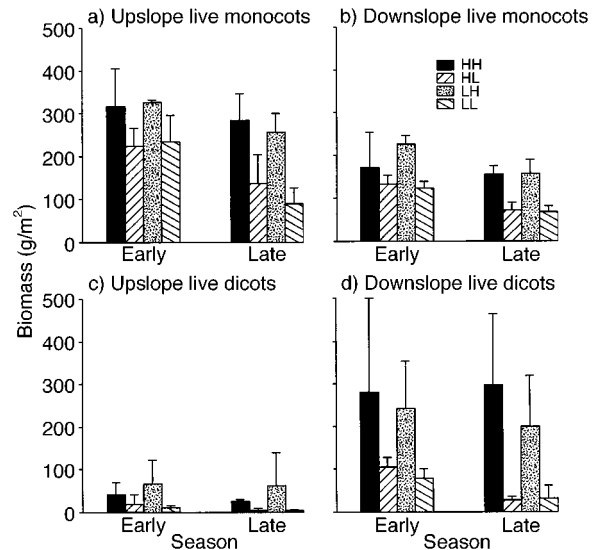

FIG. 2. Estimates of biomass for components of vegetation in different habitat types in 1995 (means + 1 SE). Vegetation samples were taken early (June) and late (October) in the growing season and differed along a gentle slope: (a) live monocots in upslope replicates, (b) live monocots in downslope replicates, (c) live dicots in upslope replicates, and (d) live dicots in downslope replicates. $N = 2$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

plant that remained palatable to both species of voles throughout the growing season (3.8–4.5 g/m^2 in 1995 and 1.5–16.1 g/m^2 in 1996). Even though an additional 15 species of plants occurred in samples from half or more of the habitat patches at sometime during this study, they generally were at least an order of magnitude less abundant than the dominant species (Table 1).

Three-way ANOVAs (food $\times$ cover $\times$ elevation) with repeated measures (season) indicated that vegetational structure differed among habitats as expected in response to manipulation, elevation, and season. Biomass of live monocots ($P = 0.002$ in 1995 and $P = 0.0009$ in 1996), live dicots ($P = 0.02$ in 1995 and $P < 0.0001$ in 1996), high-quality food ($P = 0.04$ in 1995 and $P = 0.001$ in 1996), and total biomass ($P = 0.0002$ in 1995 and $P = 0.01$ in 1996) were all significantly higher in high-cover habitats than in low-cover habitats (Figs. 2–5). Although total biomass was significantly greater in high-cover habitats over the whole growing season in 1996, this was especially true late in the season (cover $\times$ season interaction, $P = 0.09$). The amount of litter was consistently higher in high-cover habitats in 1995 ($P = 0.002$), but was higher in low-cover habitats early in the season in 1996 (cover $\times$ season interaction, $P < 0.0001$). This difference probably occurred because low-cover habitats in 1996 had been high-cover habitats in 1995, and the litter produced in 1995 carried over to the 1996 growing season.

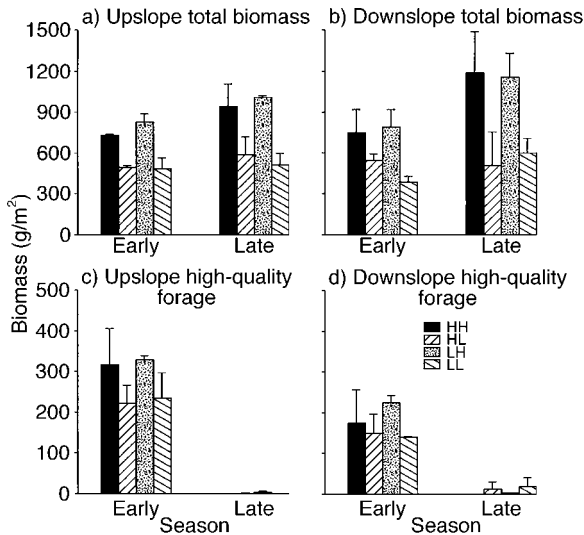Provision of supplemental food had no relationship

FIG. 3. Estimates of biomass for components of vegetation in different habitat types in 1995 (means + 1 SE). Vegetation samples were taken early (June) and late (October) in the growing season and differed along a gentle slope: (a) total biomass (live + litter) in upslope replicates, (b) total biomass in downslope replicates, (c) high-quality forage for prairie voles (see Table 1) in upslope replicates, and (d) high-quality forage in downslope replicates. $N = 2$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

to biomass for any category of the vegetation ($P > 0.54$ in all cases in 1995 and $P > 0.35$ in all cases in 1996), except for live dicots in 1996. In this year dicots were more abundant in habitats without supplemental food (food effect, $P = 0.03$), especially in habitats with high cover (food $\times$ cover interaction, $P = 0.02$).

Live monocots and high-quality forage for prairie voles had greater biomass, but live dicots had less biomass at upslope sites than at downslope sites in 1995 ($P = 0.003$, $P = 0.009$, and $P = 0.02$, respectively). Biomass of litter and total biomass did not differ with elevation ($P = 0.77$ and $P = 0.54$, respectively). In 1996 less biomass of live dicots also occurred upslope ($P < 0.0001$), but no other main effect of elevation was significant ($P > 0.21$ in all cases).

Biomass of live monocots, live dicots, and of high-quality food declined from early to late in the season in 1995 ($P < 0.0001$, $P = 0.006$, and $P < 0.0001$, respectively; Figs. 2 and 3), but biomass of litter and total biomass increased from early to late in the season ($P < 0.0001$ and $P = 0.002$, respectively). The decline in high-quality food as the season progressed was particularly striking and reflected the decline in palatability to prairie voles of the dominant monocots as they matured (Fig. 3c and d, Table 1).

Some interactions of food, cover, and elevation with season occurred in 1995. The seasonal decrease in live monocots was slightly greater in habitats without supplemental food than in those with supplemental food (food $\times$ season, $P = 0.05$), in low-cover habitats than
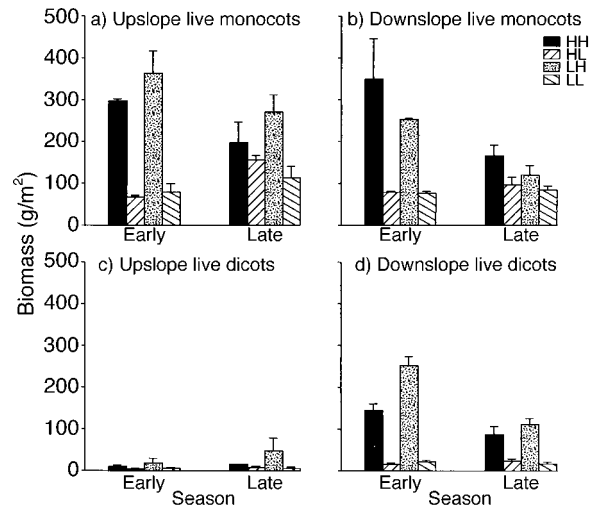

FIG. 4. Estimates of biomass for components of vegetation in different habitat types in 1996 (means + 1 SE). Vegetation samples were taken early (June) and late (October) in the growing season and differed along a gentle slope: (a) live monocots in upslope replicates, (b) live monocots in downslope replicates, (c) live dicots in upslope replicates, and (d) live dicots in downslope replicates. $N = 2$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

in high-cover habitats (cover $\times$ season, $P = 0.03$), and in upslope sites than in downslope sites (elevation $\times$ season, $P = 0.06$; Fig. 2a and b). For live dicots the seasonal decline tended to be greater in low-cover habitats than in high-cover habitats (cover $\times$ season, $P = 0.08$), in downslope sites than in upslope sites (ele-
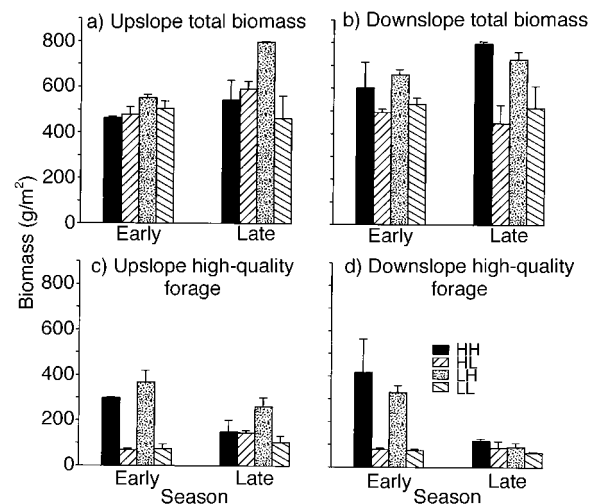

FIG. 5. Estimates of biomass for components of vegetation in different habitat types in 1996 (means + 1 SE). Vegetation samples were taken early (June) and late (October) in the growing season and differed along a gentle slope: (a) total biomass (live + litter) in upslope replicates, (b) total biomass in downslope replicates, (c) high-quality forage for meadow voles (see Table 1) in upslope replicates, and (d) high-quality forage in downslope replicates. $N = 2$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

vation × season, $P = 0.07$), and particularly in low-cover habitats at downslope sites (cover × elevation × season, $P = 0.10$; Fig. 2c and d). The seasonal increases in litter and in total biomass were greater in habitats with high cover than in those with low cover (cover × season, $P = 0.05$ and 0.005, respectively; Fig. 3a and b). High-quality forage declined more during the season in upslope sites than in downslope sites (elevation × season, $P = 0.003$) and in high-cover patches than in low-cover patches (cover × season, $P = 0.01$; Fig. 3c and d). These two interactions reflected the greater abundance of monocots upslope and in high cover and the decline in palatability of monocots during the course of the season (Table 1). No other interactions were statistically significant ($P > 0.10$ in all cases).

In 1996 biomass of live vegetation also generally declined from early to late in the season (live monocots, $P = 0.03$; live dicots, $P = 0.08$; Fig. 4), but again, several interactions occurred. Biomass of live monocots decreased in late season mainly in high-cover habitats (cover × season interaction, $P = 0.001$). Seasonal reduction of live dicots occurred only in high-cover habitats at downslope sites (cover × season interaction, $P = 0.06$; elevation × season interaction, $P = 0.02$; cover × elevation interaction, $P = 0.0001$; cover × elevation × season interaction, $P = 0.02$). Finally, biomass of high-quality forage decreased sharply over the season only in high-cover habitats (season × cover interaction, $P = 0.004$), which reflected the decline in live biomass of monocots in high-cover habitats. Both the amount of litter ($P = 0.0002$) and total biomass ($P = 0.08$) increased as the season progressed. Litter increased particularly strongly, almost threefold, in high-cover habitats (cover × season interaction, $P < 0.0001$), which had been low-cover habitats the previous year. No other interactions were significant ($P > 0.11$ in all cases).

In summary, reduction of cover by mowing had major effects on the vegetation, but provision of supplemental food had little association with vegetational composition. In both years less biomass of live monocots and dicots and less total biomass (including litter) occurred in low-cover habitats. In 1995 downslope sites had less biomass of monocots, more biomass of dicots, less biomass of high-quality forage early in the season, and more high-quality forage late in the season than did the upslope sites. In 1996 biomass of live dicots still was greater at downslope sites, but other components of the vegetation did not differ with elevation. In both years the biomass of live monocots and dicots declined during the growing season, but litter and total biomass increased. Availability of high-quality forage also declined over the season during both years and was particularly striking in 1995 for prairie voles because of the decline in palatability of monocots for them.
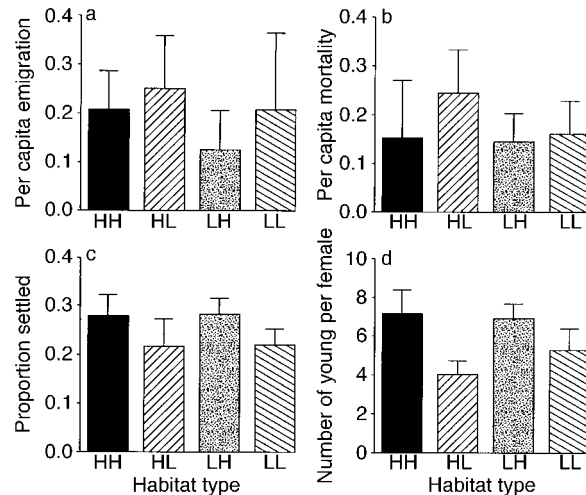

FIG. 6. Performance of founders of prairie vole (*Microtus ochrogaster*) populations (six founders per habitat patch) in different habitat types early in the experiment: (a) per capita emigration rates during the first 4 wk, (b) per capita mortality rates during the first 4 wk, (c) proportion settled after the first 4 wk, and (d) number of young recruited per female founder during weeks 6–12 (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

Performance of founders

Because three pairs of founders were released in the middle of each habitat, the total number of individuals in each replicate at the beginning of the experiment was only 24, and small differences in performance would be unlikely to be revealed by our analysis. Thus, neither cover nor food had significant effects on the per capita emigration of founding voles in either species (two-way ANOVAs, $P > 0.17$ for all main effects and interactions; Figs. 6a and 7a). Similarly, mortality of founding prairie voles did not differ with treatment (two-way ANOVA, $P > 0.41$ for main effects and interaction; Fig. 6b). Founding meadow voles that settled in low cover suffered higher mortality (three-way ANOVA, cover effect, $P = 0.0008$; Fig. 7b), especially at downslope sites (elevation effect, $P = 0.002$; cover × elevation interaction, $P = 0.004$).

