AN ABSTRACT OF THE THESIS OF

Natasha Nelson for the degree of Master of Science in Wildlife Science presented on May 24, 1996.

Title: The Effects of Patch Size and Isolation on Juvenile Emigration in Gray-tailed Voles, *Microtus canicaudus*

Redacted for Privacy

Abstract approved: _____ Jerry O. Wolff

I monitored population parameters of gray-tailed voles, *Microtus canicaudus*, residing in patchy and continuous habitats to determine the effects of patch isolation and size on juvenile emigration. The experiment was conducted in 16, 0.2-ha enclosures planted with alfalfa. I tested the hypotheses that population size, survivorship and emigration rates would be higher in control enclosures (continuous habitat, 1,850 m^2) than in three treatment enclosures in which habitat had been reduced in size by 70% and fragmented into a single large patch (625 m^2), 25 small patches (each 25 m^2) separated by 4 m of bare ground, or 4 medium-sized patches (each 156 m^2) separated by 12.5 m of bare ground. I also looked at the influence of opposite-sex relatives on juvenile emigration and sexual maturity. In May 1995, eight males and eight females were introduced to the 4-patch enclosures, and five males and eight females were introduced into the other treatments. Population size was not affected by treatments. Survivorship of males was lowest in the 4-patch treatment and highest in the 25-patch treatment, however, survivorship for females was highest in the 4-patch treatment in comparison to all others. Emigration rates were significantly

lower in the 4-patch enclosures in comparison to other treatments and juveniles emigrated at a significantly older age from the 4-patch and single-patch treatments than they did in control and 25-patch treatments. Whether an individual emigrated or stayed in residence or became sexually mature was not dependent on gender or presence/absence of opposite-sex relatives. Gray-tailed vole demographic and behavioral responses to patchy environments varied depending on patch size and isolation. Conservation biologists may need to consider how patch size and isolation affect the social environment of juveniles and how this in turn affects juvenile emigration and overall demography.

The Effects of Patch Size and Isolation on Juvenile Emigration in Gray-tailed Voles, *Microtus canicaudus*

by

Natasha Nelson

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed May 24, 1996

Commencement June 1997

Master of Science thesis of Natasha Nelson presented on May 24, 1996

APPROVED:

Redacted for Privacy

Major Professor, representing Wildlife Science

Redacted for Privacy

Chair of Department of Fisheries and Wildlife

Redacted for Privacy

Dean of Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Redacted for Privacy

Natasha Nelson, Author

ACKNOWLEDGMENT

I thank Jerry Wolff for his role in designing this research project and for his guidance in creating this manuscript. In addition, I want to thank the many special people who made the field portion of this project run smoothly, including: Renee Davis-Born, Tom Manning, Derek Lehman, Palmer Coe, Sandra Fife, Heidi Brunkel and the staff of Hyslop Agronomy Farm. I wish to give a special thank you to Eric Schauber and Dan Edge for their role in data analysis. I thank Mark Azevedo for his prodding to continue the research and Keith Moses for his support and caring.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

DEDICATION

My thesis is dedicated to the memory of my father who passed away in the middle of my field season from cancer. He was always an inspiration and always stood behind me in any decision I made.

THE EFFECTS OF PATCH SIZE AND ISOLATION ON JUVENILE EMIGRATION IN GRAY-TAILED VOLES, *Microtus canicaudus*

INTRODUCTION

A major concern in conservation biology is the loss of biodiversity (Soulé 1986; Wilson 1986). One of the greatest threats to maintaining biodiversity is loss of habitat (Harris 1984; Wilcox and Murphy 1985). Loss of habitat often results in fragmentation of the remaining habitat creating small and isolated or semi-isolated patches separated by barriers of less suitable habitat (Skole and Tucker 1993; Blackstock et al. 1995). Fragmentation in turn subdivides populations, which reduces overall population size and may alter normal demographic and social processes (Foster and Gaines 1991; see review by Andren 1994; Diffendorfer et al. 1995; Simberloff 1995). Living in patchy habitats can affect the population dynamics of subdivided populations by decreasing survival because of increased edge effects and increased exposure to predation (Wilcove 1985; Lovejoy et al. 1986; Andren 1992; Keith et al. 1993), altering movements and dispersal patterns (Lens and Dhondt 1994; Diffendorfer et. al 1995), and disrupting normal reproductive patterns (Adler 1994). Occupying edge habitat may also increase an individual's fitness by increasing the nutritional quality of the food, and this may outweigh the increased risk of predation (Bowers et al. 1996).

Isolated patches with wide dispersal barriers can lead to extinction within patches (Burkey 1989) independent of habitat reduction (Wilcove et al. 1986). Models of mountain brushtail possum (*Trichosurus caninus)* populations indicated high rates of

extinction as a result of population subdivision and low inter-patch migration (Lacy and Lindenmayer 1995). Cougars (*Felis concolor*) inhabiting a 75-km^2 habitat fragment located in the Santa Ana Mountain Range of southern California became extinct when the patch became isolated (Beier 1993). Beier concluded that if another population in an 150-km^2 habitat became isolated without a corridor, the population would become extinct without immigration. Models of spotted owls (*Strix occidentalis*) indicate that patch isolation and dispersal capabilities of owls may be the limiting factors in spotted owl recovery (Lamberson et al. 1992). Fahrig and Merriam's (1994) review of fragmented populations stressed the need to better understand the role of dispersal in relation to patch extinction.

Perhaps one of the greatest effects of fragmentation on normal demographic processes is the restriction of dispersal with increased degrees of patch isolation (Fahrig and Merriam 1985; Cummings and Vessey 1994; Bjornstad et al. in review). Work in Australia on euros, *Macropus robustus*, a large kangaroo, found movement between habitat patches was dependent on the degree of patch isolation (Arnold et al. 1993). One euro became completely isolated from other animals in a small and isolated habitat patch, and the overall movement between small isolated patches over the course of the 3-year study was extremely low (Arnold et al. 1993). Studies of prairie voles (*Microtus ochrogaster*) and deer mice (*Peromyscus maniculatus*) found that >90% of the animals never crossed 10- to16-m barriers of mowed grass (Diffendorfer et al. 1995). In another study, Wolff et al. (MS) found that only 6% of female and 15% of male gray-tailed voles (*Microtus canicaudus*) crossed 4-m barriers of bare ground between fragments during a

4-day trap period compared to 50-60% of males and females moving a comparable distance in continuous habitats. Thus, several studies have documented that dispersal is restricted in patchy environments.

Research has not addressed how isolation and restricted emigration can affect normal reproductive patterns within family groups, despite the importance of kinship (Charnov and Finerty 1980) in animal population dynamics (Wolff 1995). The normal emigration pattern for most mammals, including small mammals such as voles, is for males to emigrate from the natal site and for females to be philopatric (Dobson 1982; Boonstra et al. 1987; Wolff 1993). However, if males are inhibited from emigrating from the natal site due to the risk of crossing barriers of unsuitable habitat, interactions among relatives of the opposite sex could result in inbreeding or reproductive suppression (Pusey 1987; Brandt 1992; Wolff 1993; Wolff et al. MS). Inbreeding often results in immediate decrease of fitness to individuals (Ballou and Ralls 1982; Ralls et al. 1986; however see Wauters et al. 1994) as well as affecting demographic parameters and population growth (Simberloff and Cox 1987; Simberloff et al. 1992).

