

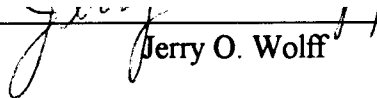
AN ABSTRACT OF THE THESIS OF

Renee Davis-Born for the degree of Master of Science in Wildlife Science presented on April 8, 1997.

Title: Influence of Movement Corridors on Enclosed Populations of the Gray-Tailed Vole: Do Immigrants Affect Reproduction and Dispersal of Residents in a Patchy Environment?

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Abstract approved: _____

 Jerry O. Wolff

I monitored demography, movement, and reproductive behavior of gray-tailed voles, *Microtus canicaudus*, in experimental habitat patches with and without corridors. I tested the hypotheses that reproductive rate, juvenile recruitment, and population size and growth rate would be affected negatively by immigrants that were introduced to resident groups (+ male and + female treatments). I hypothesized that “strangers” would commit infanticide thus decreasing juvenile recruitment. Second, I determined if movement corridors facilitated dispersal among habitat patches, thus potentially increasing infanticide, but decreasing reproductive inhibition of opposite-sex relatives by allowing them to separate (corridor treatment). Experiments were conducted in 12 0.2 ha enclosures planted with alfalfa that was fragmented into four patches (each 156 m²) separated by 12.5 m of bare ground. Introduction of unfamiliar conspecifics did not adversely affect reproductive rate, juvenile recruitment, population size, density, or growth rate. Corridors facilitated dispersal movements with males moving more than did females; however, corridors did not result in an even distribution of animals in the four patches. Unconnected habitat patches resulted in female- rather than the typical male-biased dispersal and females dispersed at lower body mass than in controls. Males that did not disperse from their natal patch exhibited a slight delay in sexual maturation. I

conclude that movement is deterred in patchy environments, enhanced with corridors, and differentially affects males and females. Behavioral factors that affect an individual's dispersal or reproductive pattern should be considered in landscape planning.

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**Influence of Movement Corridors on Enclosed Populations of the Gray-Tailed Vole:
Do Immigrants Affect Reproduction and Dispersal of Residents in a Patchy Environment?**

by

Renee Davis-Born

A THESIS

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degree of

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Master of Science thesis of Renee Davis-Born presented on April 8, 1997

APPROVED:

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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.

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Renee Davis-Born, Author

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INFLUENCE OF MOVEMENT CORRIDORS ON ENCLOSED POPULATIONS OF THE GRAY-TAILED VOLE: DO IMMIGRANTS AFFECT REPRODUCTION AND DISPERSAL OF RESIDENTS IN A PATCHY ENVIRONMENT?

INTRODUCTION

Habitat fragmentation may affect the social systems of small mammals by reducing home range size and dispersal (Yahner 1992; Diffendorfer et al. 1995; Wolff et al. *in press*). Reduced dispersal may result in the formation of familiar groups composed of kin (Kawata 1990; Pugh and Tamarin 1990; Lambin and Krebs 1991). The occurrence of kin groups should select for lower levels of aggression and infanticide, which increase the inclusive fitness of individuals in the group (Wolff 1995). Infanticide may be committed by unrelated males attempting to gain reproductive access to females (vom Saal and Howard 1982; Jeppsson 1986) or by unrelated females competing for limited resources such as nesting sites (Künkele 1992; Wolff 1993*b*). Decreased incidence of infanticide among kin should result in higher survival of young in a population of familiar individuals than would be observed among unfamiliar individuals.

The benefits of living in kin groups may be counterbalanced by reproductive suppression of juveniles and/or inbreeding, which occur when individuals do not have access to unrelated, opposite-sex conspecifics with which to mate (Noss 1987; McGuire and Getz 1991; Simberloff et al. 1992; Lambin 1994*a*). Movement corridors may lessen the occurrence of reproductive suppression and inbreeding in individuals living in a fragmented, or patchy environment by facilitating movement of individuals among habitat patches (Batzli et al. 1977; Schadler 1990; Wolff 1992). Yet, immigrants may negatively

impact juvenile survival by committing infanticide for competitive reasons discussed above. Thus movement corridors may alter the behavioral responses of a species to its environment, impacting the demographic characteristics of a population both positively and negatively.

I assessed the effect of immigrants on residents by introducing strange individuals into habitat patches composed of familiar groups and analyzing demographic parameters such as juvenile recruitment, reproductive rate, and population size and growth rate. I also determined if individuals in a patchy environment used movement corridors and whether immigrating individuals affected juvenile recruitment and rate of sexual maturation of residents in a patch. I used enclosed populations of the gray-tailed vole (*Microtus canicaudus*) to test several hypotheses.