Food and cover did not have significant main effects on settling patterns of founding prairie voles (three-way ANOVA, $P = 0.86$ and $P = 0.13$, respectively; Fig. 6c). One interaction was significant, however; a higher proportion of founders tended to settle in high-cover habitats with supplemental food in upslope sites and in high-cover habitats without supplemental food in downslope sites (food × cover × elevation, $P = 0.03$). A greater proportion of founding meadow voles settled in habitats with high cover (three-way ANOVA, cover effect, $P = 0.002$; Fig. 7c). More meadow voles settled in habitats with supplemental food in low cover, but not in high cover (food × cover interaction, $P = 0.005$), and effects of both food and cover were stronger at downslope sites (food × elevation interaction, $P =$
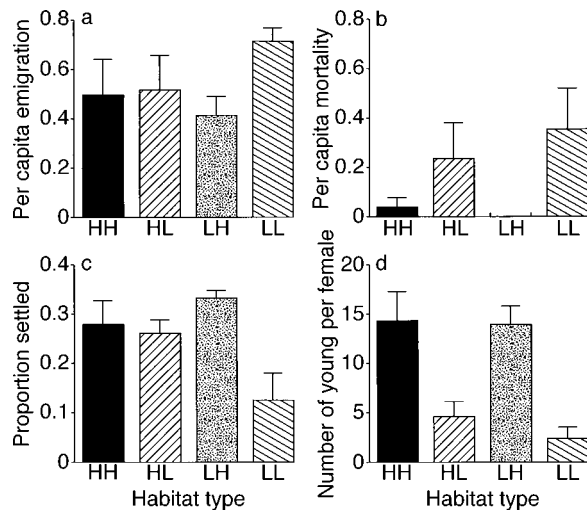
FIG. 7. Performance of founders of meadow vole (*Microtus pennsylvanicus*) populations (six founders per habitat patch) in different habitat types early in the experiment: (a) per capita emigration rates during the first 4 wk, (b) per capita mortality rates during the first 4 wk, (c) proportion settled after the first 4 wk, and (d) number of young recruited per female founder during weeks 6–12 (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

0.02; cover $\times$ elevation interaction, $P = 0.009$). The three-way interaction was not significant ($P = 0.13$).

Recruitment of young from female prairie voles was significantly higher in habitats with high cover, but not in those with high food (two-way ANOVA, $P = 0.03$ for cover and $P > 0.45$ for food and interaction; Fig. 6d). Female meadow voles that settled in high cover also had higher per capita reproductive success (two-way ANOVA, cover effect, $P = 0.0002$; Fig. 7d), but again the food effect and interaction were not significant ($P > 0.52$ in both cases).

Female founders showed no differences in body mass under different treatments at the beginning of the experiment (week 0), after settling (week 4), nor in body growth rates between weeks 0 and 4 (two-way ANOVAs, $P > 0.13$ and $P > 0.23$ for all main effects and interactions for prairie voles and meadow voles, respectively). Even though male prairie voles showed no differences in mean body mass under different treatments at the beginning of the experiment (two-way ANOVA, $P > 0.35$ for main effects and interaction), by week 4 males that had settled in habitat patches with supplemental food were larger than those in patches without supplemental food (body mass of 38.9 ± 0.3 g and 35.2 ± 1.2 g, respectively [mean $\pm$ 1 SE]; two-way ANOVA, $P = 0.008$). An interaction of food and cover ($P = 0.06$) indicated that in habitats with supplemental food males were larger in high cover than in low cover (40.0 ± 0.3 g and 37.8 ± 0.3 g, respectively), whereas the reverse was true in habitats without supplemental food (33.9 ± 1.7 g in high cover and 36.4

$\pm$ 0.8 g in low cover). Large size of males did not reflect greater growth of males that settled in habitats with greater food availability (two-way ANOVA, $P > 0.26$ for main effect of food and interaction). Rather, males that settled in high cover grew more than those that settled in low cover (mean change in body mass of 0.25 ± 0.12 g/wk and -0.05 ± 0.07 g/wk, respectively; $P = 0.02$ for main effect of cover). Thus, larger males must have settled in habitats with higher food availability.

Male meadow voles also showed no differences in mean body mass under different treatments at the beginning of the experiment ($P > 0.20$ for main effects and interactions). Because only one male (with the lowest body mass) stayed in an LL habitat, we had no replicates for this treatment for analysis of body size at week 4. We therefore compared body mass of males at week 4 and body growth rates of males for weeks 0–4 for the other three habitat types using one-way ANOVA. No significant difference in body mass occurred among habitat types at week 4 ($P = 0.97$), but mean body growth rates did differ among habitat types ($P = 0.04$). Male founders had positive growth in habitats with high cover (1.6 ± 0.8 g/wk for HH and 1.1 ± 0.5 g/wk for LH) and negative growth in low cover (-1.5 ± 0.8 g/wk for HL).

Overall, founders of both species of voles performed better in habitats with high cover. High cover was associated with greater settlement by founders, increased recruitment of young per female founder, and greater body growth of male founders. Supplemental food had less clear effects and was only associated with greater settlement by heavier male prairie voles and with greater settlement by meadow voles in HL than in LL habitats.

Population dynamics

After a slight decrease in numbers during the first 4 wk, prairie vole populations as a whole grew rapidly until week 16, after which little growth occurred (Fig. 8a). By week 20 the mean of the total populations reached 95 ± 13 voles per enclosure. Subpopulations in habitats with high cover (HH and LH) had similar population growth; their density increased nearly sixfold during the experiment to 34 ± 3 (256 voles/ha) and 34 ± 4 voles/habitat, respectively. Subpopulations in habitats with low cover grew much less; those in low cover with food addition (LH) averaged a 2.5 fold increase to 15 ± 5 voles/habitat (117 voles/ha), and those in low cover without food addition (LL) increased less than 1.5 fold to 8 ± 2 voles/habitat (62 voles/ha). Two-way ANOVA with repeated measures (no significant effects of elevation) indicated that cover and time (repeated measure) had highly significant main effects on density, but food did not ($P < 0.0001$, $P < 0.0001$, and $P = 0.85$, respectively). The effect of cover increased with time (cover $\times$ time interaction, $P < 0.0001$). Supplemental food only caused significantly
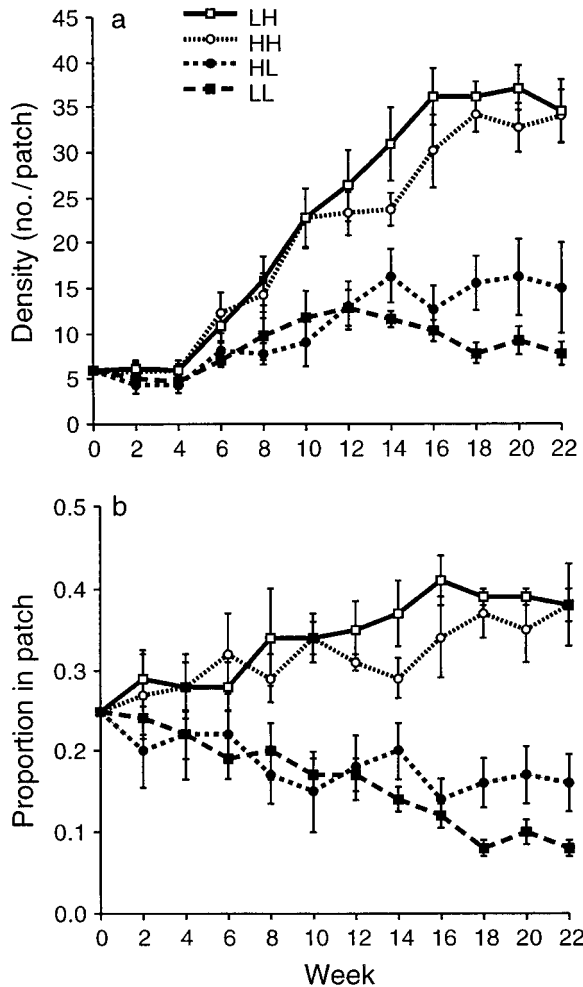
FIG. 8. (a) Number of prairie voles and (b) proportion of population known to be alive in different habitat types from early June to mid-November (means ± 1 SE). *N* = 4 in all cases. See Fig. 1 for an explanation of habitat abbreviations.

greater densities late in the season in low-cover habitats (food × cover × time interaction, *P* = 0.07; Fig. 8a). Subpopulations in all habitats remained relatively stable after week 18.

The overall pattern of population growth for meadow voles was similar to prairie voles, although larger total population size was reached. After a reduction in numbers during the first 4 wk, the mean of the total populations grew to 174 ± 22 voles per enclosure (338 voles/ha) by week 22. Again, subpopulations in different habitat types responded differently (Fig. 9a). Those in high-cover habitats (HH and LH) had similar population growth, an average increase of 12-fold. Subpopulations in HL habitats increased slowly, only two-fold overall, and subpopulations in LL habitats remained at low densities. In fact, LL subpopulations at downslope sites went locally extinct for several weeks (during weeks 4–10 and again in week 14 for one replicate and during week 8 for the other replicate), and

their population sizes generally remained <4 individuals/habitat.

By the end of the growing season, densities were highest in HH (71 ± 16 voles at upslope sites and 93 ± 22 voles at downslope sites) and LH (90 ± 27 voles at upslope sites and 54 ± 2 voles at downslope sites) habitats, intermediate in the HL (22 ± 5 voles at upslope sites and 7 ± 1 voles at downslope sites) habitats, and lowest in the LL (9 ± 2 voles at upslope sites and 4 ± 3 voles at downslope sites) habitats. Subpopulations in some HH habitats grew until regular trapping ceased at mid-November (week 22), but subpopulations in the other habitat types appeared to be stable by week 20. A three-way ANOVA (food × cover × elevation) with repeated measures indicated that population density tended to be higher in habitats with supplemental
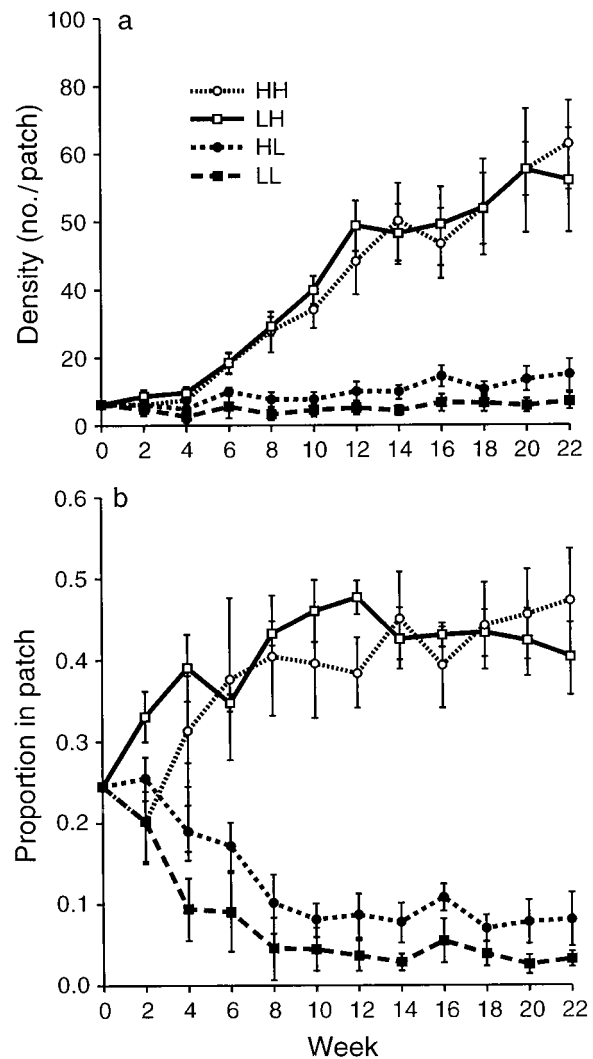

FIG. 9. (a) Number of meadow voles and (b) proportion of population known to be alive in different habitat types from early June to mid-November (means ± 1 SE). *N* = 4 in all cases. See Fig. 1 for an explanation of habitat abbreviations.

food ($P = 0.09$), in habitats with high cover ($P <$ 0.0001), and at upslope sites (elevation effect, $P =$ 0.02). Density increased with time ($P < 0.0001$), and the effect of cover increased with time (cover $\times$ time interaction, $P < 0.0001$). The effect of supplemental food occurred primarily in low-cover habitats (food $\times$ cover interaction, $P = 0.03$), and the effects of food and cover were both greater at downslope sites (food $\times$ elevation interaction, $P = 0.07$; cover $\times$ elevation interaction, $P = 0.02$). No other interactions were significant ($P > 0.23$ in all cases).