The social and demographic consequences of restricted emigration are dependent in part on the motivation for emigration. Three hypotheses have been proposed to explain juvenile emigration. Juvenile emigration may result from resource competition within the natal site (e.g. Waser 1985; Anderson 1989). This hypothesis predicts that competition for resources, primarily food, results in juveniles emigrating to areas of reduced competition. The second hypothesis predicts that juvenile emigration results from competition for mates and thus, emigration results from competition with same-sex adults

(Greenwood 1980; Dobson 1982; Moore and Ali 1984; Boonstra 1989; Ribble 1992). To support this hypothesis, emigrants should move into areas with lower densities of same-sex individuals. The third hypothesis is that juveniles emigrate to avoid inbreeding with close relatives and that emigration increases the inclusive fitness of emigrants as well as that of their nonemigrating relatives (Greenwood 1980; Pusey 1987; Wolff et al. 1988; Bollinger et al. 1993; Jacquot and Vessey 1995). Wolff (1994) proposed that juveniles that do not emigrate from their natal site, or more importantly, do not separate from their opposite-sex relatives, will experience reproductive inhibition. This model was based on empirical studies with white-footed mice (*Peromyscus leucopus*; Wolff 1992) with supportive data from gray-tailed voles (*Microtus canicaudus*; Wolff et al. MS.) and several other mammal species (Wolff 1994). From a study with gray-tailed voles in a patchy environment, Wolff et al. concluded that reproductive suppression of juveniles could have resulted from low juvenile-emigration rates across habitat barriers, leaving voles in their natal patch with relatives. Reproductive inhibition in the presence of relatives is well-documented (Batzli 1977; McGuire and Getz 1991; Wolff 1992; Lambin 1994) and is likely to occur naturally among animals restricted to patchy environments (Bjornstad in review).

Delayed sexual maturation and/or inbreeding may affect both the social dynamics of family groups, and population-level parameters (Charnov and Finerty 1980; Wolff 1995). Population growth rates and size are a result of reproductive success and survival of individuals, and growth rates ultimately determine a population's probability of persistence (Goodman 1987; Burkey 1989). Fragmented populations often show lowered growth and

persistence rates (Foster and Gaines 1991) possibly as a result of delayed reproduction and(or) subsequent inbreeding depression. Fahrig and Merriam (1985) found lower population growth rates among small populations of white-footed mice in isolated woodlots in comparison to larger connected areas. Thus, isolation can have serious consequences for population viability.

Only a few studies have addressed the relationship between patch size and barrier width and emigration in small mammals. For instance, Diffendorfer et al. (1995) found movements of cotton rats (*Sigmodon hispidus*), prairie voles and deer mice between patches with 13- to 26-m habitat barriers decreased significantly as fragmentation increased. Bjornstad et al. (in review) found dispersal differed considerably in patchy habitats for two strains of root voles (*Microtus oeconomus*), possibly as a consequence of different inbreeding tolerances. As a result of decreased patch size and increased isolation, root voles that exhibit inbreeding depression increased dispersal distances, and root voles that exhibit no inbreeding depression reduced dispersal distances. Wolff et al. (MS) found reduced dispersal in gray-tailed voles with 4-m barriers in comparison to continuous habitats of equal total area. For root voles, Andreassen et al (in press) found 2- to 4-m gaps (10-20% of a root voles normal home range) in corridors were enough to discourage male movements. However, all these studies failed to consider the importance of kinship as a force generating these emigration patterns. The objectives of my study were to determine how the demographic and social dynamics of a species were affected by patch size, kinship and distance between patches.

Specifically, I tested the hypotheses that (1) population size and survival rates would be greater in continuous than in patchy habitats; and (2) that emigration would be greater in continuous habitat than in patchy habitats and that emigration rate would decrease with increasing width of barriers. I also used observational data to discern among the three hypotheses for the motivation for juvenile emigration: resource competition, reproductive competition, and inbreeding avoidance.

To meet these objectives, I conducted an experiment with gray-tailed voles in 0.2-ha semi-natural enclosures. The gray-tailed vole is a common small mammal that inhabits grasslands in the Willamette Valley of western Oregon (Verts and Carraway 1987). Gray-tailed voles are polygamous or promiscuous, females are territorial, males have large home ranges that overlap those of several females, and juvenile emigration is male-biased (Wolff et al. 1994). Gray-tailed voles recognize relatives based on familiarity (Boyd and Blaustein 1985). Under laboratory conditions, familiar gray-tailed voles produced fewer litters than unfamiliar individuals (Boyd and Blaustein 1985) and pairings of relatives show lower pup survivorship than pairings of unrelated individuals (J. Peterson, personal communication).

METHODS

The study site and experimental units

The study was conducted at the small mammal research site located at Hyslop Agronomy Farm of Oregon State University, approximately 10 km north of Corvallis, Oregon (Edge et al. 1995). The experimental units consisted of 16 0.2 ha (45 x 45 m) enclosures planted with alfalfa. Each enclosure is constructed of galvanized sheet metal approximately 90 cm high and buried 90 cm deep to prevent escape or entry by burrowing animals. Within each enclosure, a 1-m wide strip of barren ground along the inside of the fence was kept bare to minimize use by small mammals.

Control enclosures contained a continuous patch of alfalfa (43 x 43 m = 1,850 m^2). Treatment enclosures contained 70% less habitat (each with a total of 625 m^2) arranged in three different habitat configurations. The three treatments consisted of one central large patch (25 x 25 m), four medium-sized patches (12.5 x 12.5 m each) separated by 12.5-m barriers, and 25 small patches (5 x 5 m each) separated by 4-m barriers (Fig. 1). Four replicate enclosures were randomly assigned to each treatment.

In early May, alfalfa was manipulated to create the three treatment patterns (Fig. 1). A matrix of barren ground was created initially by a herbicide treatment (RoundUp®), followed by flail mowing. Mowing and raking of the matrix maintained the habitat patterns once animals were introduced. The alfalfa was mowed to a height of 0.5 m the last week of June to increase new growth and food quality.

Vole introductions

On 15 May 1995, eight female and eight male gray-tailed voles, were introduced into the 4-patch enclosures, two females and two males in each patch. Eight female and five male voles, were introduced into the control, single- and 25-patch enclosures, two females and one or two males in each corner of each enclosure. The voles were wild-caught stock from Benton County, Oregon and presumably were not closely related. At time of release, body mass ranged from 12 to 44 g and over two-thirds the animals weighed more than 18 g when released into the enclosures.

Trapping procedures

Each control enclosure had 100 stations in a 10 x 10 matrix with one trap per station, each large-patch enclosure had 36 stations with two traps per station within the habitat patch and 20 traps were placed at 9-m intervals along the fence perimeter across the bare ground barrier (total 92 traps). Each 4-patch enclosure had nine stations per patch with two traps per station (total 72 traps), and each 25-patch enclosure had four stations per patch with one trap per station (total 100 traps). Trap stations were 4.3 m apart in all enclosures except the 25-patch. Within the 25-patch enclosures, trap stations were located 1 m from each patch's edge with 3 m between traps.

Sherman live-traps were baited with oats and sunflower seeds, set in the evening and checked once a day at sunrise. Traps were propped open and prebaited during non-

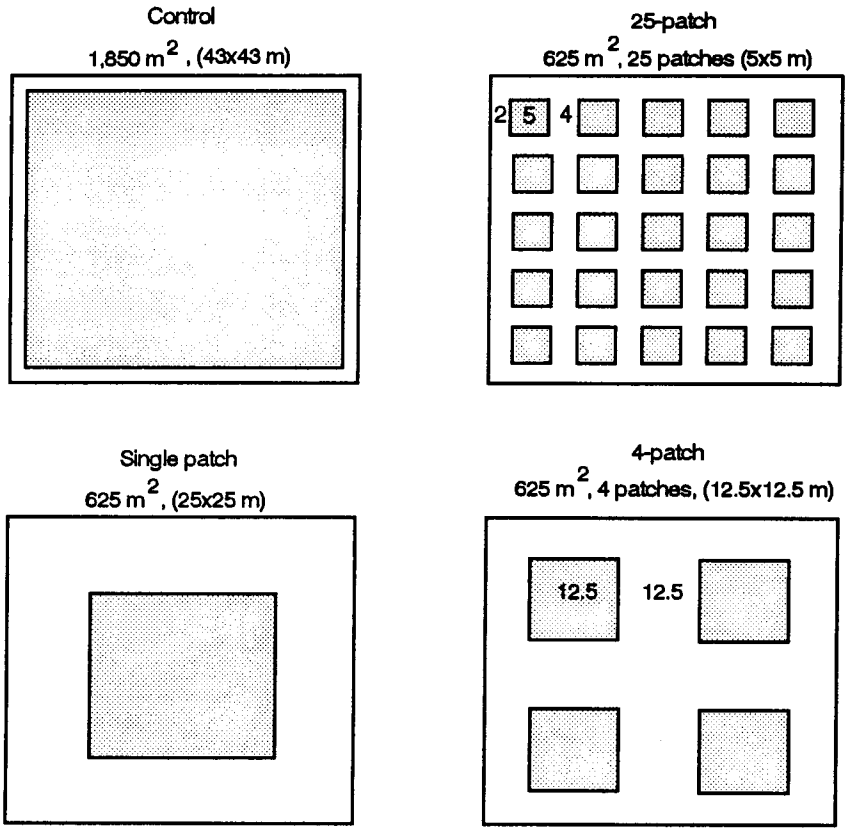

Figure 1. Alfalfa distribution (shaded boxes) in control, single-patch, 25-patch, and 4-patch enclosures for the study of emigration and social structure in gray-tailed voles living in a patchy environment.

trapping periods. Voles were trapped for four consecutive nights (trap period) at two-week intervals from May through September 1995. The 4-patch enclosures were trapped one week prior to all other treatments and the data from these weeks were associated with the next previous week's data. Voles were ear-tagged for identification. Body mass, gender, reproductive condition, and trap location were recorded for each capture. Animals $\geq$ 30 g were considered adults.