CHAPTER 1: THE EFFECTS OF IMMIGRANTS ON JUVENILE RECRUITMENT OF RESIDENTS IN A PATCHY ENVIRONMENT

A common feature of many microtine populations is that they cycle on a 3 to 5 year periodicity (Krebs and Myers 1974; Taitt and Krebs 1985). Numerous hypotheses have been proposed to explain these cycles (Lidicker 1988) including one that focuses on the formation of female kin groups and familiarity with neighbors (Charnov and Finerty 1980). The model presented by Charnov and Finerty (1980) states that at low population densities, neighbors are primarily kin who behave amicably toward one another, whereas at high densities neighbors are primarily non-kin who behave aggressively toward one another. Tests of this model have produced mixed results (Boonstra and Hogg 1988; Ylönen et al. 1990; Sera and Gaines 1994), but in general do not support the model (Kawata 1990; Pugh and Tamarin 1990; Lambin and Krebs 1991). For example, the level of relatedness and familiarity was highest at the highest and not the lowest densities in studies with Townsend's voles, *M. townsendii* (Lambin and Krebs 1991) and prairie voles, *M. ochrogaster* (Getz et al. 1993). Another contradiction to the Charnov and Finerty model proposed by Wolff (1995), states that at increased densities, dispersal rates should decrease because of a social fence of territorial individuals (Hestbeck 1982). Subsequently, kin and familiar groups are formed, thus individuals are more likely to be "friends" at high than at low densities. Isolated populations in which familiar kin groups have been formed may be negatively impacted if unfamiliar individuals invade and disrupt social structure within familiar groups (Wolff 1995). In particular, these unfamiliar, intruding individuals are often subadult females attempting to overtake an occupied territory (Wolff 1993b) and

subadult males trying to secure access to females in an unfamiliar area (Wolff and Cicirello 1991).

Females of many species of mammals actively defend territories or exclusive space that isolates them and their offspring from neighboring or potentially intruding infanticidal females (e.g., *Peromyscus* sp., Wolff and Cicirello 1991; *Microtus townsendii*, Lambin 1994b; *Clethrionomys glareolus*, Mappes et al. 1996; and see Wolff 1993b and references cited therein). During field trials, female *M. pennsylvanicus* acted aggressively towards nonresident females with which they had no previous familiarity (Yoder et al. 1996). Laboratory and field studies demonstrated that infanticide is committed by unrelated or unfamiliar females as a form of resource competition in an attempt to take over an occupied territory (Sherman 1981; Künkele 1992; Lambin and Krebs 1993; Wolff 1993b). Resource competition and the potential for infanticide by females should be greater at high densities when all nest sites and territories are occupied than at low densities when vacant space is available for colonization (Wolff and Cicirello 1991). A previous study of *M. canicaudus* determined that, at high densities, juvenile recruitment was inversely proportional to the presence of unrelated adult females competing for limited territories (Wolff and Schaubert 1996). At high densities, related female small mammals often nest and rear litters together without killing each other's pups (Madison and McShea 1987; Lambin and Krebs 1991, 1993; Wolff 1992, 1994b; Mappes et al. 1996). Communal nesting by related female house mice, *Mus musculus*, increased inclusive fitness by decreasing the incidence of conspecific infanticide by males and females (Manning et al. 1995). Therefore, the potential for female infanticide should be positively associated with density, and negatively associated with coefficient of relatedness.

Killing of unrelated offspring by strange males to acquire reproductive access to the infants' mother is well documented in mammals (Hausfater and Hrdy 1984 and references cited therein) and has been demonstrated experimentally in several species of small mammals (Webster et al. 1981; vom Saal and Howard 1982; Labov et al. 1985; Wolff and Cicirello 1989, 1991). The act of copulation, and in some cases cohabitation, suppresses infanticide in males by increasing male-female familiarity (Webster et al. 1981; Labov et al. 1985; Jeppsson 1986). Males also may be inhibited from committing infanticide on any pups within their home range or where they have copulated (Wolff and Cicirello 1989, 1991). The most significant advantage of male-female familiarity is to increase confidence of paternity which decreases chances of infanticide (see references above). A second advantage is that if males remain in residence they may provide some defense against intrusion by infanticidal males, which are dispersing into a new territory to gain access to reproductive females (Madison and McShea 1987; Getz et al. 1990; McGuire and Getz 1991). The relative importance of males being familiar with given females or a given location with respect to whether or not they will commit infanticide is not known.