Proportions of prairie voles in each habitat type changed gradually through week 16, with proportions increasing in high-cover habitats and decreasing in low-cover habitats (Fig. 8b). From week 18 to week 22 the proportions changed little, and mean values in HH, LH, HL, and LL habitats at week 22 were 0.38 $\pm$ 0.05, 0.38 $\pm$ 0.02, 0.16 $\pm$ 0.3, and 0.08 $\pm$ 0.01, respectively. A two-way ANOVA with repeated measures again indicated that cover had a highly significant effect on the proportion of the population in each habitat ($P < 0.0001$) and that the effect increased significantly with time (cover $\times$ time interaction, $P <$ 0.0001). Food had no main or interactive effects ($P >$ 0.40 in all cases).

Many meadow voles released in low-cover habitats emigrated or died, which resulted in sharp increases in the proportions of populations in high-cover habitats in the first 8 wk. After that proportions remained relatively constant (Fig. 9b). Mean proportions of the populations in HH, LH, HL, and LL habitats at week 22 were 0.37 $\pm$ 0.01, 0.46 $\pm$ 0.04, 0.12 $\pm$ 0.05, and 0.05 $\pm$ 0.00, respectively, at upslope sites; 0.58 $\pm$ 0.05, 0.35 $\pm$ 0.06, 0.04 $\pm$ 0.00, and 0.02 $\pm$ 0.02, respectively, at downslope sites. A three-way ANOVA with repeated measures indicated that cover had a highly significant effect on the proportion of the population found in a habitat type (cover effect, $P < 0.0001$), and the effect increased significantly with time (cover $\times$ time interaction, $P < 0.0001$). The effect of cover was stronger at downslope sites (cover $\times$ elevation interaction, $P =$ 0.02). The positive effect of supplemental food only occurred in low-cover habitats (food $\times$ cover interaction, $P = 0.06$), particularly at downslope sites (food $\times$ elevation interaction, $P = 0.03$) late in the season (food $\times$ cover $\times$ elevation $\times$ time interaction, $P =$ 0.06). No other main effect or interactions were significant ($P > 0.11$ in all cases).

In summary, populations of both species increased during the season and reached their highest densities in habitats with high cover, although considerably higher densities were reached by meadow voles. Supplemental food only caused increased density in low-cover habitats, particularly at downslope sites for meadow voles. Prairie voles maintained subpopulations continuously in all habitats, but two subpopulations of meadow voles in low-cover, low-food habitats went extinct, then were reestablished by immigration. Similarly, the proportion of each population found in different habitats largely reflected the amount of cover. In prairie voles the proportion of the population in high cover continued to increase until late in the season (week 18) when densities stabilized, but in meadow voles proportional differences among habitats were established early (week 8) and remained relatively constant thereafter.

Sex and age structure

For prairie voles none of the sex ratios of any cohort (adults, subadults, or juveniles) within any habitat type differed significantly from 1:1, either early or late in the growing season ($P > 0.1$ for all chi-square tests). Similarly, neither the sex ratios for the total populations in each enclosure nor the sex ratios for each habitat type pooled over all the replicates differed significantly from 1:1 ($P > 0.1$ for all chi-square tests).

For meadow voles sex ratios of cohorts within habitat types did not differ significantly from 1:1 ratio in the early season ($P > 0.20$ for all chi-square tests, numbers pooled over replicates and averaged for weeks 8–14), except that subadults in LH habitats were skewed toward males (female/male = 0.50; $\chi^2 = 3.5$, df = 1, P = 0.06). Sex ratios of more subpopulations were skewed late in the season, however. More females occurred among adults in habitats with supplemental food (female/male = 1.53; $\chi^2 = 6.5$, df = 1, $P = 0.03$ for HH habitats, and female/male = 2.99; $\chi^2 = 5.3$, df = 1, $P = 0.02$ for HL habitats). More males occurred among subadults in LH habitats (female/male = 0.47; $\chi^2 = 16.2$, df = 1, $P = 0.001$). The sex ratio of juveniles was not skewed in any habitat ($P > 0.37$ in all habitats). Too few individuals occurred in LL habitats to warrant testing. Finally, as for prairie voles, the sex ratios of total populations (all ages in all habitats combined) were not different from 1:1 within any replicate during either season ($P > 0.12$ for all chi-square tests).

Adults formed the greatest proportion of trappable prairie vole populations, followed by subadults and juveniles (Fig. 10). The proportion of adult prairie voles in the total population increased slightly late in the growing season and was greater for subpopulations in habitat patches with high cover, particularly later in the growing season (two-way ANOVA with repeated measures, $P = 0.008$ for cover effect, $P = 0.05$ for season effect, and $P = 0.02$ for the cover $\times$ season interaction; Fig. 10a). The main effect of supplemental food, more adults in habitats with food added, was marginally significant ($P = 0.08$), but no other interaction was significant ($P > 0.13$ in all cases).

Adults also formed the greatest proportion of meadow vole populations (Fig. 11), but juveniles were generally more common than subadults. Contrary to the results for prairie voles, the proportion of adult meadow voles in the total populations decreased over the season, but was slightly higher for subpopulations in habitat patches with low cover, particularly later in the season
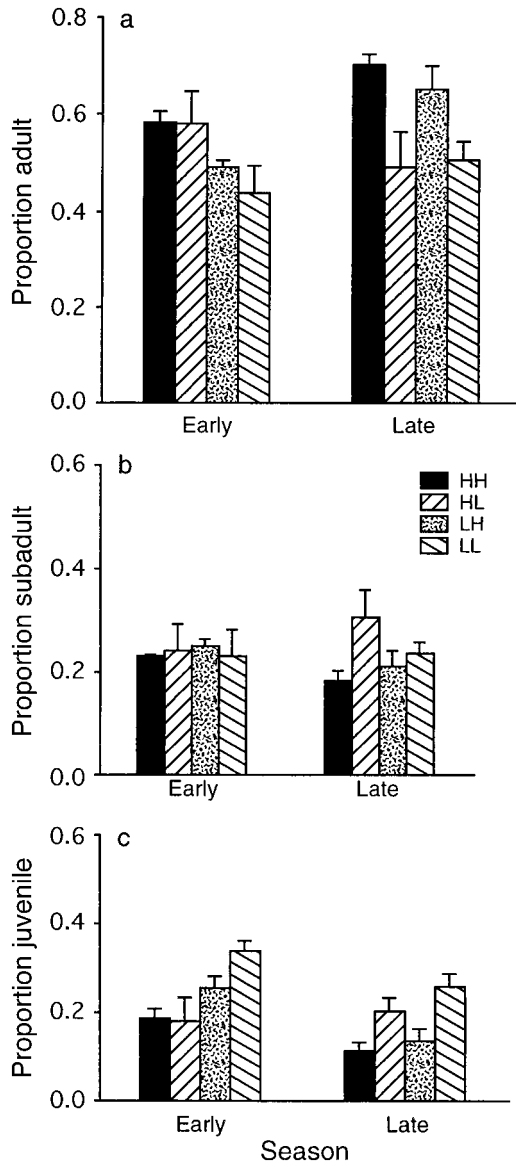
FIG. 10. Age structure of prairie vole populations in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment. Proportions of population are given for (a) adults, (b) subadults, and (c) juveniles (means + 1 SE). $N = 4$ in all cases. No significant differences occurred in sex ratios. See Fig. 1 for an explanation of habitat abbreviations.

(three-way ANOVA with repeated measures, season effect, $P = 0.02$; cover effect, $P = 0.05$; cover × season interaction, $P = 0.05$; Fig. 11a) and in LL habitats (food × cover interaction, $P = 0.07$). The proportion of adults tended to be higher in low-food habitats at downslope sites (food × elevation interaction, $P = 0.10$), especially late in the season (food × elevation × season interaction, $P = 0.07$). The main effect of supplemental food and other interactions were not significant ($P > 0.10$ in all cases).

The proportion of subadult prairie voles in habitat

patches with low cover was slightly greater than in high cover, but no other significant main effects or interactions occurred (two-way ANOVA with repeated measures, $P = 0.06$ for cover, $P > 0.10$ in all other cases; Fig. 10b). Again contrary to prairie voles, the proportion of subadult meadow voles in habitat patches with high cover was greater than in low cover, particularly later in the season (three-way ANOVA with repeated measures, cover effect, $P = 0.02$; cover × season interaction, $P = 0.005$; Fig. 11b). Early in the season, the proportion of subadults was greater in habitats with
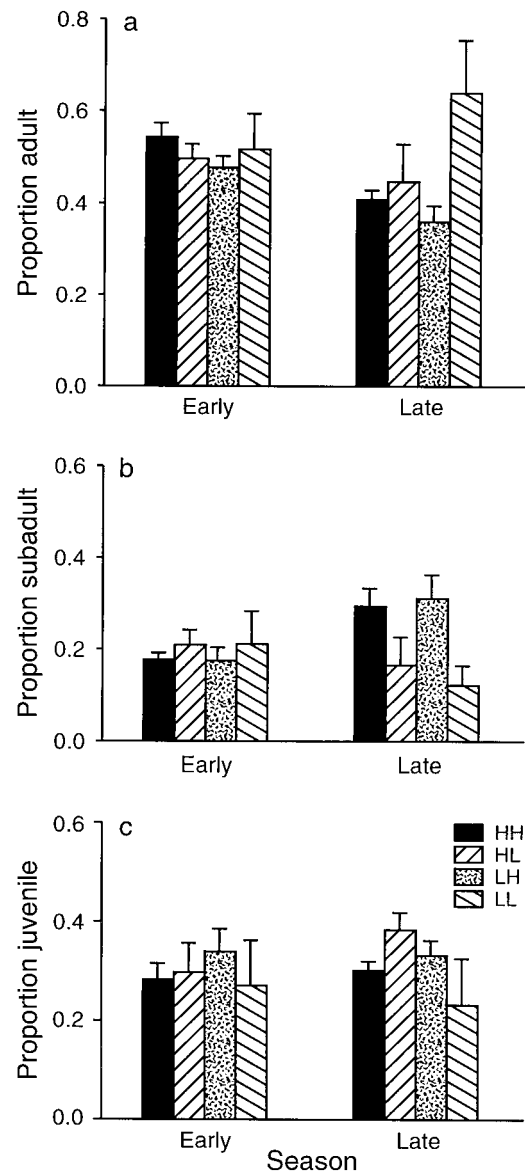

FIG. 11. Age structure of meadow vole populations in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment. Proportions of population are given for (a) adults, (b) subadults, and (c) juveniles (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

supplemental food at upslope sites and greater in habitats without supplemental food at downslope sites; a trend that reversed late in the season (food $\times$ elevation $\times$ season interaction, $P = 0.03$). No other significant main effects or interactions occurred ($P > 0.17$ in all cases). In general, patterns for subadult meadow voles were just the opposite of those for adults.

Juvenile prairie voles formed a greater proportion of subpopulations in habitats without supplemental food than in those with supplemental food (two-way ANOVA with repeated measures, $P = 0.004$; Fig. 10c), in habitats with low cover than in those with high cover ($P = 0.001$), and earlier in the season than later in the season ($P = 0.007$). This pattern likely reflected the movement of older voles out of habitats with low food and low cover, which occurred particularly early in the season. The effect of cover was greater later in the season (cover $\times$ season interaction, $P = 0.05$). No other significant interactions occurred ($P > 0.14$ in all cases). The proportion of juvenile meadow voles was not affected by any main effects or interactions ($P > 0.25$ in all cases; Fig. 11c).

In general, overall population sex ratios remained 1:1 for both species of voles. Sex ratios within age categories and habitat types also remained 1:1 for prairie voles; the sex ratio for adult meadow voles favored females in habitats with supplemental food late in the growing season. Adult voles formed the largest age category of trappable voles for both species. However, whereas the proportion of adult prairie voles increased during the growing season and tended to be greater in habitats with high cover or supplemental food, the opposite trends occurred for meadow voles. Similarly, subadult prairie voles were more numerous than juveniles and formed a greater proportion of populations in low cover, but the trends for subadult meadow voles were the opposite. Juvenile prairie voles contributed more of subpopulations in habitats with low cover and without supplemental food, but the proportion of juvenile meadow voles did not differ with cover or food.

Demographic variables

Per capita rates of in situ recruitment for prairie voles were not significantly different among habitat types (two-way ANOVA with repeated measures, $P = 0.20$ for food and $P = 0.18$ for cover; Fig. 12a), but recruitment declined later in the season ($P = 0.002$). None of the interactions were significant ($P > 0.13$ in all cases). In situ recruitment of meadow voles was not significantly affected by any main effects or interactions (two-way ANOVA with repeated measures, $P > 0.12$ in all cases; Fig. 13a).