Reproduction and recruitment

All newly tagged animals were considered recruits that were born in the enclosure. A newly tagged animal <18 g was considered recently weaned and still in the natal site (gray-tailed voles in a laboratory colony are weaned when they are 15-17 g). Females were considered sexually mature when they weighed 30 g and in reproductive condition if they were lactating, pregnant, or had widely parted pubic symphyses. Testes of males are relatively small and cannot be measured externally, so males were considered reproductive if their body mass was $\geq$30 g (Wolff et al . 1994). Recruitment was measured by the number of recruits captured in an enclosure per adult female captured in the same enclosure 4 weeks (two trap periods) earlier. The time lag allowed recruits to reach trappable size.

I assigned pups to a litter if the two animals under comparison were located within 3 trap stations or in the same patch, and weighed within 3 g of each other. Litters were not assigned if other litters were within two trap stations and seemed to overlap the litter

under question. Mothers were assigned to litters if they were lactating the week of capture or the previous trap week and if they were using the same traps or were within the same patch as the litter. The criteria for litters were determined post-hoc and I felt it to be critical enough keep errors of admission low, but relaxed enough that at least 20% of recruits could be assigned to litters. More stringent testing via genetic analysis was not feasible.

Juvenile emigration

I documented emigration of juveniles by comparing the location of the natal site for juveniles that weighed $\leq$18 g to their location at time of sexual maturity. Emigrants were recruits that emigrated on their own volition and remained >2 trap stations away from their natal site or in another patch for $\geq$2 weeks and did not return to their natal site. A resident was an animal that lived at least two consecutive trap periods and was never found outside its natal site. Animals that made excursions to another patch for one week, but returned to their natal patch were still considered residents.

Data analysis

Demography

I used the Statistical Analysis System (SAS Version 6.0; SAS Institute, Inc. 1989) to conduct all analyses. Population size of animals (Minimum Number Alive; MNA) was estimated using a program written in SAS. Population growth rates were determined by taking the log of $(MNA_{i+1} / MNA_i)/2$.

Survivorship

I calculated sex-specific survival rates (ϕ_i) using derivations of the Cormack-Jolly-Seber mark-recapture methodology (Cormack 1964; Jolly 1965; Seber 1982). I adopted the modeling philosophy espoused by Burnham et al. (1987) and Lebreton et al. (1992), in which the goodness-of-fit of each model and the number of parameters for survival (ϕ_i) and capture probabilities (ρ_i) are evaluated. Good models are those that fit the data, with small numbers of parameters, and reflect what is already known about the species. The most parsimonious models were identified using Akaike's Information Criterion (AIC; Lebreton et al. 1992). I used the programs RELEASE (Burnham et al. 1987) and SURGE (Pradel and Lebreton 1991) for survival modeling. Survival rates are expressed as survival per 2 weeks.

Demographic responses to fragmentation.

A two-factor analysis-of-variance (ANOVA) was used to test for the effects of treatment and sex on the mean proportion of emigrants, the mean number of weeks past weaning when emigration occurred, and mean mass at time of emigration. All proportions were arcsine transformed before analysis. A two-factor ANOVA was used to test for the effects of treatment, emigration category (emigrant or resident) and interactions of treatment and emigration category on the proportion of animals becoming reproductive. A paired t-test was used to test if animals moved to patches of lower or higher density of total, same-sex or opposite-sex individuals in the 4-patch and 25-patch enclosures. Because of the limited number of emigrants in the 4-patch enclosures, emigration data were obtained from voles in eight additional 4-patch enclosures (R. Davis-Born, unpublished). A chi-squared analysis was used to test if the choice of patches made by the animals was significantly different from random, if emigration was dependent on the presence of opposite-sex or same-sex relatives and if sex ratios were biased in each treatment. A Fisher's exact test was used to test if sexual maturity was associated with the presence of an opposite-sex relative. A repeated-measures ANOVA (RMANOVA) was used to test for the effects of time, treatment and time by treatment interactions on population size, population density, population growth rates, and the number of recruits per adult female (any female $\geq$30 g) from 4 weeks prior. Wilk's Lambda was the test statistic evaluated in all RMANOVA analysis.

RESULTS

Demography

I caught 635 voles 5,008 times between 6 June and 27 September, 1995. The sex ratio was not biased for any treatment (all $\chi^2 < 1.37$, $P > .24$). The mean maximum population sizes ranged from 26 (SE 2.5) animals in the single patch to 39 (SE 3.4) in the control enclosure. Population size differed significantly over time ($F_{7,6} = 4.24$; $P < .05$; Fig. 2a), but not among treatments ($F_{3,12} = 0.24$, $P = .89$) and no week by treatment interactions occurred ($F_{21,8} = 17.78$; $P > .19$).

Mean peak density estimates, based on the amount of habitat available in each enclosure (control was 0.185 ha and all other treatments were 0.0625 ha) were 181 animals/ha in control, 424 animals/ha in the single-patch, 420 animals/ha in 25-patch and 416 animals/ha in 4-patch enclosures (Fig. 2b). Density did not differ among treatments ($F_{3,12} = 2.90$, $P = .08$) or time ($F_{7,6} = 2.94$; $P = .10$) and no week by treatment interactions occurred ($F_{21,18} = 1.22$; $P = .33$). Population growth rates peaked 20 June - 5 July with production of the first litters, but were relatively stable after that date (Fig. 3). Population growth rates differed over time ($F_{8,5} = 6.54$; $P = .03$), but not among treatments ($F_{3,12} = 1.56$, $P = .25$) and no week by treatment interactions occurred ($F_{24,15} = 1.29$; $P = .32$). The highest proportion of captured voles that were recruits occurred in two peaks: 6 June for all but the control, and 1 August for all but the 4-patch enclosures (Fig. 3). The