If, in fact, familiarity and maintenance of kin or mating groups are important to promote nepotism and deter infanticide, fragmentation of habitats and isolation of small breeding demes can both help and hinder these relationships. For instance, many aspects of small mammal social systems, including intraspecific social interactions, are known to be affected by habitat fragmentation, which may result in reduced movements and small home ranges with considerable overlap among individuals (Yahner 1992; LaPolla and Barrett 1993; Diffendorfer et al. 1995; Wolff et al. *in press*). In response to reduction and

fragmentation of habitat, densities of gray-tailed voles, *Microtus canicaudus*, increased from approximately 400 animals/ha to over 2,000 animals/ha (Wolff and Schauber 1996; Wolff et al. *in press*). Fragmentation, which contributed to high densities of gray-tailed voles, may have additional effects on the social composition and demography of fragmented populations such as decreased juvenile recruitment and a breakdown of territoriality (Wolff and Schauber 1996). When an unfamiliar individual immigrates into a semi-isolated population, aggressive interactions among unfamiliar conspecifics may occur (Hobbs 1992; Wolff 1995). In particular, individuals may commit infanticide when entering an unfamiliar area (Sherman 1981; Wolff and Cicirello 1989).

The objective of my study was to assess the role of familiarity among individuals on juvenile recruitment and subsequent population size and growth rate in a small mammal population living in a patchy environment. I used the gray-tailed vole, a species common to the area, as the study species. Experimental vole populations were studied in three treatments, one in which I experimentally introduced strange females to established resident populations in isolated habitat patches, one in which strange males were introduced to residents in habitat patches, and a control in which individuals remained in their natal habitat patch or dispersed on their own volition. I tested the hypotheses that juvenile survival and recruitment, female reproductive rate, population growth rate, and population size would be greater in control enclosures than in treatment enclosures. I assumed intrusion by strange males and females would result in infanticide, disrupting normal reproduction by resident females.

METHODS

Study Species

The gray-tailed vole is the common, grassland, arvicoline species of the Willamette Valley, Oregon. Gray-tailed voles are similar in appearance, behavior, and ecology to other *Microtus* spp., especially closely related *M. montanus* (Verts and Carraway 1987). Breeding occurs from March through November, gestation time is 21 days, modal litter size is six, juveniles are weaned at 15–18 days, and females can start breeding when they are 18 g (about 18–20 days old). The mating system, like that of most mammals, is polygynous (Wolff et al. 1994). In the field, females have relatively small ($\bar{x} = 56 \text{ m}^2$) home ranges (Wolff et al. 1994); home ranges of males are larger than those of females and overlap those of one or more females. Like many other vole species, juvenile dispersal is male-biased (e.g., Wolff 1985; Getz et al. 1990; Lambin 1994a; Bollinger et al. 1993; Bjørnstad et al. *in review*).

Research Facilities

The study was conducted at the vole enclosure research site located at the Hyslop Agronomy Farm of Oregon State University approximately 10 km north of Corvallis, Oregon (Wolff et al. 1994, Edge et al. 1995). The experimental units consisted of eight 0.2 ha (45 x 45 m) enclosures planted with alfalfa (*Medicago sativa*). 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. A 1-m wide strip along the inside of the fence within each plot is kept bare to minimize use by small mammals.

The control and treatment enclosures contained four small isolated patches, each 12.5 x 12.5 m (156 m²; Fig. 1). Each patch was separated from adjacent patches by a 12.5-m wide barren strip to serve as a barrier of unsuitable habitat. In late April 1995, alfalfa was sprayed with a herbicide (RoundUp®), flail-mowed, and debris removed to create the habitat configuration. Matrices were maintained by herbiciding, mowing, and removal of debris. In late June, the remaining alfalfa was mowed to a height of 0.5 m to promote new growth. Four replicate enclosures were randomly assigned as controls, while two replicate enclosures were assigned to each treatment.

Experimental Procedures

Eight male and eight female voles were introduced to each enclosure on 15 May 1995; two animals of each sex were placed in each of four patches for all treatments. All animals were trapped from wild populations in Benton County, Oregon and were unfamiliar with each other. Body mass of introduced animals ranged from 11–52 g for males and 13–42 g for females. Over 90% of the introduced animals weighed > 18 g when released into the enclosures.