Per capita mortality of prairie voles tended to be higher in low-cover habitats (two-way ANOVA with repeated measures, $P = 0.10$; Fig. 12b) and increased dramatically with season ($P = 0.002$). No other main effects or interaction terms were significant ($P > 0.14$ in all cases). Per capita mortality of meadow voles
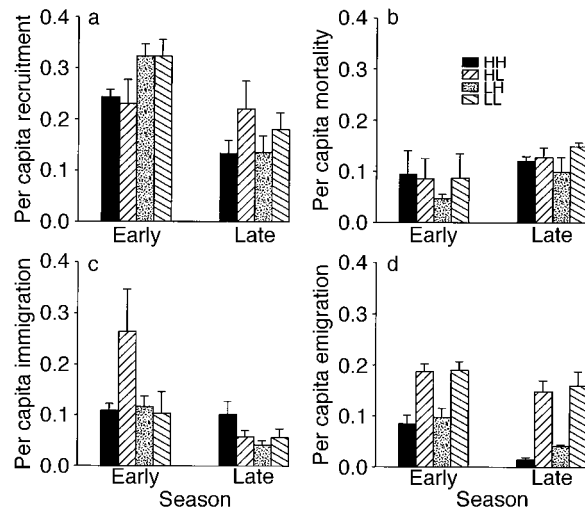

FIG. 12. Biweekly estimates of demographic variables for populations of prairie voles in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment: (a) per capita in situ recruitment of young, (b) per capita mortality rates, (c) per capita immigration rates, and (d) per capita emigration rates (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

tended to be higher in high-cover habitats early in the season, but not late in the season (cover $\times$ season interaction, $P = 0.07$; Fig. 13b). As for prairie voles, mortality of meadow voles increased significantly with season (season effect, $P < 0.0001$). The main effects of supplemental food and cover and other interactions were not significant ($P > 0.25$ in all cases).

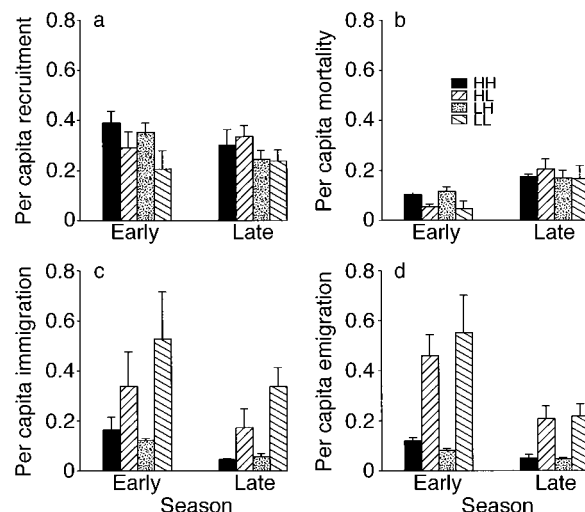In situ recruitment minus mortality (net in situ re-

FIG. 13. Biweekly estimates of demographic variables for populations of meadow voles in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment: (a) per capita in situ recruitment of young, (b) per capita mortality rates, (c) per capita immigration rates, and (d) per capita emigration rates (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

cruitment) was positive throughout the season for both species of voles, but declined substantially later in the season (two-way ANOVAs with repeated measures, season effect, $P < 0.001$ for prairie voles and $P = 0.006$ for meadow voles; Figs. 14a and 15a). No other significant main effects occurred ($P = 0.16$ for food and $P = 0.77$ for cover). Greater net recruitment of prairie voles tended to occur in habitats with low food early in the season but not late (food $\times$ season interaction, $P = 0.09$). No other interactions approached significance for either species ($P > 0.22$ in all cases).

Per capita immigration of prairie voles also decreased significantly with season (two-way ANOVA with repeated measures, $P = 0.005$; Fig. 12c). A marginally significant effect of food ($P = 0.06$) and a significant interaction (food $\times$ cover $\times$ season, $P = 0.05$) indicated that supplemental food tended to cause greater immigration in low-cover habitats early in the season and in high-cover habitats late in the season. No other main effects or interactions reached significance ($P > 0.12$ in all cases). For meadow voles per capita immigration rates were much higher in low-cover habitats (three-way ANOVA with repeated measures, cover effect, $P = 0.007$; Fig. 13c), especially at downslope sites (cover $\times$ elevation interaction, $P = 0.08$). The rates decreased significantly with season (season effect, $P = 0.004$), especially at downslope sites in high cover (elevation $\times$ season interaction, $P = 0.05$; cover $\times$ elevation $\times$ season interaction, $P = 0.009$). The main effects of food and elevation and the other interaction terms were not significant ($P > 0.16$ in all cases).

Per capita emigration of prairie voles was slightly greater in low-food habitats, much greater in low-cover habitats, but lower later in the season (two-way ANOVA with repeated measures, $P = 0.08$, $P < 0.0001$, and $P = 0.0007$, respectively; Fig. 12d). The effect of cover was greater later in the season (cover $\times$ season interaction, $P = 0.05$). No other interactions approached significance ($P > 0.28$ in all cases). Per capita emigration rates for meadow voles also were greater in low-cover habitats (two-way ANOVA with repeated measures, cover effect, $P < 0.0001$; Fig. 13d) and also declined later in the season (season effect, $P = 0.0002$). The seasonal reduction was greater in low-cover habitats (cover $\times$ season interaction, $P = 0.03$). The main effect of food and the other interaction terms were not significant ($P > 0.42$ in all cases).

Immigration minus emigration (net movement) for prairie voles was consistently negative in LL habitats and consistently positive in high-cover habitats, which indicated consistent net movement into habitats with high cover (Fig. 14b). Net movement tended to be greater with greater food availability (two-way ANOVA with repeated measures, $P = 0.03$) and greater cover ($P = 0.01$), except that net movement was greatest in HL habitats early in the season but in HH habitats late in the season (cover $\times$ season, $P = 0.05$; food $\times$ cover $\times$ season, $P = 0.05$). The other main effect (sea-

son) and interactions were not significant ($P > 0.20$ in all cases).

Net movement of meadow voles also differed among habitat types (Fig. 15b). Habitats with supplemental
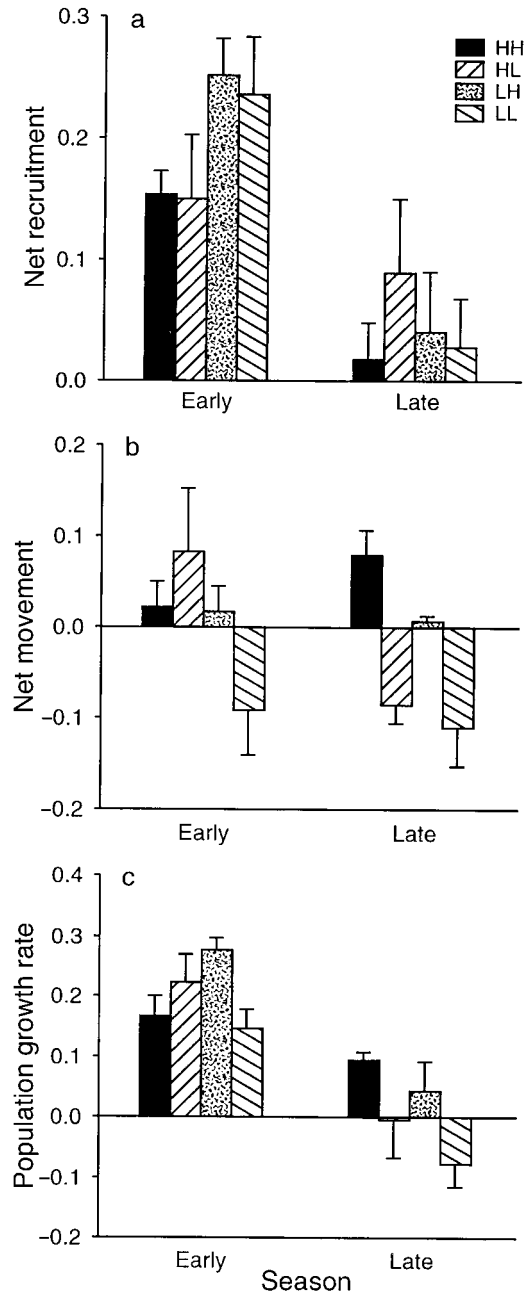

FIG. 14. Biweekly estimates of net demographic variables for populations of prairie voles in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment: (a) net per capita rate of in situ recruitment (in situ recruitment of young − mortality), (b) net per capita rate of movement (immigration − emigration), (c) per capita rate of population growth (net in situ recruitment + net movement) (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.
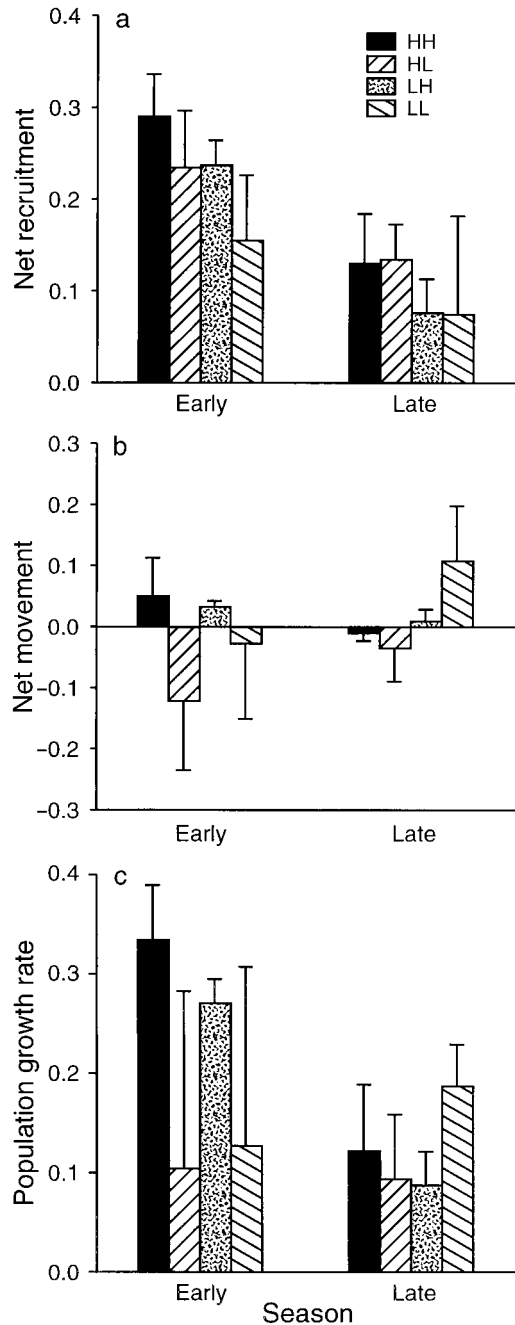
FIG. 15. Biweekly estimates of net demographic variables for populations of meadow voles in different habitat types early (weeks 8–14) and late (weeks 16–22) in the experiment: (a) net per capita rate of in situ recruitment (in situ recruitment of young − mortality), (b) net per capita rate of movement (immigration − emigration), and (c) per capita rate of population growth (net in situ recruitment + net movement) (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

food had overall negative net movement, whereas habitats without supplemental food had overall positive net movement (three-way ANOVA with repeated measures, food effect, $P = 0.06$), especially among low-cover habitats (food × cover interaction, $P = 0.08$). At upslope sites, but not downslope sites, net movement was greater in high-cover habitats (cover × elevation interaction, $P = 0.04$), especially in the early season (cover × elevation × season interaction, $P = 0.08$). No other main effects or interactions were significant ($P > 0.13$ in all cases).

Population growth rates (per capita growth per 2 wk) were obtained by summing all four demographic factors (in situ recruitment, mortality, immigration, and emigration). Mean values for prairie voles were greater than zero in all habitat types, except for habitats with low cover in the late season (Fig. 14c). The strongest trend was decreased population growth late in the season (two-way ANOVA with repeated measures, $P < 0.0001$). Population growth was also greater in habitats with high cover ($P = 0.03$). Both trends were consistent with the changes in population density (Fig. 8a). No other significant main effects or interactions occurred ($P > 0.11$ in all cases). Population growth of meadow voles was not significantly related to either main effects or interactions (two-way ANOVA with repeated measures, $P > 0.16$ in all cases; Fig. 15c). Not even the strong seasonal declines in survival and net in situ recruitment (Figs. 13b and 15a) were clearly reflected in population growth, much less patterns of net movement away from habitats with supplemental food in low cover and toward high cover at upslope sites. Therefore, differences of density of meadow voles among habitat types late in the season appeared to largely reflect patterns of survival and settlement by founders early in the season.