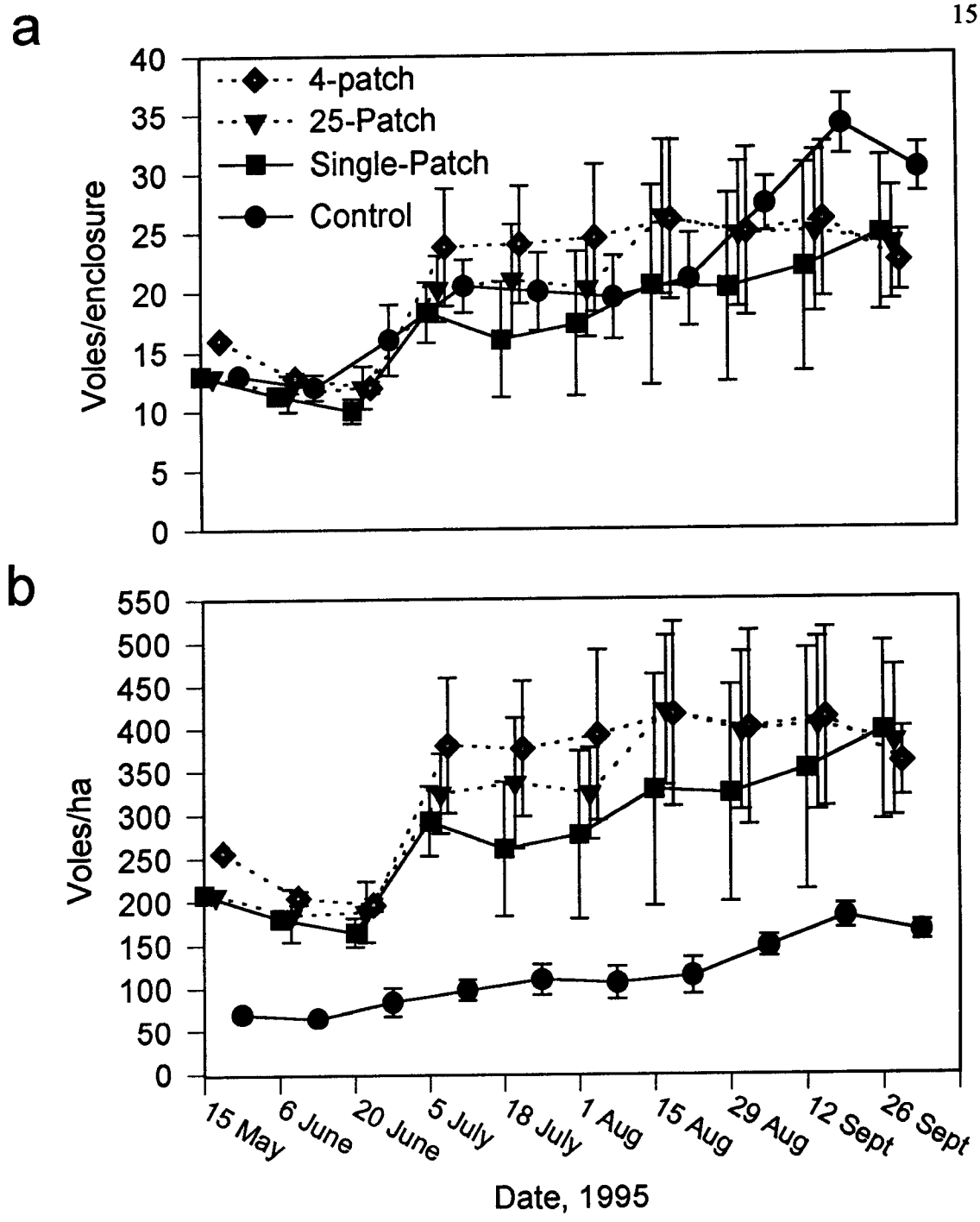

Figure 2. Mean (± SE) population size (a) and density (b) of gray-tailed voles in control, single- patch, 25-patch and 4-patch enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995. Population density refers to number of animals per total area of alfalfa habitat.

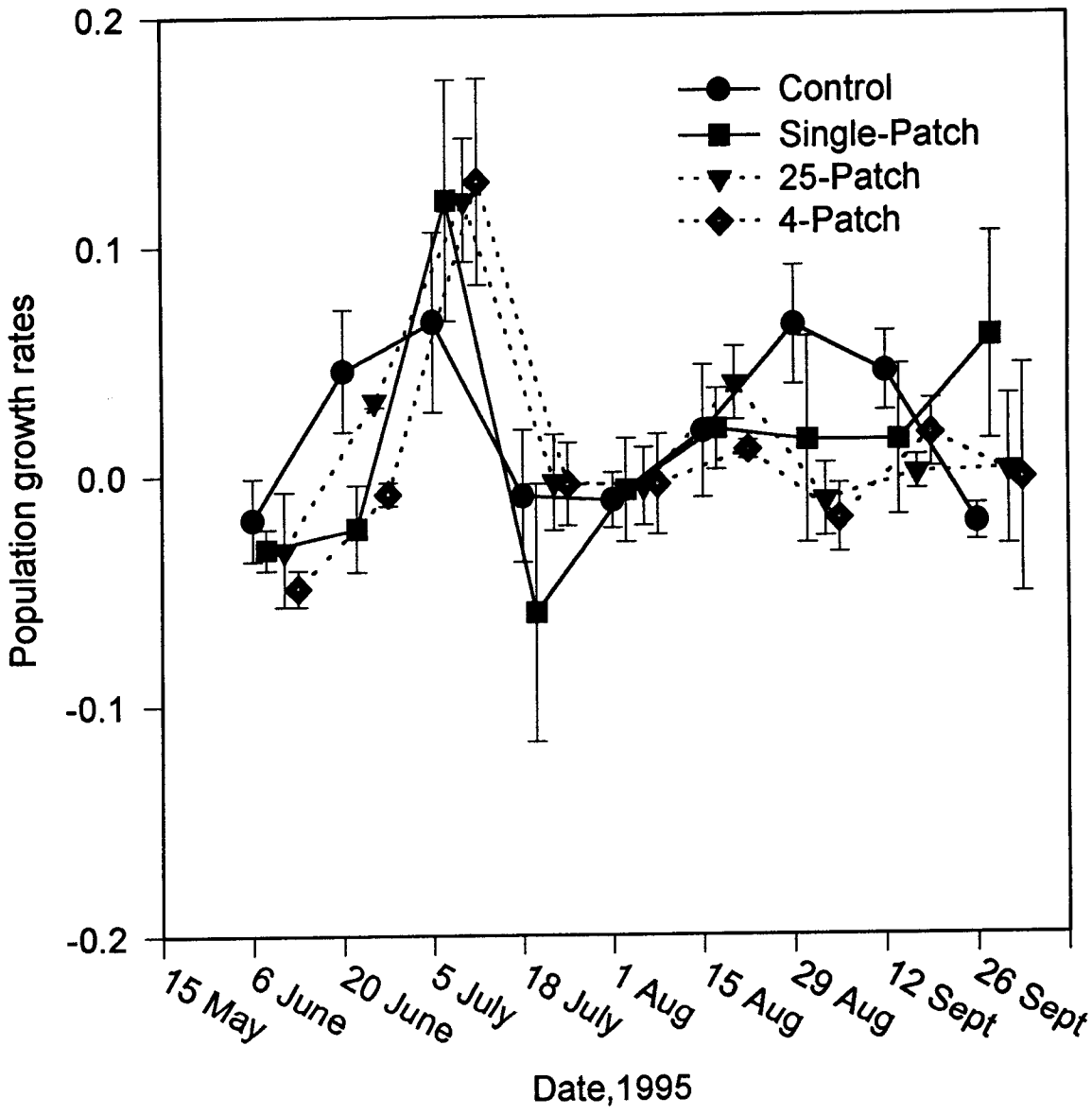

Figure 3. Mean (± SE) population growth rates of gray-tailed vole populations in control, single-patch, 25-patch and 4-patch enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

mean number of recruits/adult female did not differ among treatments ($F_{3,12} = 0.46$, P = .71; Table 1) or time ($F_{5,8} = 2.13$; P = .16) and no week by treatment interaction occurred ($F_{15,22} = 1.05$; P = .44).

Survival

Survival rates (ϕ) differed by gender, were partially time dependent for males but not for females, and in most cases differed among treatments (Fig. 4). Capture probabilities (ρ) for both genders were constant for all trap periods (ρ_c). In the most parsimonious model (AIC = 129) out of the 21 models tried, male survivorship in the control enclosures did not differ over time; males in the single-patch enclosure had low survivorship in August as a result of predation and trap mortality; males in the 4-patch had extremely low survivorship in the last four 2-week intervals in comparison to the first four intervals; males in the 25-patch enclosures had higher survivorship in the last four 2-week intervals than the first four intervals. The most parsimonious model for females (AIC = 278) out of the 18 models tried, showed a difference between survivorship in the 4-patch enclosure and the other three treatments. The longevity of animals did not differ significantly among treatments or treatment by emigration category interaction, but was significantly affected by emigration category (Table 1). Longevity was shorter for residents than for emigrants except in the single-patch enclosures where the reverse was true.