I experimentally tested for the effects of disrupting the social environment of small breeding demes on demographic parameters by removing residents and adding unfamiliar males and females (to simulate mortality and immigration) in the four treatment enclosures. Beginning 12 June 1995, one resident male was removed from each patch in

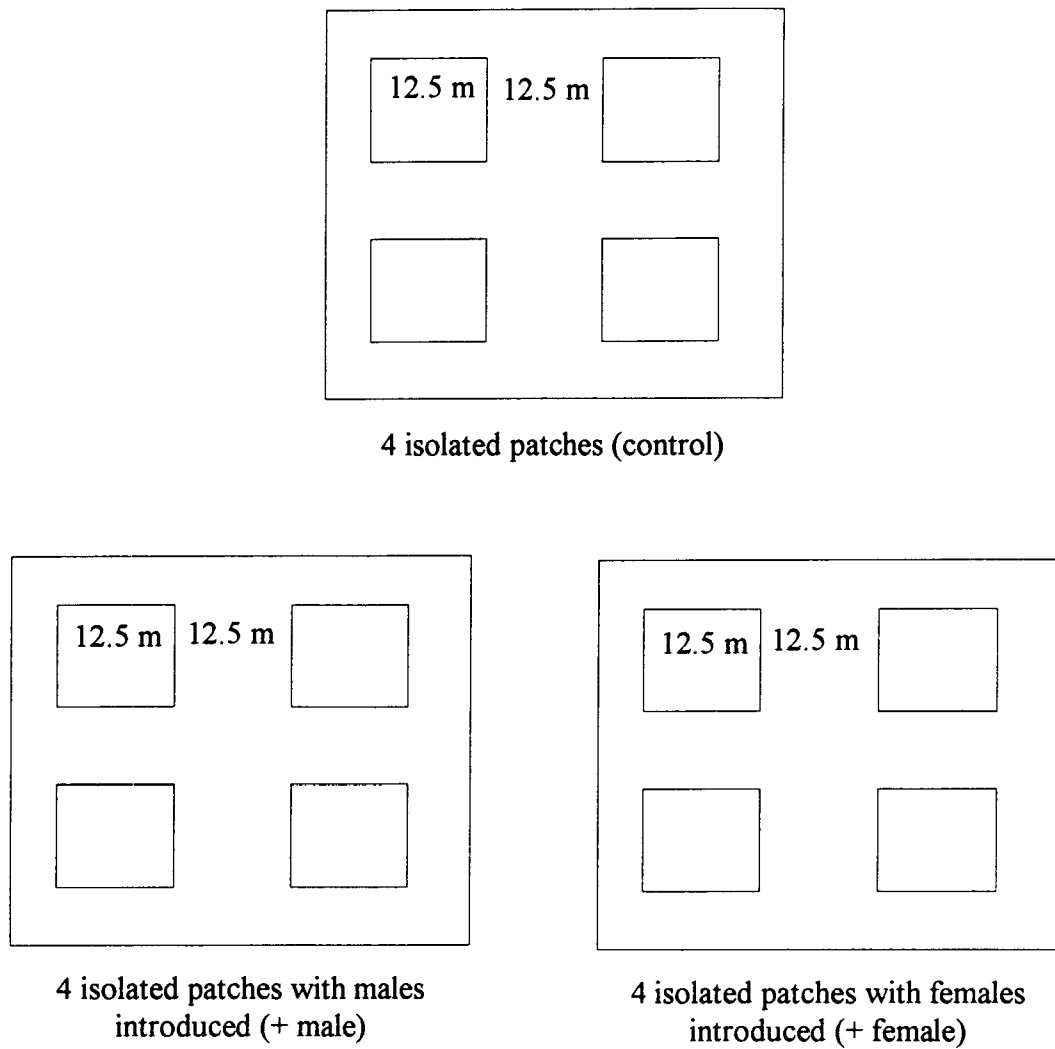


Figure 1. Habitat configurations for control, + male, and + female enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

two of the enclosures each week and one strange male was added to each patch to simulate loss of residents and immigration of strangers (+ male). Body mass of introduced males ranged from 18–49 g. A similar procedure was used in the remaining two treatment enclosures; one female was removed from each patch each week and one strange female was added. Introduced females did not exhibit signs of pregnancy: swollen abdomen, lactating nipples, or open pubic symphysis. Body mass of introduced females ranged from 18–42 g. The removal of one animal/patch/week is comparable to normal survival rates (90% survival/week) observed in these enclosures during previous studies (Edge et al. 1995, Wolff et al. *in press*).