In summary, in situ recruitment decreased with season for prairie voles and mortality increased with season for both species of voles, which led to much lower net recruitment late in the season for both species. Per capita movements for both species of voles also declined with season, but net movement did not. Food and cover had little effect on net in situ recruitment for either species. Net movement of prairie voles was positive in habitats with high cover and negative in habitats with low cover, at least late in the season, whereas net movement of meadow voles tended to be positive in habitats without supplemental food and negative in habitats with supplemental food. Population growth rates of prairie voles declined with season but remained highest in habitats with high cover and were reflected in the differences in densities among habitat types. For meadow voles, however, population growth rates did not reflect differences in habitat types, and differences in density among habitats appeared to reflect the patterns of survival and movements of the founding voles.
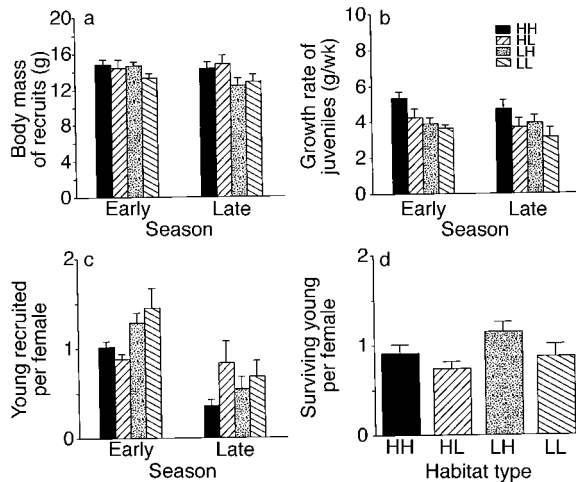
FIG. 16. Estimates of fitness correlates for populations of prairie voles in different habitat types: (a) body mass of juvenile recruits, (b) body growth rate of juveniles, (c) young recruited per adult female, and (d) young born before week 14 that survived to adulthood per adult female (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviation.

Fitness correlates

For prairie voles, body mass of new recruits first captured as juveniles was slightly greater in habitats with supplemental food and earlier in the season (two-way ANOVA with repeated measures, $P = 0.06$ and $P = 0.09$, respectively; Fig. 16a), but no other main effects or interactions were significant ($P > 0.10$). Body mass of meadow voles first captured as juveniles did not differ among habitat types (two-way ANOVA with repeated measures, $P > 0.17$ in all main effects and interactions; Fig. 17a). Body growth rate of juvenile prairie voles was higher in habitats with supplemental food and with greater cover (three-way ANOVA with repeated measures, $P = 0.03$ for food and $P = 0.04$ for cover; Fig. 16b). Body growth declined with season, particularly at downslope sites ($P = 0.03$ for season and $P = 0.04$ for elevation $\times$ season interaction). A strong four-way interaction (food $\times$ cover $\times$ elevation $\times$ season, $P = 0.0003$) indicated that for downslope sites the effect of food was greater in low-cover habitats early in the season and in high-cover habitats later in the season, but the pattern was reversed in upslope habitats. No other interactions approached significance ($P > 0.29$ in all cases). Again, body growth rates of juvenile meadow voles did not differ among habitat types, although they decreased over the season (season effect, $P = 0.0001$; $P > 0.21$ in all other main effects and interactions; Fig. 17b).

Recruitment of young per adult female prairie vole was less in habitats with supplemental food, with high cover, and later in the season (two-way ANOVA with repeated measures, $P = 0.008$, $P = 0.02$, and $P = 0.002$, respectively; Fig. 16c). No interaction was sig-

nificant ($P > 0.14$). For meadow voles, recruitment of young per adult female was greater in high-cover habitats (two-way ANOVA with repeated measures, cover effect, $P = 0.07$; Fig. 17c). Other main effects and interactions were not significant ($P > 0.17$ in all cases).

Overall reproductive success of adult female prairie voles, measured as number of young that survived to adult size, tended to be greater in habitats with high cover and without supplemental food (two-way AN-OVA, $P = 0.06$ and $P = 0.10$, respectively; Fig. 16d). The interaction of food $\times$ cover was not significant ($P > 0.57$). For female meadow voles the number of young that survived to adult size did not differ significantly among habitat types (two-way ANOVA, $P > 0.18$ for both main effects and interaction; Fig. 17d).

In summary, lower recruitment of young per adult female prairie vole occurred with supplemental food, in high cover, and late in the season, all of which were generally associated with higher densities. High cover was also associated with greater survival of young and greater survival in general (Fig. 12b), and both high cover and supplemental food were associated with increased growth rates of young, which may have reduced their age at reproductive maturity. Thus, fitness correlates of prairie voles other than recruitment, which probably responded more to density than the other measures, tended to be higher in habitats with higher quality, particularly those with higher cover. Fitness correlates of meadow voles differed little among habitat types.

Density-dependent effects

The relationship of population demography to density varied among habitat types (Table 2). Density of
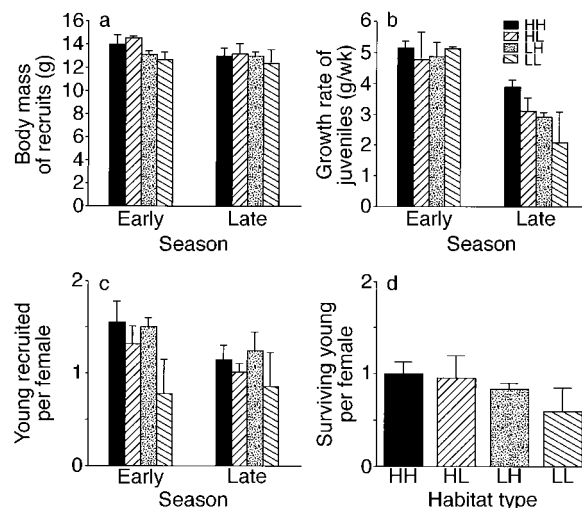

FIG. 17. Estimates of fitness correlates for populations of meadow voles in different habitat types: (a) body mass of juvenile recruits, (b) body growth rate of juveniles, (c) young recruited per adult female, and (d) young born before week 14 that survived to adulthood per adult female (means + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

TABLE 2. Sign of slopes ($-$, $+$) and coefficients of determination (R^2) for linear regressions of in situ per capita recruitment, per capita deaths, per capita immigration, and per capita emigration on density (N) of prairie vole (MO) and meadow vole (MP) subpopulations in four habitat types (HH, high food, high cover; HL, high food, low cover; LH, low food, high cover; LL, low food, low cover).

| | Habitat types | | | | | |
| | HH | | HL | | LH | |
Regression	MO	MP	MO	MP	MO	MP
Recruitment $\times N$	$-$, 0.20**	$-$, 0.01	$+$, 0.00	$-$, 0.00	$-$, 0.49****	$-$, 0.14*
Death $\times N$	$+$, 0.14*	$+$, 0.36***	$+$, 0.02	$+$, 0.04	$+$, 0.21**	$+$, 0.10*
Immigration $\times N$	$-$, 0.21**	$-$, 0.41****	$-$, 0.26**	$-$, 0.23***	$-$, 0.30**	$-$, 0.48****
Emigration $\times N$	$-$, 0.22**	$-$, 0.26***	$-$, 0.01	$-$, 0.19**	$-$, 0.16*	$-$, 0.11*
Emigration $\times \lambda$	$+$, 0.21**	$+$, 0.00	$-$, 0.20**	$-$, 0.02	$+$, 0.02	$+$, 0.06

Notes: Emigration was also regressed against the finite rate of population increase (λ) in each habitat type. Data include observations for four replicates during eight sampling periods (weeks 8–22) in each regression ($n = 32$). Only values with $P < 0.01$ are significant using a sequential Bonferroni correction.

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$.

prairie voles had significant correlations with in situ processes (negative with recruitment and positive with mortality, both directly density dependent) in habitats with high cover, but not in habitats with low cover. Movement generally decreased as density increased, with significant negative relationships to immigration (directly density dependent) in all habitat types and to emigration (inversely density dependent) in habitats with high cover. When all of these BIDE factors were summed, the resultant rates of population growth were more strongly density dependent in habitats with high cover, where densities reached the higher levels, than in low cover (Fig. 18a).

In situ net recruitment within habitat patches ($B - D$) and net movement between habitats ($I - E$) responded differently to density of prairie voles. Net recruitment decreased significantly as density increased in habitats with high cover but not in those with low cover (Fig. 18b). On the other hand, net movement decreased significantly as density increased in habitats with low cover but not in those with high cover (Fig. 18c). Per capita emigration rates had no consistent relationship with current rate of population growth (Table 2).

Population density of meadow voles had little relationship to in situ recruitment (Table 2). Density was more strongly related to mortality, however, with a significant positive relationship in habitats with high cov-

er. As with prairie voles, density of meadow voles had significant negative relationships with movement. Per capita immigration decreased with density in all except LL habitats, in which densities remained low. A similar pattern occurred for per capita emigration (dispersal), although most significance levels were marginal.

When all of per capita demographic factors were summed for meadow voles, similar to prairie voles, the rate of population growth showed significant negative relationships with density in all but LL habitats (Fig. 19a). Again, in situ net recruitment ($B - D$) within habitat patches and net movement ($I - E$) between habitat patches responded differently to density (Fig. 19b and c). In high-cover habitats, unlike prairie voles, population density of meadow voles was negatively related to both net in situ recruitment and net movement. In HL habitats, population density was negatively related to net movement only. In LL habitats, where little variation in density occurred, no demographic factor was related to density. Per capita emigration rates had no significant relationship with current rate of population growth of meadow voles (Table 2).

In summary, for both species, subpopulations that grew substantially during the experiment showed effects of density on per capita demographic parameters and on rates of population growth. Density had a negative relationship with in situ recruitment for prairie

TABLE 3. Cumulative frequency of net in situ recruitment (number recruits $-$ number deaths) and net movement (number immigrants $-$ number emigrants) of prairie voles (MO) and meadow voles (MP) for four habitat types (HH, high food, high cover; HL, high food, low cover; LH, low food, high cover; LL, low food, low cover).

| | Net recruitment | | | Net movement | | |
| | MO | | MP | MO | | MP |
Habitat	Weeks 8–22	Weeks 20–22	Weeks 8–22	Weeks 8–22	Weeks 20–22	Weeks 8–22
HH	13.0 $\pm$ 4.8	-2.5 ± 2.0	68.4 $\pm$ 12.6	9.6 $\pm$ 4.0	2.1 $\pm$ 0.8	0.73 $\pm$ 5.01
HL	12.5 $\pm$ 5.4	0.2 $\pm$ 3.7	13.9 $\pm$ 4.0	-3.5 ± 3.4	-0.3 ± 0.8	-6.30 ± 3.58
LH	24.7 $\pm$ 6.0	1.1 $\pm$ 2.7	57.9 $\pm$ 20.2	1.5 $\pm$ 2.7	-1.2 ± 0.3	5.27 $\pm$ 4.06
LL	11.0 $\pm$ 1.6	0.8 $\pm$ 1.4	3.6 $\pm$ 1.7	-8.3 ± 2.0	-0.6 ± 0.3	0.30 $\pm$ 2.73

Note: Means $\pm$ 1 SE are given over weeks 8–22 and weeks 20–22 ($n = 4$).

Table 2. Extended.

| | Habitat type | |
| | LL | |
MO		MP
+, 0.03		−, 0.01
+, 0.00		+, 0.05
−, 0.13*		−, 0.08
−, 0.10		−, 0.08
−, 0.09		−, 0.09

voles and but not for meadow voles. A positive relationship between density and mortality and a negative relationship between density and movement (inversely density dependent for emigration and directly density dependent for immigration) occurred for both species. For prairie voles directly density-dependent net recruitment only occurred in high cover, and directly density-dependent net movement only occurred in low cover. Both net recruitment and net movement were directly density dependent for populations of meadow voles in habitats with high cover, but only net movement was directly density dependent in habitats with low cover. Emigration showed no consistent relationship to rate of population growth for either species.

Dispersal patterns

After founding voles settled, all habitat types supported at least some population growth for both species, but population growth declined late in the growing season (Figs. 8a and 9a). For the breeding season as a whole (weeks 8–22) the cumulative number of in situ recruits generally exceeded the number of deaths in all habitats (Table 3). Neither the main effects of food and cover nor their interaction were significant for prairie voles (two-way ANOVA, $P > 0.15$ in all cases); for meadow voles net in situ recruitment was greater in high-cover habitats (two-way ANOVA, cover effect, $P = 0.0007$), but the main effect of food and the interaction were not significant ($P > 0.40$ in both cases).

The patterns of net movement for weeks 8–22 did differ among habitats for prairie voles. In high cover there were more immigrants than emigrants, whereas in low cover there were more emigrants than immigrants (Table 3; two-way ANOVA, $P = 0.005$ for main effect of cover). There also tended to be relatively more immigrants into habitats with supplemental food ($P = 0.07$), but no significant interaction occurred between food and cover ($P = 0.57$). Neither the main effects nor the interaction were significant for cumulative net movement of meadow voles (two-way ANOVA, $P > 0.18$ in all cases).