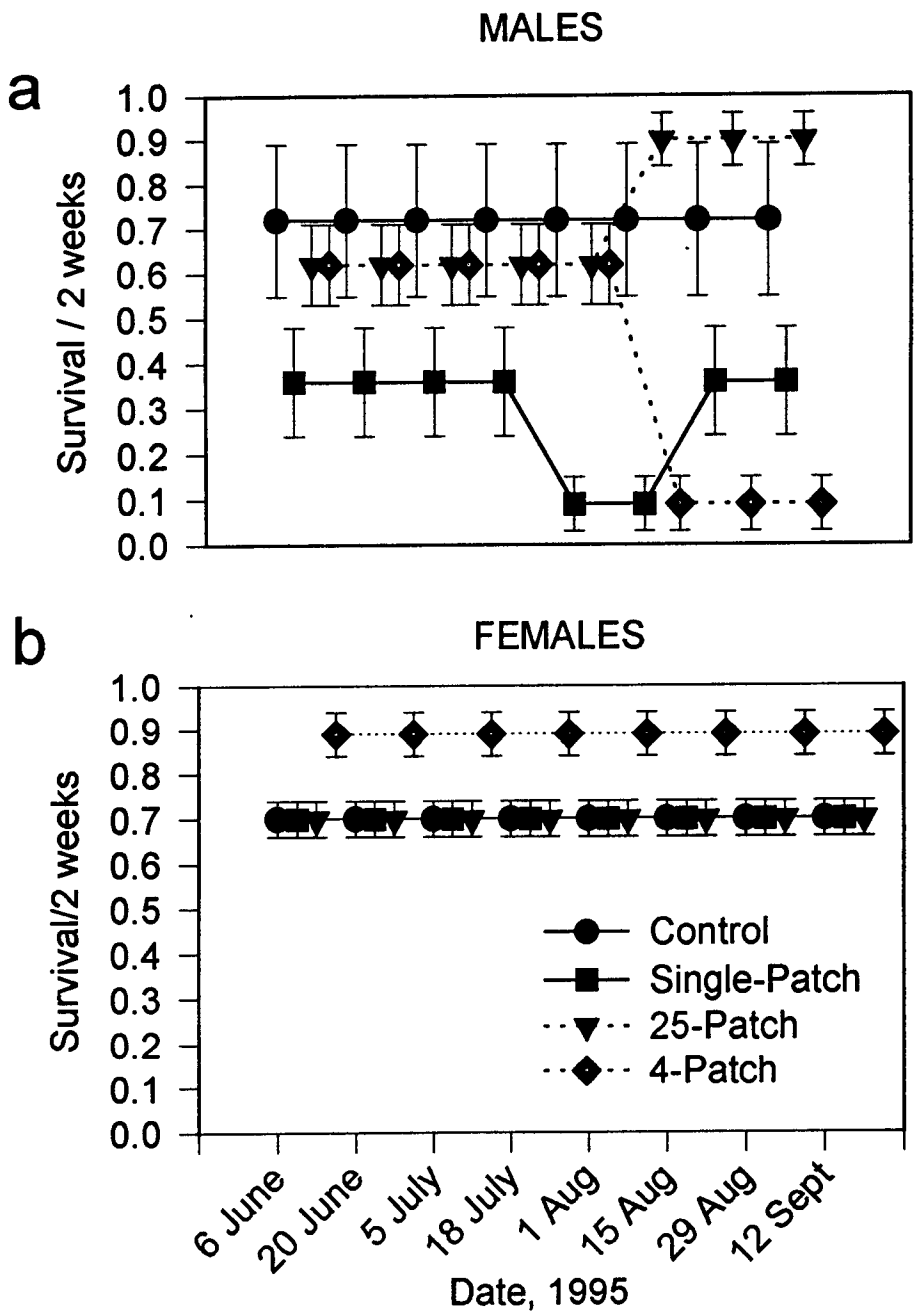

Figure 4. Mean (± SE) survivorship over time of gray-tailed voles in control, single-patch, 25-patch and 4-patch enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

Table 1. Demographic parameters of gray-tailed voles in control, single-patch, 25-patch and 4-patch enclosures at Hyslop Agronomy Farm, Benton County, Oregon, during summer, 1995. Mean (± SE).

Demographic Parameter	Control	Single-Patch	25-Patch	4-Patch	ANOVA	P
N ≥ 4 weeks[a]	69	50	53	59		
N ≥ 6 weeks	49	43	48	51		
Recruits per female	1.16 (0.23)	0.88 (0.31)	0.81(0.41)	0.65 (0.35)	Trt.[b]	$F_{3,12}$ = 1.75; P = .21
					Time	$F_{5,8}$ = 3.24; P = .07
					Trt. * time	$F_{15,22}$ = 0.72; P = .74
Longevity (weeks)						
					Trt.	$F_{3,21}$ = 2.25; P = .11
Emigrants	8.8 (1.00)	8.4 (0.96)	9.1 (0.60)	10.4 (0.18)	Emg/Res.[c]	$F_{1,21}$ = 4.04; P = .05
Residents	6.5 (0.75)	9.6 (1.48)	6.2 (1.03)	8.8 (0.32)	Trt.*Emg./Res.	$F_{3,21}$ = 1.99; P = .15
Number of weeks past weaning when individuals first emigrate						
					Trt.	$F_{3,20}$ = 4.37; P = .01
Males	2.8 (0.37)	4.3 (0.72)	3.5 (0.48)	4.3 (1.44)		
					Sex	$F_{1,20}$ = 0.20; P = .67
Females	2.7 (0.40)	4.8 (0.97)	2.7 (0.26)	4.3 (0.55)		
					Trt.* Sex	$F_{3,20}$ = 0.23; P = .88

Table 1, Continued

Mean mass at time of emigration (grams) [d]						
					Trt.	$F_{3,20} = 1.73$; $P = .19$
Males	26.4 (1.90)	30.5 (5.60)[1]	28.7 (2.00)[1]	25.3 (5.20)	Sex	$F_{1,20} = 2.96$; $P = .09$
Females	24.8 (2.95)	26.1 (1.71)[1]	27.1 (1.05)[1]	29.7 (1.03)	Trt*Sex	$F_{3,20} = 0.45$; $P = .72$
Proportion of animals emigrating						
					Trt.	$F_{3,24} = 7.09$; $P = .001$
Male	0.67 (0.07)	0.35 (0.13)	0.89 (0.06)	0.23 (0.10)	Sex	$F_{1,24} = 0.15$; $P = .71$
Female	0.50 (0.12)	0.64 (0.16)	0.68 (0.07)	0.25 (0.10)	Trt. * Sex	$F_{3,24} = 2.84$; $P = .06$
Number becoming reproductive (%)						
Male					Trt.	$F_{3,16} = 0.48$; $P = .70$
Emigrant	17/19 (90)	5/7 (71)	19/20 (95)	3/3 (100)	Emg./Res.	$F_{1,16} = 0.02$; $P = .90$
Resident	6/7 (86)	9/11 (82)	4/4 (100)	21/22 (95)	Trt.*Emg./Res	$F_{3,16} = 0.16$; $P = .92$

Table 1, Continued

Female					Trt.	$F_{3,17} = 0.49$; P = .69
Emigrant	11/14 (79)	8/14 (57)	9/19 (47)	7/10 (70)	Emg./Res.	$F_{1,17} = 1.13$; P = .30
Resident	6/9 (67)	9/11 (82)	3/5 (60)	14/16 (88)	Trt* Emg./Res.	$F_{3,17} = 0.41$; P = .75
Time to sexual maturity from weaning date (weeks)						
Male					Trt.	$F_{3,16} = 0.73$; P = .54
Emigrant	4.5 (0.90)	4.8 (0.77)	4.6 (0.48)	6.0 (0)	Emg./Res.	$F_{1,16} = 0.80$; P = .39
Resident	5.1 (0.60)	6 (0.80)	3.3 (0.40)	5.1 (0.87)	Trt.*Emg./Res.	$F_{3,23} = 1.70$; P = .21
Female					Trt.	$F_{3,16} = 2.17$; P = .13
Emigrant	6.1 (1.60)	5.9 (1.00)	5.7 (1.23)	8 (1.46)	Emg./Res.	$F_{1,16} = 0.27$; P = .61
Resident	5.7 (1.70)	6.6 (1.60)	6 (1.60)	6.8 (1.30)	Trt.*Emg./Res.	$F_{3,23} = 1.42$; P = .27

[a] $N \geq 4$ weeks denotes number of juveniles that lived more than 4 weeks after first capture, $N \geq 6$ denotes number of juveniles that lived more than 6 weeks after first capture

[b] Trt. = Treatment; [c] Emg./Res. = Emigrants versus Residents

[d] Matched numbers denote a significant difference ($p < .05$) under a multiple range analysis

Juvenile emigration and recruitment

A total of 303 recruits that weighed ≤ 18 g when first captured were caught in the 16 enclosures during the study. Seventy-eight percent (231/303) of recruits lived ≥ 4 weeks past weaning, long enough to emigrate, and were used in the emigration analysis. The number of weeks past weaning before an animal emigrated from its natal site differed among treatments (Table 1). The length of time before emigration was longer for animals in the single-patch and the 4-patch enclosures than for animals in the control and the 25-patch enclosures. The number of weeks past weaning before an animal emigrated and the mass at which an animal first emigrated, did not show a gender or gender by treatment interaction effect (Table 1). The proportion of voles emigrating differed significantly among treatments (Table 1), but not by gender or gender by treatment interaction. A greater proportion of animals dispersed in the control and 25-patch enclosures than they did in single-patch and 4-patch enclosures.