Trapping Procedures

I established nine trap stations in each patch with 4 m between traps for a total of thirty-six trap stations in each enclosure. Two 8 x 9 x 23-cm Sherman live trap (model LFATG; H.B. Sherman Traps, Inc., Tallahassee, Florida) were placed at each station for a total of 72 traps per enclosure. Animals were trapped for four consecutive nights at 2-week intervals (trap period) from late May through September. 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 nontrapping periods. All captured animals were ear-tagged for identification and data on body mass (measured to the nearest 1 g with Pesola spring scales), sex, age, reproductive condition and trap location recorded at first capture each week; trap location was recorded at subsequent captures within the same week.

Reproduction and Recruitment

Animals were considered adults if their body mass is ≥ 30 g. Females were in reproductive condition if they are lactating, pregnant, or have widely parted pubic symphyses. Testes of male gray-tailed voles cannot be measured externally, thus males were considered to be reproductive if body mass ≥ 30 g.

Laboratory Study of Infanticide

The objective of my laboratory study was to determine if male and female gray-tailed voles commit infanticide and, if so, at what stage of pup development infanticide occurs. Adult voles were housed individually in 30.5 x 20 x 13 cm cages at the Laboratory Animal Research Center (LARC) on the Oregon State University campus. Cages were provided with a thin layer of wood shavings and cotton bedding material. Alfalfa pellets and water were provided daily *ad libitum*.

The study involved placing an adult vole with a pup and observing if infanticidal behavior occurred. I used adults of both sexes. The treatment was age of the pup at time of exposure to adult voles; treatments were 1–3, 5–6, 7–9, and 14 days of age. I used ≤ 10 replicates per treatment to minimize the number of pups exposed to potential infanticide; 22 nonreproductive adult females and 28 adult males were used. Each adult vole was used only once for experimental trials. For each trial, a pup was placed in a clean 30.5 x 30.5 x 61-cm polypropylene cage and an adult vole was released into the cage. I observed for 15 minutes after release into the cage or until I observed infanticidal behavior. Upon seeing signs of infanticidal behavior (i.e., biting by the adult), I removed

the pup from the cage. Behavior was recorded for all trials. If the pup sustained a wound that would be fatal, I immediately euthanized the animal using the LARC euthanasia chamber. I minimized fatal physical interaction between adults and pups by intently observing the animals and removing pups at the first sign of infanticidal behavior. If the pup was removed from the trial unharmed, it was returned to its mother and littermates.

Data Analysis

Population size and growth

Population size was estimated using Minimum Number Alive (MNA), a program written for the Statistical Analysis System (SAS Version 6.0; SAS Institute, Inc. 1989). Population growth rates were determined by $\log(MNA_{i+1}) - \log(MNA_i)$. Population density was calculated by dividing population size estimates by the area of alfalfa within each enclosure.

Reproduction, recruitment, and rate of sexual maturation

I measured reproductive rate by the proportion of adult females (≥ 30 g) in reproductive condition. I measured recruitment by the number of recruits captured in an enclosure per adult female captured in the same enclosure 4 weeks (two trap periods) before. The time lag allowed recruits to reach trappable size.

Survivorship

I calculated sex-specific survival rates (ϕ_i) using derivations of the Cormack-Jolly-Seber mark recapture methodology (Cormack 1964; Jolly 1965; Seber 1965). 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 programs RELEASE (Burnham et al. 1987) and SURGE (Pradel and Lebreton 1991) for survival modeling. I express survival rates as survival/2 weeks.

Statistical analyses

I used the Statistical Analysis System (SAS Version 6.0; SAS Institute, Inc. 1989) to conduct analyses of population size, density, and growth, reproduction, and juvenile recruitment. Three parameters, population size and density and juvenile recruitment (number of recruits per adult female four weeks before) were natural-log-transformed, and the arcsine square-root of proportions was analyzed to satisfy assumptions of statistical tests. I used univariate repeated-measures analysis of variance (RMANOVA) to test for effects of treatment and time on demographic parameters (Huynh and Feldt 1970). A Huynh-Feldt-corrected P -value is reported. Back-transformed means and standard errors are presented for transformed data.

I used Chi-square analysis to test if the incidence of infanticide by males and females against pups of various ages differed from random. For each age category of pups, I compared the proportion of adults committing infanticide per total number of trials and analyzed these proportions separately for adult males and females. Statistical significance was assumed when $P \leq 0.05$.