After populations of prairie voles had stabilized (week 18, Fig. 8a), patterns of recruitment and movement balanced one another (weeks 20–22 in Table 3).
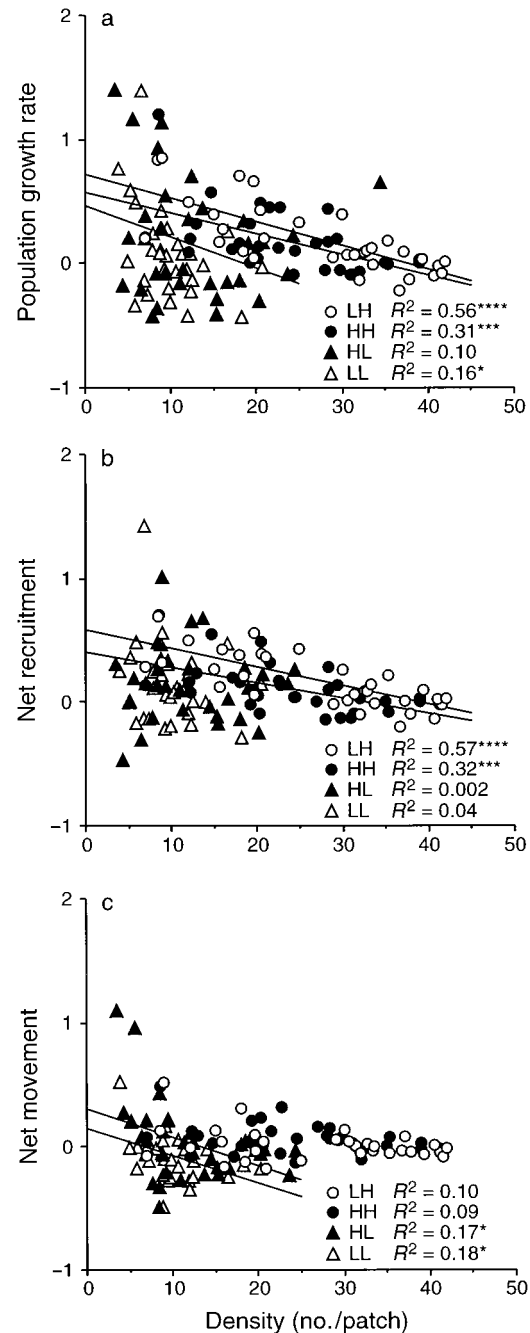

Fig. 18. Relationship of (a) per capita rates of population growth, (b) net in situ recruitment, and (c) net movement to density of prairie voles in different habitat types for weeks 8–22 of experiment. Coefficients of determination (R^2) are given for linear regression of data from each habitat ($N = 32$ in all cases). *$P < 0.05$, ***$P < 0.001$, ****$P < 0.0001$. See Fig. 1 for an explanation of habitat abbreviations.

Recall that demographic variables were calculated from week $t − 2$ to week t, so the value for week 20 represented weeks 18–20. Our treatments had no significant effects on net in situ recruitment when populations were stable (two-way ANOVA, $P > 0.43$ for main ef-
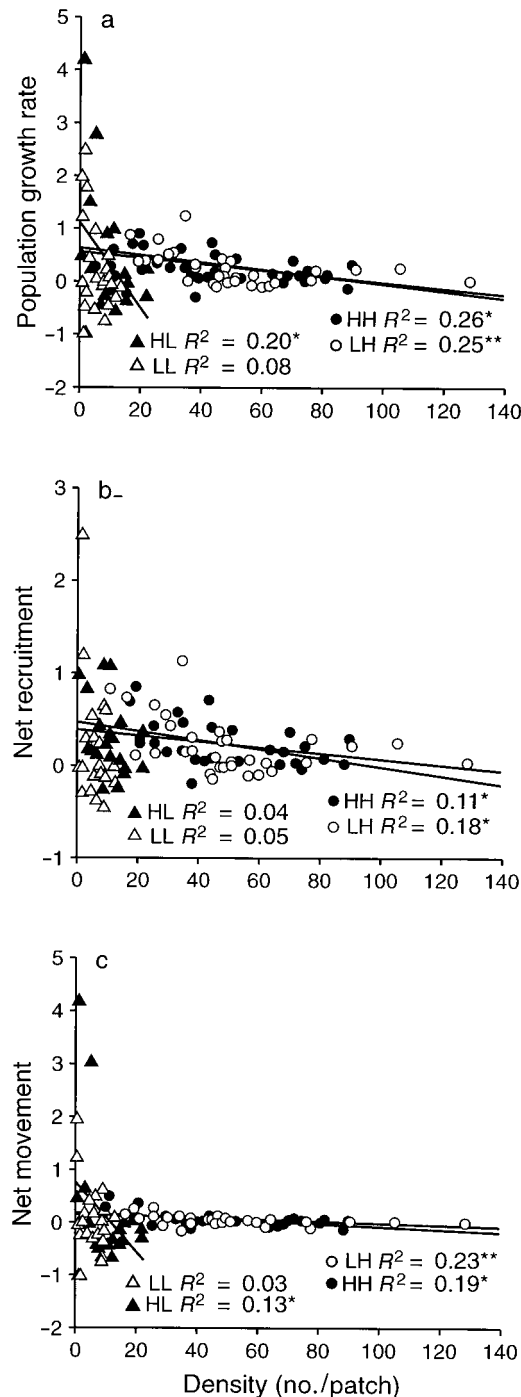
Fig. 19. Relationship of (a) per capita rates of population growth, (b) net in situ recruitment, and (c) net movement to density of meadow voles in different habitat types for weeks 8–22 of experiment. Coefficients of determination (R^2) are given for linear regression of data from each habitat ($N = 32$ in all cases). *$P < 0.05$, **$P < 0.01$. See Fig. 1 for an explanation of habitat abbreviations.

fects and interaction). Net movement, however, remained relatively greater in habitats with supplemental food, an effect that largely occurred in high cover (two-way ANOVA, $P = 0.01$ for food effect, $P = 0.41$ for cover effect, and $P = 0.05$ for interaction).

When habitat types were paired to compare the exchange of prairie voles between two specific habitat types, net movement of prairie voles was consistently from low-quality to high-quality habitats during the course of the season, even though net movement was not always significant for individual pairs of habitats (weeks 8–22 in Table 4). Comparisons in which food treatment remained the same but cover differed indicated that net movement was from low cover to high cover ($P = 0.002$). Comparisons in which cover remained the same but food treatment differed indicated that net movement was from lower to higher food availability, but the trend was only marginally significant ($P = 0.08$). Because the patterns of net movement were consistent, we combined all six possible two-way comparisons of four habitat types to compare overall movement between low-quality and high-quality habitats. Based upon our earlier results, we expected that when food availability and cover conflicted (LH–HL comparison), the habitat with high cover (LH) should be higher quality. This overall comparison indicated highly significant net movement from lower quality habitats to higher quality habitats ($P = 0.0004$). Near the end of the season, after populations had stabilized, the patterns of net movement between pairs of habitats appeared to be balanced (not significantly different from 0; Table 4).

Movement of meadow voles between pairs of habitats showed no significant net dispersal between higher and lower quality habitats, except for positive movement from high-food, low-cover habitat to low-food, high-cover habitat ($P > 0.38$ in all cases except $P = 0.009$ for LH–HL; Table 4). Pooling results for combinations of pairs did not lead to significant net movement between high- and low-cover habitats ($P = 0.79$), between habitats with and without supplemental food ($P = 0.47$), or between higher and lower quality habitats in general ($P = 0.44$). Thus, dispersal of meadow voles between habitats generally appeared to be balanced.

Linear regression analyses indicated that per capita emigration rate (dispersal) tended to decrease as population density increased in habitats with high cover for both species of voles (Table 2), an inverse density-dependent effect. Because population growth declined with density in high cover (Figs. 18a and 19a), one might expect per capita emigration for both species to be positively related to population growth, but it showed no clear pattern when compared to finite rate of population growth (Table 2). For prairie voles in one high-quality habitat type (HH), emigration was positively associated with population growth; in one poor-quality habitat type (HL), emigration was negatively

TABLE 4. Net dispersal of prairie voles (MO) and meadow voles (MP) between pairs of habitat types for weeks 8–22 and weeks 20–22 (means ± 1 SE).

		MO				MP	
Habitat pairs	N	Weeks 8–22	P	Weeks 20–22	P	Weeks 8–22	P
HH–HL	4	3.91 ± 1.11	0.04	−0.92 ± 0.42	0.11	1.80 ± 2.91	0.58
LH–LL	4	2.88 ± 1.01	0.07	0.29 ± 0.41	0.53	−0.88 ± 1.83	0.67
High–low cover	8	3.40 ± 0.73	0.002	−0.31 ± 0.50	0.41	0.46 ± 1.67	0.79
HH–LH	4	2.06 ± 1.46	0.25	−0.06 ± 0.41	0.89	−1.90 ± 2.96	0.57
HL–LL	4	1.21 ± 0.84	0.25	0 ± 0	...	−0.25 ± 0.25	0.39
High–low food	8	1.64 ± 0.80	0.08	−0.03 ± 0.27	0.88	−1.07 ± 1.41	0.47
HH–LL	4	3.79 ± 1.68	0.11	−0.79 ± 0.63	0.30	0.83 ± 1.28	0.56
LH–HL	4	0.54 ± 2.11	0.81	0.92 ± 0.44	0.13	4.25 ± 0.70	0.009
High–low quality	24	2.40 ± 0.58	0.0004	−0.09 ± 0.48	0.65	0.64 ± 0.82	0.44

Notes: Habitat types are as follows: HH, high food, high cover; HL, high food, low cover; LH, low food, high cover; LL, low food, low cover. Positive values indicate net dispersal toward the first habitat type (higher quality) from the second habitat type (lower quality) in each pair. High–low cover includes pairs for which only cover differs, high–low food includes pairs for which only food differs, and high–low quality includes all pairs. Values for probability levels (P) are based on paired t tests. N = sample size.

associated with population growth, and for the remaining two habitat types, emigration had no significant relationship with population growth. Meadow voles showed no significant relationships between emigration and population growth. When mean per capita emigration over the whole season was compared to peak population densities (mean of weeks 20 and 22), rather than comparing current emigration to current population density, a strong negative relationship occurred over all habitat types for both species (Figs. 20 and 21).

In summary, the overall pattern of movement for prairie voles during our experiment was emigration from low-cover habitats and immigration to high-cover habitats. Comparison of pairs of habitats indicated that net dispersal was consistently from lower quality to higher quality habitats. Not until the end of the growing season, when populations had stabilized, did dispersal of prairie voles between habitats appear to be balanced. After the founders had settled, meadow voles did not show the same propensity for emigration from low cover to high cover that prairie voles did, and movement of meadow voles appeared to be balanced for the experiment as a whole. Emigration rates tended to be inversely density dependent for both species, but neither species showed a consistent relationship between emigration and population growth. Both species showed a strong inverse relationship between mean per capita emigration over the whole season and carrying capacity (maximum stable density) of the habitats.

Overwinter demography

By March of 1996 the mean population sizes of prairie voles had declined to low densities in all habitat patches (Fig. 22a). Of the 24 individuals captured, 20 had been marked the previous fall, so little recruitment
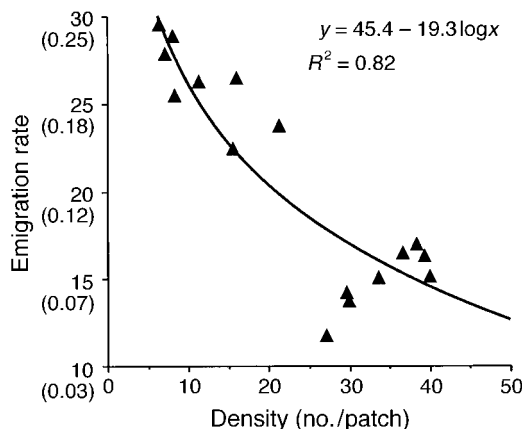

FIG. 20. Relationship of mean per capita emigration of prairie voles (arcsine-transformed data) during weeks 8–22 to peak population densities across all habitat patches (N = 16). The coefficient of determination (R^2) is given for logarithmic regression, $P < 0.001$. Values in parentheses on ordinate give untransformed values for emigration.
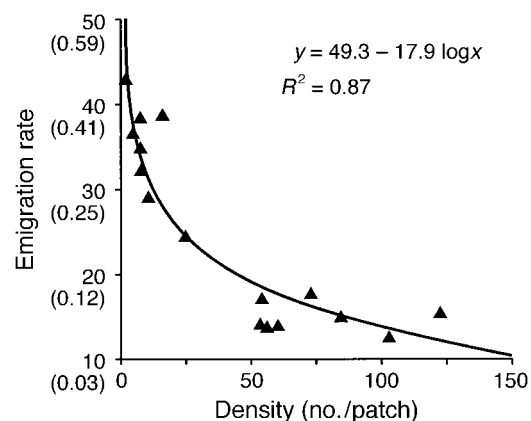

FIG. 21. Relationship of mean per capita emigration of meadow voles (arcsine-transformed data) during weeks 8–22 to peak population densities across all habitat patches (N = 16). The coefficient of determination (R^2) is given for logarithmic regression, $P < 0.001$. Values in parentheses on ordinate give untransformed values for emigration.
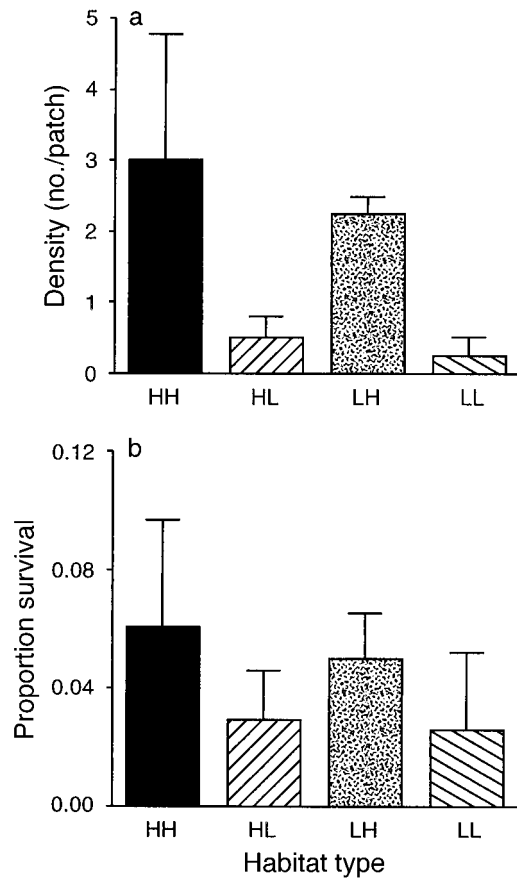
FIG. 22. (a) Density in March 1996 and (b) survival of prairie voles over winter (November–March) in different habitat types (mean + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

had occurred. Densities remained significantly higher in habitats with high cover (two-way ANOVA, $P = 0.03$), but neither the food effect nor the food $\times$ cover interaction were significant ($P > 0.59$ in both cases). Survival from late November to early March also appeared to be higher in habitats with high cover, but because of high variability neither main effects nor interactions were significant (two-way ANOVA, $P > 0.76$ in all cases; Fig. 22b).