A higher proportion of males changed patches in the 25-patch enclosures (89%, SE 0.06) than in the 4-patch enclosures (22%, SE 0.10; $F_{1,6} = 20.80$, $P = .004$). A significantly higher proportion of females changed patches in the 25-patch enclosures (68%, SE 0.06) than in the 4-patch enclosures (25%, SE 0.10; $F_{1,6} = 12.60$, $P = .01$). Between the genders, a higher proportion of males moved in the 25-patch enclosures than did females, but a lower proportion of males moved in the 4-patch enclosures than did females, however, neither difference was significant (All $F_{1,6} < 4.71$, $P > .07$). Thus, 12.5-m barriers lowered emigration rates for both genders, but 4-m barriers did not.

A total of 191 recruits lived ≥ 6 weeks past weaning, long enough to become reproductive (Table 1). For males, the proportion becoming reproductive did not differ significantly among treatments, by emigration category, or treatment by emigration category (Table 1). For females, the proportion becoming reproductive did not differ by treatment, emigration category, or treatment by emigration category. For males, the time to sexual maturity did not differ by treatment, emigration category, or treatment by emigration category interaction (Table 1). For females, the time to sexual maturity did not differ by treatment, emigration category or treatment by emigration category (Table 1).

Influence of vole density

Males in the 4-patch treatment tended to move to patches that contained lower densities of males, but with total and female densities that did not differ from that of the natal patch, while females moved to patches with a lower density of total, same-sex and opposite-sex individuals (Table 2; data for 4-patch treatment obtained from R. Davis-Born, unpublished). Males in the 25-patch enclosure moved to patches of lower densities of males and lower total densities, but with females densities that did not differ from that of the natal patch. Females moved to patches that did not differ from that of the natal patch with regards to density of total, same-sex and opposite-sex individuals (Table 2). The tendency to move to patches of lower density however, did not differ from expected based on the frequency distribution of low and high density patches available for either males or females in the 25-patch or in the 4-patch enclosures (All $X^2 < .51$, $P > .47$).

Table 2. The mean (±SE) total, male and female densities in natal patches and the new patch into which individuals immigrated in the 4-patch and 25-patch enclosures.

	Males		Females		Total	
Tratment/Sex	Natal patch	New patch	Natal patch	New patch	Natal patch	New patch
4-Patch						
Males (N = 14)	4.0 (0.42) [1]	2.5 (0.47) [1]	3.7 (0.55)	3.4 (0.61)	7.7 (0.91)	5.9 (1.00)
Females (N = 25)	3.9 (0.42) [2]	2.3 (0.45) [2]	4.9 (0.43) [3]	2.8 (0.30) [3]	8.8 (0.67)[4]	5.0 (0.52) [4]
25-Patch						
Males (N = 21)	1.2 (0.20) [5]	0.6 (0.20) [5]	1.0 (0.07)	0.6 (0.11)	2.2 (0.21)[6]	1.1 (0.36)[6]
Females (N = 21)	1.5 (1.4)	1.0 (0.14)	0.6 (0.17)	0.4 (0.10)	2.0 (0.51)	1.4 (0.19)

Matched numbers denote a significant difference ($P < .05$).

For residents of the 4-patch enclosures, 38 of 42 males and 33 of 40 females had patches of lower density available to them within their enclosures but did not emigrate. For residents of the 25-patch enclosures, four of five males and all 10 females had patches of lower density available to them within their enclosures but did not emigrate.

Influence of relatives

Because of the limited number of individuals that could be identified in kin groups (Table 3) the data on the effect of opposite-sex relatives was combined for all treatments in analysis. In all cases, animals that remained in residence were exposed to an unrelated member of the opposite-sex the week of, or two weeks prior to becoming sexually mature (Table 3). Emigration and sexual maturity were independent of the presence or absence of an opposite-sex relative for males or females (Table 4).

Table 3. For individuals in which kinship is known, the number of individuals emigrating or remaining in residence and the number of animals that were exposed to an opposite-sex stranger the week of or 2 weeks prior to becoming sexually mature. The number of individuals becoming sexually mature is shown in parenthesis.

	Male		Female		Number exposed to opposite-sex strangers	
	Emigrant	Resident	Emigrant	Resident	Males	Females
Control	12 (11)	3 (3)	5 (5)	4 (4)	15	9
Single-patch	5 (3)	8 (6)	7 (4)	9 (7)	13	16
4-patch	2 (2)	16 (16)	7 (6)	14 (12)	18	21
25-patch	14 (13)	4 (4)	11 (7)	4 (3)	18	15

Table 4. Number of individuals becoming reproductive and emigrating in the presence or absence of opposite-sex relatives (all treatments combined)

		Opposite sex relative present	Opposite sex relative absent	Statistic
Males				
	≥30g (Reproductive)	11	6	Fisher's 2-tail P = 1.0
	<30g (Non-reproductive)	2	0	
	Emigrants	21	12	$X^2 = 1.14$; P = .29
	Residents	19	12	
Females				
	≥30g (Reproductive)	10	12	Fisher's 2-tail P = .48
	<30g (Non-reproductive)	1	0	
	Emigrants	18	12	$X^2 = 1.99$; P = .16
	Residents	13	18	

DISCUSSION

Many studies have concluded that fragmentation has negative effects on population size and survivorship (e.g. Burkey 1989; Andrean 1994) because fragmentation increases edge effects and exposes animals to predation as they cross barriers (Wilcove 1985; Lovejoy et al. 1986; Andren 1992; Keith et al. 1993). I found no difference in population size among treatments and crossing barriers seemed to have no negative effect on survival. Despite the high proportion of emigrants crossing 4-m barriers of bare ground, the survival of males and females in 25-patch enclosures was higher or equal to the survival of males and females in a continuous single-patch of equal area. The lowest survival rate was for males in the 4-patch enclosure, which also had the lowest emigration rate. Two factors could have masked any differences in survival among treatments in my study. First, because patches were large and densities were low, animals could have remained within the core of the patch and thus avoided edge effects. Two, I believe predation was not a factor because few mammalian or avian predators were seen at the study site and the tall alfalfa provided adequate cover from avian predators. Other studies on *Microtus* have shown individuals may be attracted to edges for the food quality, and that the food quality outweighs the risk of living on the edge (Bowers et al. 1996). Because of a low predation risk within the alfalfa, population size and survivorship of gray-tailed voles did not decrease as a consequence of living in a patchy environment.

The growth rate of a population is dependent in part on the emigration of individuals which allows gene flow (Gaines and McClenaghan 1980, Barton 1992), and averts the

negative consequences of inbreeding and reproductive suppression (Ballou and Ralls 1982; Ralls et al. 1986; Pusey 1987; Wolff 1992). I found no difference in population growth rates among treatments despite large differences in the proportion of individuals emigrating. In the 4-patch enclosures the majority of the animals remained in residence, while in all other treatments the majority of animals emigrated. However, for all treatments, the animals that remained in residence either shared a patch with an unrelated member of the opposite-sex, or were living in a continuous environments where several unrelated members of the opposite-sex overlapped their home ranges. The exposure to unrelated individuals could explain the high levels of sexual maturity despite animals remaining in residence and as a consequence, why there were no differences in population growth rates among treatments.