RESULTS

Demography

I caught 378 voles 3,986 times between 31 May and 21 September 1995. Population size increased from the initial 16 animals per enclosure in May to means of 22 in control, 30 in + male, and 29 in + female enclosures (Fig. 2). Mean peak density estimates, based on the amount of habitat available (0.0625 ha for all treatments) were 358 animals/ha in control, 485 animals/ha in + male, and 464 animals/ha in + female enclosures (Fig. 2). Population-size and density estimates did not differ over time (both $F_{9,54} = 1.51$, both $P = 0.25$) or among treatments (all $F_{2,5} \leq 0.36$, $P \geq 0.72$) except for 12–16 June ($F_{2,5} = 27.08$, $P = 0.002$). During this period, population and density estimates in the control enclosures were less than those in the + male and + female enclosures (both $P < 0.01$). Population growth rates did not differ among treatments (all $F_{2,5} \leq 4.99$, $P \geq 0.06$) except between the periods 31 May–2 June and 12–16 June ($F_{2,5} = 161.30$, $P = 0.0001$; Fig. 3). Between these periods, population growth rates in the control enclosures were less than those in the + male and + female enclosures ($P < 0.001$).

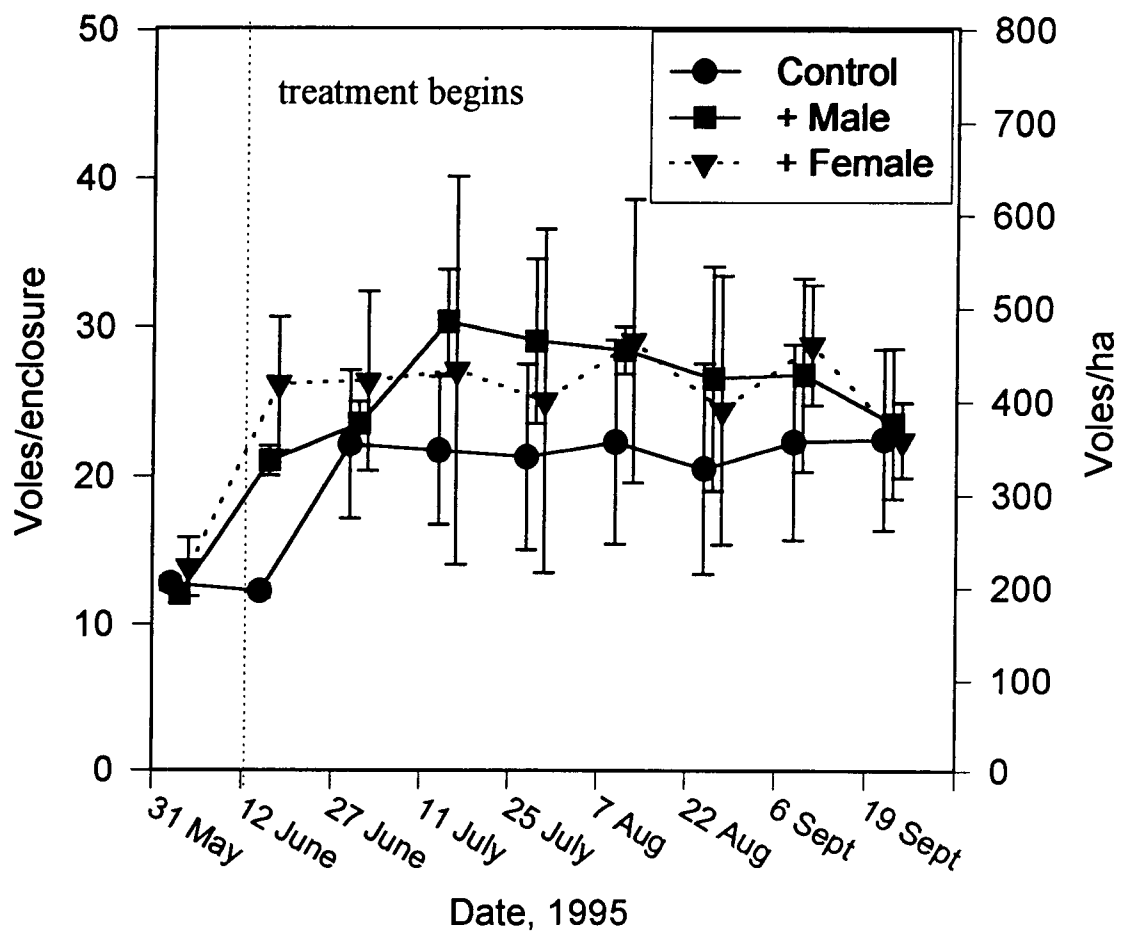


Figure 2. Mean (S.E.) population size (left) and density (right) of gray-tailed voles in control, + male, and + female enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995. Population density refers to number of animals per total area of alfalfa habitat.