Mean population sizes of meadow voles also had declined substantially by March of 1997 (Fig. 23a). Of the 66 individuals that were captured, 60 had been marked the previous fall, so again little additional recruitment had occurred. Spring densities again remained significantly higher in high-cover habitats (two-way ANOVA, cover effect, $P = 0.0003$). Neither the main effect of food nor the interaction was significant ($P > 0.76$ in both cases). Survivorship from late November to early March also tended to be higher in habitats with high cover (cover effect, $P = 0.09$; Fig. 23b). Again, the main effect of food and the interaction were not significant ($P > 0.17$ in both cases).

DISCUSSION

Basic habitat quality

Responses to our treatments by founding voles early in the experiment should indicate basic quality of the different habitat types that we created, and both species of voles had better performance in unmowed (high-cover) habitats. As expected, mowing substantially reduced the biomass of vegetation, except for litter early in 1996, and dramatically reduced overall cover (Figs. 2–5). More founders of both species settled in habitats with high cover (Figs. 6c and 7c), early recruitment of young was greater in habitats with high cover (Figs. 6d and 7d), and body growth rates of males were greater in high cover. Populations reached much higher densities in unmowed habitats (Figs. 8a and 9a), and even after substantial declines in density over winter, most voles remained there.

The only effects of food on founders were that larger male prairie voles settled in habitats with supplemental food and that meadow voles settled more in low cover with supplemental food than in low cover without it. The lack of response to food early in the season may
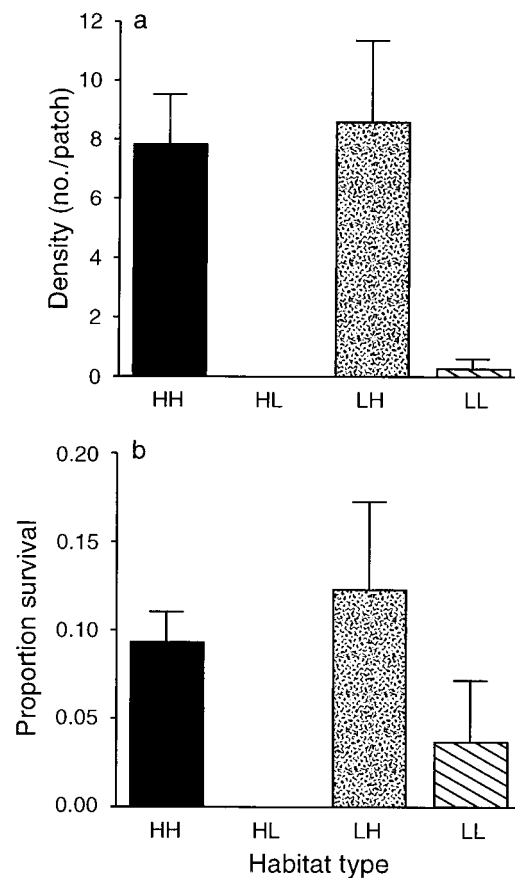

FIG. 23. (a) Density in March 1997 and (b) survival of meadow voles over winter (November–March) in different habitat types (mean + 1 SE). $N = 4$ in all cases. See Fig. 1 for an explanation of habitat abbreviations.

have reflected the abundance of high-quality food in all habitat types at that time (Figs. 3c, d and 5c, d). Late in the season the availability of high-quality food from the natural vegetation was lower, particularly for prairie voles, and only then did supplemental food have an effect on population densities in low cover (Figs. 8 and 9). A particularly important effect of supplemental food on population density of meadow voles occurred in low-food, low-cover habitats where two different replicates went temporarily extinct. Subpopulations in high-food, low-cover habitats never went extinct, presumably because of the supplemental food.

We conclude that our manipulations did influence basic habitat quality as expected. The effect of mowing was greater than the effect of adding supplemental food, however, perhaps because mowing reduced the amount of natural food as well as the amount of cover. One might argue that mowed habitats should contain more succulent, higher quality vegetation because of regrowth, but we did not observe such a response. Mowed plants, particularly monocots, did regrow, but the plants continued to mature as the season progressed and appeared similar in toughness to plants in unmowed habitats. Finally, although substantial differences in the composition of vegetation occurred between upslope (more monocots) and downslope (more dicots) sites, these had surprisingly little effect on the performance of the founding voles. These results support our ranking of basic quality for the four habitat types in our experimental landscape as HH ≥ LH > HL > LL.

Habitat selection

The ideal despotic model of habitat selection (IDD), rather than the ideal free model (IFD), seemed likely to apply to both species of voles before our experiment because females occupy exclusive territories (Madison 1985, Getz and Hofmann 1986). We therefore expected higher fitness in habitats that had higher basic quality.

Correlates of individual fitness generally did not vary consistently with habitat quality, however. Growth rates of juvenile prairie voles and the number of young that survived to adulthood per adult female were both greater in habitats with high cover (Fig. 16b and d). Lower rates of in situ recruitment occurred in high cover (Fig. 16c), however, which may have reflected the higher densities generally found there (Fig. 8a). Body mass of juvenile prairie voles at first capture and growth rates of juveniles were greater in habitats with supplemental food, but in situ recruitment of young per adult female was lower (Fig. 16a, b, and c). Lower in situ recruitment may have reflected the greater proportion of adults in habitats with supplemental food late in the season (Fig. 10a), which in turn was associated with net movement into habitats with supplemental food (Fig. 14b). Overall, prairie voles residing in habitats with higher cover appeared to have greater overall fitness, but those in habitats with supplemental

food may not have. Nevertheless, these results supported IDD habitat selection for prairie voles.

For meadow voles more young per adult female were originally recruited in habitats with high cover (Fig. 17c), but the number of young that survived to adulthood, which should be a better indicator of fitness, did not differ with habitat quality (Fig. 17d). Furthermore, no significant differences were detected for either size or growth rates of juveniles. Thus, we detected relatively little difference in the fitness of meadow voles in different habitats, which supported IFD habitat selection for meadow voles.

Although fitness correlates supported IDD for prairie voles, the actual distribution of voles among habitat patches did not. Recall that the IDD model predicted that the proportion of the population in low-quality habitats should increase as populations increased, whereas the IFD model predicted that the proportion in low-quality habitat should remain constant after the founders had settled and population growth was well under way. Neither of these patterns occurred for prairie voles during our experiment (Fig. 8b). Founders only showed a slight tendency to move to high-quality habitats or to survive better in them. As new recruits came into the populations, the proportion in low-quality habitats continued to decline, rather than increase as predicted by the IDD model. Only when the population densities stabilized late in the season did the proportions in each habitat stabilize, as predicted by the IFD model.

For meadow voles, after the initial movements of founders, the proportion of populations in different habitats stabilized by week 8 and remained relatively constant throughout the growing season. Apparently, dominant individuals could not keep subordinates out of high-quality habitats as population density increased. Thus, the pattern of habitat use supported the IFD model of habitat selection for meadow voles, agreeing with the results for fitness correlates.

A whole suite of different factors, such as costs of traveling, ability to sample surrounding habitats, and constraints on perceptual capabilities, could cause unequal fitness among habitats even if the underlying mechanism is IFD habitat selection (reviewed in Sutherland 1996). A common effect of these factors is that animals tend to stay in their resident habitats, even if their potential fitness would be greater in alternative habitats. The cost of habitat selection, which involves such factors as increased mortality and lost breeding opportunities during emigration and colonization stages of dispersal, also may be important (Metzgar 1967, Anderson 1989 and references therein). Even if animals are free to select the habitat which would provide the highest fitness, they are unlikely to disperse unless the benefit to fitness is greater than the cost of habitat selection (Morris 1987, 1992).

The cost of habitat selection may have reduced dispersal and maintained unequal fitness among prairie

vole populations in different habitats even though habitat selection eventually followed the IFD model. Despotism was not sufficient to prevent immigrants of either species of vole from entering high-quality habitats even at relatively high densities (Figs. 12c and 13c), which suggests that it may be unable to enforce IDD habitat selection. The considerable plasticity of territory size of voles, which decreases dramatically as population density increases (Desy et al. 1990), is also consistent with a relatively small effect of despotism.

Even if despotic behavior does not prevent immigration, fitness may vary among residents within a habitat because territory quality can vary within a habitat. Dominant individuals may still enjoy higher fitness than subordinates within habitats (as in the ideal preemptive habitat selection model of Pulliam and Danielson 1991), and despotic behavior may still impose a cost of habitat selection. For example, Whitham (1980) found that fitness of *Pemphigus* aphids was equal among habitats (individual leaves), but was unequal within habitats. Although he did not measure the cost of habitat selection, there likely was one because these aphids fight for the best positions on the leaves. Nevertheless, only in cases when the cost of habitat selection is low is equal fitness among habitats likely to be observed, even for a species with IFD.

Dispersal patterns

The source–sink model of dispersal predicts positive net recruitment ($B > D$) and negative net movement ($I < E$) in high-quality habitats and the opposite pattern for low-quality habitats. Over the growing season, the number of in situ recruits generally exceeded the number of deaths in all habitat types for both species (Table 3). Although local extinction of meadow voles occurred in LL habitats during several weeks, it was a result of negative net movement and not negative net in situ recruitment. On all three occasions when local extinction occurred, the last animals emigrated. Analysis of the frequency of movements also indicated no net movement of voles from high-quality to low-quality habitats for either species (Table 3). Thus, the source–sink model did not apply to vole populations in our experimental system.

When pairs of habitat types were considered, there was net movement of individuals from lower quality habitats to higher quality habitats for prairie voles, which supported an unbalanced dispersal model (Table 4). However, late in the season population density stabilized, little dispersal occurred, and the balanced dispersal model could not be rejected. Mean per capita emigration was inversely related to the asymptotic densities (carrying capacity) for our populations (Figs. 20 and 21), as required by the model for balanced dispersal (McPeek and Holt 1992), and it may be that time lags associated with the relatively sedentary nature of prairie voles (Desy et al. 1990) delayed their achievement of balanced dispersal.

Population dynamics

Patterns of dispersal in relation to population density did not suggest a key role for dispersal in generating long-term patterns of population dynamics for prairie voles. The relationship of per capita emigration to population growth rate in high-cover habitats was inconsistent, a significant positive relationship in one high-cover habitat but not in the other (Table 2). Per capita emigration was inversely density dependent in high-cover (high-quality) habitats, in which population cycling of prairie voles might be expected. Although this relationship supports the idea that increased social interactions may deter movement through dense populations of voles (the social fence of Hestbeck 1982), it does not support the idea that dispersal strongly influences population dynamics. The positive feedback from decreased emigration at high densities should have favored continued population growth, but densities stabilized.

Some might argue that the short period of time that we observed our populations was insufficient to support conclusions about the environmental factors promoting stability or instability over longer time spans (years). We do not disagree. Our experiment, however, was conducted to examine the relationships of habitat quality to demographic processes and habitat use by voles as their density changed. It was not meant to determine which environmental factors are most important for long-term population dynamics. We expect the relationships of demographic processes to density to be consistent over time, even if the environmental factors that influence the long-term population dynamics of voles change.