Isolation of patches reduces emigration in mammals (Beier 1993; Diffendorfer 1995, Lacy and Lindenmeyer 1995; Wolff et al. MS) and birds (Lovejoy et al. 1986). In my experiment, I found 12.5-m barriers severely restricted emigration of gray-tailed voles and 4-m barriers did not. This result is in agreement with the prediction that as barrier width increases the proportion of small mammals emigrating will decrease (Andreassen in press). In contrast to my study, Wolff et al. (MS) found 4-m barriers reduced emigration rates of gray-tailed voles to <20% for both sexes, however vole population sizes averaged >100 animals/enclosure and all patches were occupied; my population sizes remained between 12 and 40 animals/enclosure and several patches remained empty at any time. Thus, Wolff et al.'s animals may have been inhibited from emigration because the patches surrounding

them had high densities of strangers (social fences; Hestbeck 1982; habitat saturation; Jones et al. 1988), while my animals still had empty patches available to them. However, the effect of barrier width can not be separated from patch size in my study, and these results should be interpreted with caution.

The three hypotheses for explaining the proximate and ultimate causation of juvenile emigration has undergone considerable discussion (Waser 1985; Pusey 1987; Moore and Ali 1984; Wolff 1993). However, little empirical testing has been done (but see Wolff 1992, and references in Wolff 1994). In unmanipulated environments, small mammals display a negative relationship between emigration and population density (Jones et al. 1988; Wolff et al. 1988; Sandell 1991, Wolff 1992), which is contrary to the predictions of the resource competition hypothesis. In this study, emigration varied by gender, patch size and barrier width. Males in the 25-patch (4-m barriers) and females in the 4-patch (12.5-m barriers) treatments moved to patches of lower total density, but males in the 25-patch and females in the 4-patch treatment did not move to patches of lower total density. However, movements to these patches of lower density did not differ from random based on the frequency distribution of patches of various densities. I found no indication that food or breeding space was limited. In the previous 3-years of study using these enclosures, densities frequently exceeded 100 voles/enclosure and in some cases > 2,000 voles/ha (Schauber et al. in press; Wolff et al. MS). Thus, it is unlikely that resource competition played a significant role in juvenile emigration with densities of 400 voles/ha in my experiment.

The hypothesis that sex-biased dispersal in mammals results from mate competition as proposed by Dobson (1982) has been supported by some studies (*e.g. Peromyscus californicus*, Ribble 1992), but not in others (*P. leucopus*, Wolff et al. 1988; Wolff 1992; Jacquot and Vessey 1995; and see Wolff 1993, 1994 for reviews). In this study, emigration was from patches of higher same-sex density to patches of lower same-sex density in all cases except for females in the 25-patch enclosures, where there were no differences between the natal patch and the new patch. However, movements to patches of lower same-sex density did not differ from random based on the frequency distribution of patches of various densities, thus I was unable to support the mate-competition hypothesis.

The inbreeding avoidance hypothesis predicts that individuals should emigrate to areas away from opposite-sex relatives and if they do not emigrate, they will undergo reproductive suppression. Support for the presence of relatives as a cause of sex-biased emigration has some experimental support (*Peromyscus*, Wolff 1992; *Microtus*, Bollinger et al. 1993). Juveniles exposed to relatives exhibit higher emigration rates than those exposed only to strangers (Wolff 1992; Bollinger et al. 1993). In my study, male and female emigration was independent of the presence of opposite-sex relatives. Additionally, I found that male and female sexual maturity was independent of the presence of opposite-sex relatives and that sexual maturation rates were quite high even in patches where little or no emigration had taken place (see above). However, sample sizes were limited and may not have provided an adequate test of this hypothesis. Thus, I had

insufficient data to reject the inbreeding avoidance hypothesis or the model presented by Wolff (1994).

Because of small samples sizes, I may not have provided an adequate test of the resource competition and mate competition hypotheses. Furthermore, my definitions of relatives may contain enough admission errors to mask the effects predicted by the inbreeding avoidance hypothesis. I can not reject nor support any of the hypotheses for juvenile emigration with my data.

CONCLUSIONS

The survivorship and population sizes of gray-tailed voles were not affected by isolation and a 70% reduction of habitat. My study could have been too short-term to observe treatment differences. Alternatively, the gray-tailed vole may be evolutionally adapted to living in patchy environments, and thus exhibited no differences in survivorship and population size. Further studies on the effects of habitat fragmentation should be conducted long-term or during harsh (e.g. winter) conditions to determine how isolated populations respond to annual bottlenecks.

The 4-patch treatment with 12.5-m barriers supported the prediction that barriers can severely restrict emigration, however, the 25-patch treatment with 4-m barrier did not support this prediction. Previous studies had found 4-m barriers inhibited emigration of gray-tailed voles (Wolff et al. MS), but their densities were nearly four times higher the number found in my study. Different social factors, such as territoriality and "social fences," could have created the disparity in vole emigration responses found between these two studies. Further studies should consider how overall enclosure density influences juvenile emigration.

The 4-patch treatment did not support the prediction that isolation has negative demographic consequences. The 4-patch animals became isolated, but I detected no differences among treatments in growth rates, recruits per adult female ratios, time to sexual maturity, proportion of animals becoming sexually mature or timing of sexual maturity. However, if the study had continued for several generations, I speculate that the

animals in the 4-patch treatment could have become severely inbred (Wauters et al. 1994) because of the extremely low emigration rates ('genetic clumping'; Bjornstad in press), resulting in lower population growth rates and population sizes in comparison to all other treatments.

None of the hypotheses explaining juvenile emigration can be rejected by my data. Emigration patterns were independent of patch density and the presence of opposite-sex individuals. However, I was limited to small population sizes and I propose that future research should explore the role these hypotheses play in patchy environments with larger enclosures and variable densities.

BIBLIOGRAPHY

Adler, G. H. 1994. Tropical forest fragmentation and isolation promote asynchrony among populations of a frugivorous rodent. Journal of Animal Ecology **63**: 903-911.

Anderson, P. K. 1989. Dispersal in rodents: a resident fitness hypothesis. Special Publication 9, American Society of Mammalogist, Allen Press, Manhattan, Kansas, USA.

Andreassen, H. P., R. A. Ims, and N.C. Steinseth. 1996. Discontinuous habitat corridors: effects on male root vole movements. Journal of Applied Ecology in press.

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

Andren, H. 1992. Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. Ecology **73**:794-804.

Arnold, G. W., D. E. Stephens, J. R. Weeldenburg, and E. A. Smith. 1993. Influences of remnant size, spacing pattern and connectivity on population boundaries and demography in euros Macropus robustus living in a fragmented landscape. Biological Conservation **64**:219-230.

Ballou, J. and K. Ralls. 1982. Inbreeding and juvenile mortality in small populations of ungulates; a detailed analysis. Biological Conservation **24**:239-272.

Barton, N. H. 1992. The genetic consequences of dispersal. Pages 38-59 in N. C. Stenseth, and W. Z. Lidicker, Jr. editors. Animal dispersal; small mammals as a model. Chapman & Hall, London, England.

Batzli, G. O., L. L. Getz, and S. S. Hurley. 1977. Suppression of growth and reproduction of microtine rodents by social factors. Journal of Mammalogy **58**: 583-591.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7: 94-108.

Bjornstad, O. N., H. P. Andreassen, and R. A. Ims. 1996. Effects of habitat patchiness and connectivity on the spatial ecology of the root vole (Microtus oeconomus). Ecology in review.

Blackstock, T. H., J. P. Stevens, E. A. Howe, and D. P. Stevens. 1995. Changes in the extent and fragmentation of heathland and other semi-natural habitats between 1920-22 and 1987-88 in the Lllyn peninsula, Wales, UK. Biological Conservation **72**:33-44.

Bollinger, E. K., S. J. Harper, and G. W. Barrett. 1993. Inbreeding avoidance increase dispersal movements of the meadow vole. Ecology **74**:1153-1156.

Boonstra, R. 1989. Life history variation in maturation in fluctuating meadow vole populations (Microtus pennsylvanicus) Oikos **54**:265-274.

Bowers, M. A., K. Gregario, C. J. Brame, S. F. Matter, J. L. Dooley, Jr. 1996. Use of space and habitats by meadow voles at the home range, patch and landscape scales. Oecologia **105**:107-115.