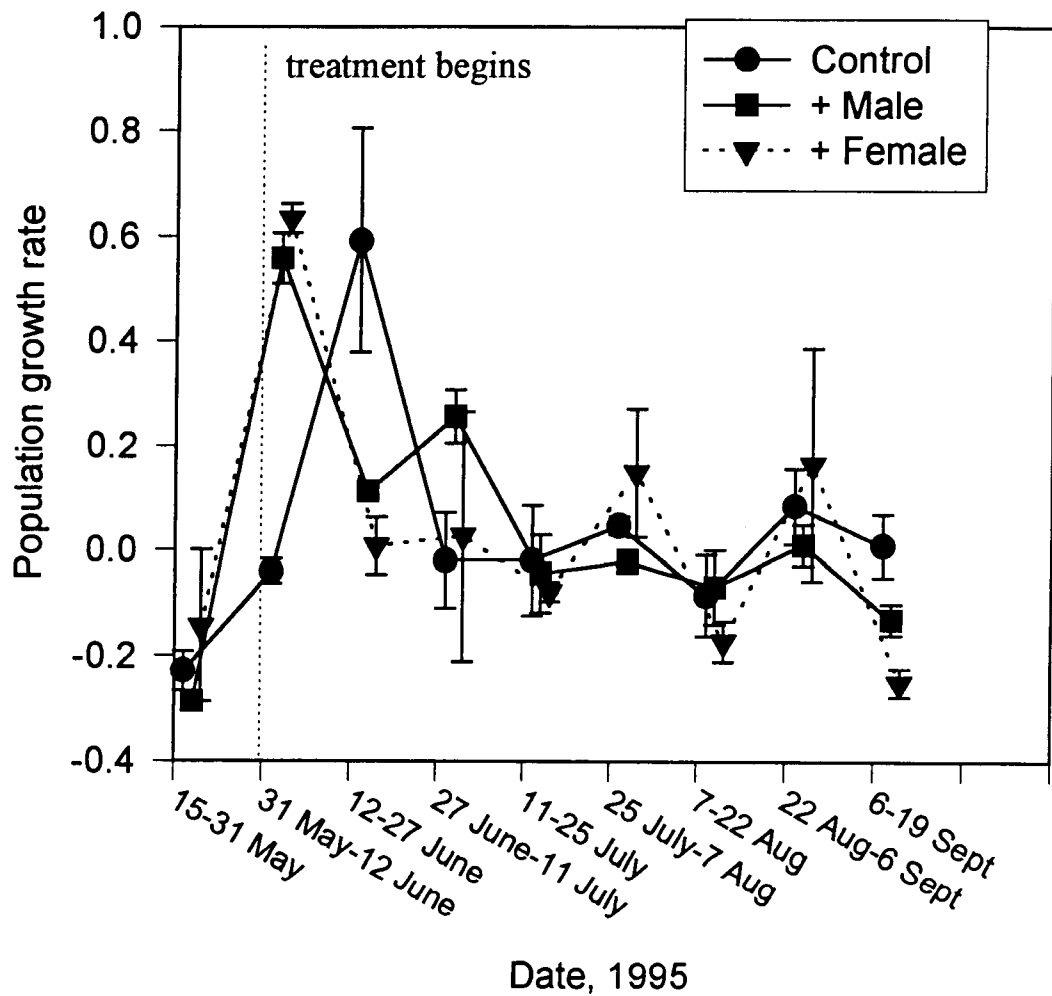


Figure 3. Mean (S.E.) population growth rates of gray-tailed vole populations in control, + male, and + female enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

Reproduction

The proportion of reproductive females fluctuated over time in all treatments. The proportion of adult females that were in reproductive condition differed over time ($F_{7,35} = 4.02$, $P = 0.003$), but not by treatment ($F_{2,5} = 3.19$, $P = 0.13$; Fig. 4). Proportion of reproductive females in control, + male, and + female enclosures followed a bi-modal curve when graphed against time. Juvenile recruitment measured by the number of recruits per adult female four weeks prior did not differ over time ($F_{6,30} = 2.80$, $P = 0.06$) or by treatment ($F_{2,5} = 3.40$, $P = 0.12$; Fig. 5).