In habitats with high cover, both species showed strong population growth that was directly density dependent (Figs. 8a and 9a), which implies that some demographic process is acting to stabilize population size. In low cover, where population density varied less, the results were less consistent. Detection of density dependence for populations over short intervals of time can be problematic because of autocorrelation, but experimental manipulation of density has shown that direct density-dependent reproduction does occur in meadow voles (Ostfeld and Canham 1995). Time series analyses of longer intervals also have found strong density dependence in population growth from year to year for a variety of small mammal species (Fryxell et al. 1998, Stenseth 1999), although long-term stability may not be caused by the same processes as short-term stability. Some of our subpopulations had not stabilized by the end of the experiment, and we do not claim that particular demographic processes actually had stabilized meadow vole populations in all cases. Rather we call attention to those processes that had the potential to do so.

A particularly interesting result of our experiment was that subpopulations in different habitats appeared

to have different stabilizing processes. For prairie voles the two populations that reached the highest densities (HH, LH) showed a negative relationship between net in situ recruitment and density, but net movement in those populations was unrelated to density (Fig. 18b and c). The two populations in low cover (HL, LL) grew much less and showed little relationship of net in situ recruitment to density, but their net movement was negatively related to density (Fig. 18b and c). Meadow vole subpopulations in high-cover habitats displayed significant negative relationships between density and both net in situ recruitment (Fig. 19b) and net movement (Fig. 19c). Subpopulations in HL habitats grew much less and showed no relationship between net in situ recruitment and density (Fig. 19b), but their net movement was negatively related to density (Fig. 19c). Subpopulations in LL habitats showed little variation in density, and we detected no density-dependent net in situ recruitment or net movement (Fig. 19b and c). Thus, it appears that densities of voles in habitats with high cover were stabilized primarily by birth and death processes, but densities in low-cover habitats were stabilized more by movement.

Although previous studies have reported differences in the performance of voles in habitat patches with different vegetation (Batzli 1974, Cole and Batzli 1979, Ostfeld et al. 1985, Ostfeld and Klosterman 1986), we know of no previous study that reports different mechanisms for stabilizing subpopulations of small mammals in different habitat patches. Apparently, this phenomenon was a straightforward result of preference for high-cover habitats by voles. Greater population growth in populations with higher cover did not occur simply because of greater net in situ recruitment, but because of a combination of net in situ recruitment and immigration. Thus, even when net in situ recruitment was similar in high-cover and low-cover habitats, growth rates differed because of net movement from the low-cover to the high-cover habitats.

This scenario also helps to explain why the results for individual fitness supported the IDD model of habitat selection for prairie voles, whereas the distribution of the populations among habitat types did not. Even though population densities had reached relatively high levels, in situ recruitment remained positive (Fig. 16a), and fitness remained higher in high quality habitats, at least as indicated by body growth rates (Fig. 18b). Under these conditions net movement to high cover continued (Fig. 16b), as might be expected if patterns of habitat selection respond to natural selection. Prairie voles may simply not have responded rapidly enough to habitat differences to achieve similar fitness and balanced dispersal among habitat types until after population densities in high quality habitats had stabilized. Unfortunately, stable populations were only reached late in the growing season, and we have insufficient data to examine fitness correlates at that time.

Seasonal effects

An important question is what environmental factors actually stabilized our populations at the end of the growing season? We have so far viewed the processes as simply density dependent, but habitat deterioration as the season progressed could have occurred because of seasonal environmental changes independent of density. For instance, density-dependent responses for net in situ recruitment and net movement that we observed could have been responses to the deterioration of habitats, such as the decline of natural food or increase of predation pressure, which could have occurred independently of population density as the season progressed. We have documented a severe decline in availability of high-quality food as vegetation matured (Figs. 3c, d and 5c, d), and the lower net recruitment late in the season (Figs. 14a and 15a) could have reflected poor availability of natural foods. If a seasonal reduction in the availability of high-quality food alone were responsible for the cessation of population growth, however, we would expect lower measures of individual performance known to be associated with nutrition of voles, particularly body growth of young and recruitment of young per adult female (Batzli 1985), in habitats without supplemental food. This did not occur. Body growth rates of juveniles late in the season were similar to those early in the season for prairie voles (Fig. 16b), and body growth of subpopulations of meadow vole declined late in the season whether or not supplemental food was present (Fig. 17b). Recruitment of young per adult female declined late in the season for both species of voles, but again the decline occurred whether or not supplemental food was present (Figs. 16c and 17c).

Our earlier work indicated that predation pressure on voles increases late in the growing season in east–central Illinois (Lin and Batzli 1995), and per capita mortality did increase in all of our habitat types late in the growing season (Figs. 12b and 13b). A greater increase in mortality would likely occur in lower cover as predation pressure increased, but this did not happen for prairie voles (Fig. 12b) and only occurred marginally for meadow voles (Fig. 13b). Increased predation pressure should also cause less movement within habitats with low cover, where voles would be the most vulnerable (Desy et al. 1990). Although movement of prairie voles between captures in successive trapping periods did decline slightly with season (9.3 ± 0.5 m early and 7.9 ± 0.7 m late; two-way ANOVA with repeated measures, season effect, $P = 0.03$), there were no main effects of food or cover and no season × treatment interactions ($P > 0.22$ in all cases). A similar seasonal decrease in movement occurred for meadow voles, but movement actually was greater in low-cover habitats. Mean distances moved were 9.9 ± 0.5 m and 12.2 ± 1.2 m for high-cover and low-cover habitats, respectively, in the early season and 7.4 ± 0.3 m and

TABLE 5. A comparison of the effects of supplemental food and vegetative cover on prairie voles and meadow voles.

Population metric	Prairie voles		Meadow voles	
	Food effect	Cover effect	Food effect	Cover effect
Founders				
Mortality	0	0	0	−#
Emigration	0	0	0	0
Settlement	0	(+)	+¶#	+#
Recruitment†	0	+	0	+
Male body size	+	0	0	0
Male growth rate	0	+	0	+
Post-founder population				
In situ recruitment	0	0	0	0
Mortality	0	(−)	0	(+)§
Net in situ recruitment	(−)§	0	0	0
Immigration	(+)	0	0	−§#
Emigration	(−)	−‖	0	−§
Net movement	+	+	(−)	0
Population growth	0	+	0	0
Population density	(+)‖¶	+‖	(+)¶#	+‖#
Population proportion	0	+‖	+¶#	+‖#
Fitness correlates				
Growth of young	+	+	0	0
Body mass of young	(+)	0	0	0
Recruitment†	−	−	0	(+)
Reproductive success‡	(−)	(+)	0	0

Notes: The section for founders gives results for weeks 0–4, except for recruitment which occurred during weeks 5–10; the section for post-founder populations gives per capita demography for weeks 8–22; the section for fitness correlates gives information on the performance of all juveniles, but only for female adult voles. A significant positive treatment effect ($P < 0.05$) is indicated by +; a significant negative treatment effect is indicated by −; a nonsignificant treatment effect is indicated by 0. Signs in parentheses indicate a marginally significant treatment effect ($0.05 < P < 0.1$).

† Number of young recruited per adult female.
‡ Number of young surviving to adult size per adult female.
§ Greater early in season (weeks 8–14).
‖ Greater late in season (weeks 16–22).
¶ Greater in low cover.
# Greater at downslope sites.

8.4 ± 0.5 m for high- and low-cover habitats, respectively, in the late season. A two-way ANOVA with repeated measures showed that both the season effect ($P = 0.0002$) and the cover effect ($P = 0.04$) were significant. Neither the main effect of food nor any interaction was significant ($P > 0.30$ in all cases).

A final consideration is that photoperiod decreases late in the growing season, and laboratory experiments indicate that shorter daylengths can inhibit reproduction of some arvicoline rodents (Negus and Berger 1988). Reproduction in prairie voles and meadow voles can continue through the winter, however, if densities are not high or if supplemental food is available (Keller and Krebs 1970, Cole and Batzli 1978). We conclude that density-dependent demographic responses and population stability late in the growing season are unlikely to be explained by seasonal effects that are independent of density.

Comparison of species

Because we conducted the experiments of prairie voles and meadow voles in different years, differences between species could reflect differences in weather between years. Direct effects of weather were unlikely to have been important because neither growing season had unusual patterns of temperature or rainfall. Nevertheless, the vegetation in our enclosures did differ between years, particularly because of less production of monocots and associated litter in 1996 (Table 1). On balance, 1996 should have been a less favorable year for meadow voles because of their dependence on monocots for food, but meadow voles reached much higher densities in high-cover habitats than did prairie voles in 1995.

In fact, meadow voles and prairie voles had many similar responses to our experimental landscapes (Table 5). Neither species responded to the food treatment as strongly as to the cover treatment. Female founders of both species had greater reproductive success and male founders grew better in high-cover habitats. After the establishment of founders, emigration rates were much higher in low-cover habitats and populations reached higher density in high-cover habitats. The effects of supplemental food were less obvious. Population density was slightly higher in habitats with supplemental food, but only in low-cover habitats late in the season. Klatt (1986) previously reached the conclusion that vegetative structure was a better predictor of relative abundance of prairie voles and meadow voles than was floristic composition, which could be

interpreted as a greater impact of cover compared to food.

Several major differences between the two species also existed. First, meadow voles had poorer performance in low-cover habitats than did prairie voles, which supports the finding of previous studies that meadow voles have lower tolerance for low vegetative cover (reviewed in Klatt 1986). Meadow voles responded to low-cover habitats soon after they were released. The proportion of populations in low-cover habitats declined abruptly, while prairie vole populations had slower response (Figs. 8b and 9b). By week 22, the proportion of population in high-cover habitats was greater for meadow voles than for prairie voles (88% and 75%, respectively). Even though meadow voles reached higher overall density than prairie voles, the density of prairie voles in low-cover habitats was at least as high as that for meadow voles (Figs. 8a and 9a). Prairie voles never went locally extinct in low-food, low-cover habitats, as did meadow voles. Founding meadow voles suffered greater mortality in low-cover habitats, but prairie voles did not. After founders settled, the reproductive success of adult females was greater in high-cover habitats for meadow voles, but not for prairie voles. Finally, meadow voles showed worse performance at downslope sites, but prairie voles did not (Table 5).

Poorer performance in low-cover habitats for meadow voles could not be explained by the differences in vegetation between the two years. The total biomass of vegetation in low-cover habitats was similar both years, and the differences between high- and low-cover habitats were more extreme in the prairie vole experiment of 1995 (Figs. 3 and 5). The amount of high-quality natural food available in low-cover habitats late in the season was actually greater for meadow voles. Late in the season meadow voles favor monocots as food more than do prairie voles (Table 1), which may explain the poorer performance of meadow voles at downslope sites where more dicots, but fewer monocots, occurred late in the season (Figs. 2 and 4).

Except for its impact on extinction of meadow voles in low cover, supplemental food appeared to affect prairie voles more than meadow voles (Table 5), and prairie voles had lower availability of high-quality forage late in the season than did meadow voles (Figs. 4 and 6). Per capita immigration rates and net movement were greater in habitats with supplemental food for prairie voles, but not for meadow voles. Young prairie voles in high-food habitats were heavier when they were first captured and enjoyed greater body growth rates; neither effect occurred in meadow voles. The apparent negative effect on per capita reproduction of adult female prairie voles may have been linked to the greater net immigration to habitats with supplemental food (Fig. 14b), which may have resulted in more young, non-reproductive adult females and decreased per capita reproductive rates.

Perhaps the greatest difference between the two species was that prairie voles showed significant net dispersal from low- to high-quality habitats, whereas meadow voles did not. Assuming that voles disperse to maximize fitness, if the difference in fitness between habitats more than compensates for the cost of habitat selection, then net movement from low- to high-quality habitats should occur. Balanced dispersal will not be observed until the difference in density between habitats is sufficient to make the difference in realized quality of the two habitats similar to the cost of habitat selection. Prairie vole dispersal did appear to be balanced by the end of the growing season (weeks 20–22; Table 4), and the IFD may not have been achieved until then.

Why did we observe unbalanced dispersal for most of the season in prairie voles, but not in meadow voles? Meadow voles have greater mobility (Madison 1985), so they probably can respond more quickly to differences in quality among habitat patches. Both movement within habitats and dispersal rates between habitats were greater for meadow voles than for prairie voles, at least in low cover where densities were low (Figs. 12c, d; 13c, d; 20; and 21). Mobility of a species relative to the distance that must be traversed seems likely to influence the time required to equalize fitness among habitats (Morris 1992). Even so, lower vagility may not have been sufficient to cause the delay for prairie voles at a spatial scale as small as our experimental system, and other factors could have contributed to a greater cost of habitat selection for prairie voles.

Unbalanced dispersal, even with IFD, may be relatively common in natural populations that are constantly perturbed or that live in habitats with changing carrying capacities (McLeod 1997). After such events, natural populations are likely to deviate from balanced dispersal and equal fitness (even after allowing for cost of habitat selection). The length of time required to reestablish a balanced state is likely to be a function of several factors; low vagility, strong social organization, and lack of cover can all reduce dispersal (Merriam 1995). In general, however, we expect unbalanced dispersal to be less common for more vagile species, such as large mammals or birds, that can cross an unfavorable matrix within a landscape relatively easily (Doncaster et al. 1997).

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APPENDIX

Tables presenting ANOVA statistics are available in ESA's Electronic Data Archive: *Ecological Archives* M071–005.