Boyd, S. K., and A. R. Balustein 1985. Familiarity and inbreeding avoidance in the gray-tailed vole (Microtus canicaudus). Journal of Mammalogy **66**:348-352.

Brandt, C. A. 1982. Social factors in immigration and emigration. Pages 96-141 in N.C. Stenseth and W. Z. Lidicker, Jr. editors. Animal dispersal; small mammals as a model. Chapamn & Hall, London, England.

Burkey, T. V. 1989. Extinction in nature reserves: the effect of fragmentation and the importance of migration between reserve fragments. Oikos **55**:75-81.

Burnham, K.P., D. R. Andreson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis method for fish survival experiments based on release-recapture. American Fisheries Society Monograph **5**.

Charnov, E.L., and J. P. Finerty. 1980. Vole population cycles: a case for kin selection? Oecologia **45**:1-2.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika **51**:429-238.

Cummings, J. R. and S. H. Vessey. 1994. Agricultural influences on movement patterns of white-footed mice (Peromyscus leucopus). American Midland Naturalist **132**:209-218.

Diffendorfer, J. E., M.S. Gaines, and R. D. Holt. 1995. Habitat fragmentation and movement of three small mammals (Sigmon, Mictrotus, and Peromyscus). Ecology **76**:827-839.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. Animal Behavior **30**:1183-1192.

Edge, W. D., J. O. Wolff, and R. L. Carey. 1995. Density-dependent responses of gray-tailed voles to mowing. Journal of Wildlife Management **59**:245-251.

Fahrig, L. and G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology **66**:1762-1768.

Fahrig, L., and G.Merriam. 1994. Conservation of fragmented populations. Conservation Biology **8**:50-59.

Foster, J., and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal. Ecology **72**:1358-1373.

Gaines, M. S., and L. R. McClenaghan, Jr. 1980. Dispersal in small mammals. Annual Review of Ecological Systems **11**:163-196.

Goodman, D. 1987. The demography of chance extinction. Pages 11-34 in M.E. Soulé editor. Viable population for conservation. Cambridge University Press, London, England

Greenwood, P. J. 1980. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior **28**:1140-1162.

Harris, L. D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, Illinois, USA.

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

Jacquot, J. J., and S. H. Vessey. 1995. Influence of the natal environment on dispersal of white-footed mice. Behavior Ecology and Sociobiology **37**:407-412.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika **52**:225-247.

Jones, W. T., P. M. Waser, L. F. Elliott, N. E. Link, and B. B. Bush. 1988. Philopatry, dispersal, and habitat saturation in the banner-tailed kangaroo rat Dipodomys spectabilis. Ecology **69**:1466-1473.

Keith, L. B., S. E. M. Bloomer, and T. Willebrand. 1993. Dynamics of a snowshoe hare population in fragmented habitat. Canadian Journal of Zoology **71**: 1385-1392.

Lacy, R. C., and D. B. Lindenmeyer. 1995. A simulation study of the impacts of population subdivision on the mountain brushtail possum Trichosurus caninus ogilby (Phalangeridae: marsupialia) in south-eastern Australia. II. Loss of genetic variation within and between subpopulations. Biological Conservation **73**: 131-142.

Lamberson, R. H., R. McKelvey, B. R. Noon, and C. Voss. 1992. A dynamic analysis of Northern spotted owl viability in a fragmented landscape. Conservation Biology **6**:505-512.

Lambin, X. 1994. Natal philopatry, competition for resources, and inbreeding avoidance in Townsend's voles (Microtus townsendii). Ecology **75**:224-235.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Andreson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecology Monographs **62**:67-118.

Lens, L., and A. A. Dhondt. 1994. Effects of habitat fragmentation on the timing of Crested Tit Parus Cristatus natal dispersal. Ibis. **136**:147-152.

Lovejoy, T. E., R. O. Bierregaard, Jr., A. B. Rylands, J. R. Malcolm, C.E. Quintela, L. H. Harper, K. S. Brown, Jr., A. H. Powell, B. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on amazon forest fragments. Pages 257- 285 in M.E. Soulé editor. Conservation Biology; the science of scarcity and diversity. Sinauer Assoc. Inc. Sunderland, Massachusetts, USA.

McGuire, B. and L. L. Getz. 1991. Response of young prairie voles (Microtus ochrogaster) to nonresident males; implications for population regulation. Canadian Journal of Zoology **69**:1348-1355.

Moore, J., and R. Ali. 1984. Are dispersal and inbreeding avoidance related? Animal Behavior 32:94-112.

Pradel, R. J. and Lebreton, J. D. 1991. User's manuel for program SURGE version 4.1.Mimeographed Document, C.E.P.E./C.N.R.S. BP 5051, 34033 Montpellier-cédex, France.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology and Evolution 2:295-299.

Ralls, K., P. H. Harvey, and A. M. Lyles. 1986. Inbreeding in natural populations of birds and mammals. Pages 35-56 in M.E. Soulé editor. Conservation Biology; the science of scarcity and diversity. Sinauer Assoc. Inc. Sunderland, Massachusetts, USA.

Ribble, D. O. 1992. Dispersal in a monogamous rodent, Peromyscus californicus. Ecology **73**:859-866.

Sandell, M., J. Argrell, S. Erlinge, and J. Nelson. 1991. Adult philopatry and dispersal in the field vole Microtus agrestis. Oecologia **86**:153-158.

SAS Institute Inc. 1989. SAS/STAT user's guide. Version 6. SAS Institute, Inc. Cary, Indiana, USA.

Schauber, E. M., W. D. Edge, and J. O. Wolff. Insecticide effects on small mammals.; influence of vegetation structure and diet. Ecological Applications in press.

Seber, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd edition. MacMillan Publishing Company, New York, New York, USA.

Simberloff, D. 1995. Habitat fragmentation and population extinction of birds. Ibis **137**: S105-S111.

Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. Conservation Biology **1**:63-71.

Simberloff, D., J. A. Farr, J. Cox., and D. W. Mehlman. 1992. Movement corridors: conservation bargins or poor investments. Conservation Biology **6**:493-504.

Skole, D. and Tucker, C. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. Science **260**:1905-1910.

Soulé, M.E. editor. 1986. Conservation Biology; the science of scarcity and diversity. Sinauer Assoc. Inc. Sunderland, Massachusetts, USA.

Vert, B. J., and L. Carraway. 1987. Microtus canicaudus. Mammalian Species **267**:1-4

Waser, P. M. 1985. Does competition drive dispersal? Ecology **66**:1170-1175.

Wauters, L.A., Y. Hutchinson, D. T. Parkin and A. A. Dhondt. 1994. The effects of habitat fragmentation on demography and on the loss of genetic variation in the red squirrel. Proceedings of the Royal Society of London; Series B. **255**: 107-111.

Wilcove, D.S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. Ecology **85**: 1211-1214.

Wilcove, D.S., C. H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. p237-256 in M.E. Soulé editor. Conservation Biology; the science of scarcity and diversity. Sinauer Associates Inc. Sunderland, Massachussetts, USA

Wilcox, B. A., and Murphy, D. D. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist **125**:879-887.

Wilson, E.O. 1986. Editor. Biodiversity. National Academy Press, Washington, D.C., USA.

Wolff, J. O. 1992. Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. Nature **359**: 409-410.

Wolff, J. O. 1993. What is the role of adults in mammalian juvenile dispersal? Oikos **68**:173-176.

Wolff, J. O. 1994. More on juvenile dispersal in mammals. Oikos **71**:349-352.

Wolff, J. O. 1995. Friends and stangers in vole population cycles. OIKOS **73**:411-414.

Wolff, J. O., W. D. Edge, and R. Bentley. 1994. Reproductive and behavioral biology of the gray-tailed vole. Journal of Mammalogy **75**:873-879.

Wolff, J. O., K. I. Lundy, and R. Baccus. 1988. Dispersal, inbreeding avoidance, and reproductive success in white-footed mice. Animal Behavior **36**:456-465.

Wolff, J. O., E. M. Schauber, and W. D. Edge. In review. The effects of habitat fragmentation on the demography and social structure of the gray-tailed vole. Conservation Biology.