Survival

Due to human-related trap mortality and predation by a feral cat, survival estimates were excluded for one of the control enclosures. Survival rates ranged from 0.781 to 0.965 for males in control enclosures, 0.879 to 0.965 for males in + male and + female enclosures, and 0.826 to 0.977 for females in all three treatments. The majority of biweekly survival rates did not differ by treatment or sex, except in + female enclosures. Between the weeks of 11 July and 25 July and the weeks 7 August and 22 August, survival for males ($\phi = 0.965$, $S.E. = 0.093$) was higher than that for females ($\phi = 0.826$, $S.E. = 0.024$); however, between 6 September and 19 September, female survival ($\phi = 0.977$, $S.E. = 0.008$) was higher than male survival ($\phi = 0.879$, $S.E. = 0.028$). Survival of individuals that have reached the age of recruitment did not differ by treatment.

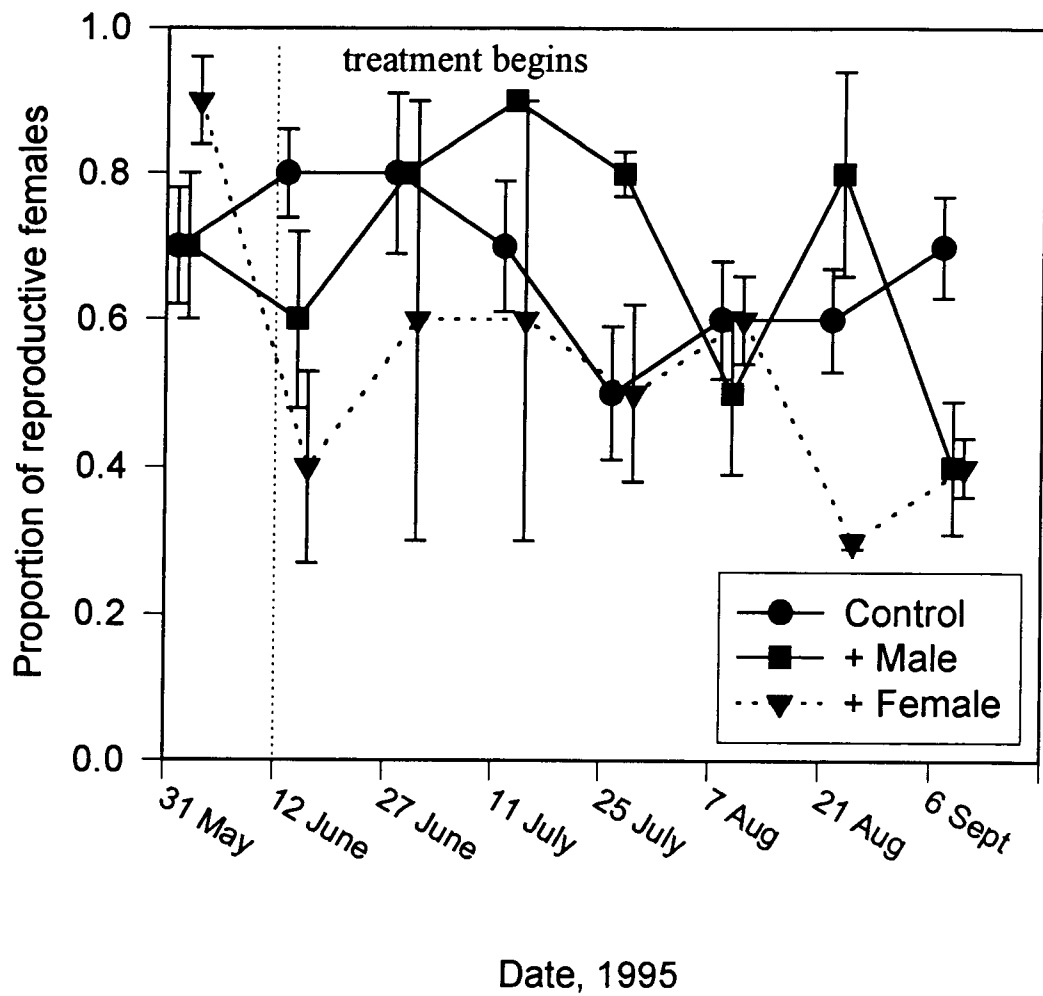


Figure 4. Mean (S.E.) proportion of females in reproductive condition, expressed as the number of reproductive females per total number of adult females, in control, + male, and + female enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

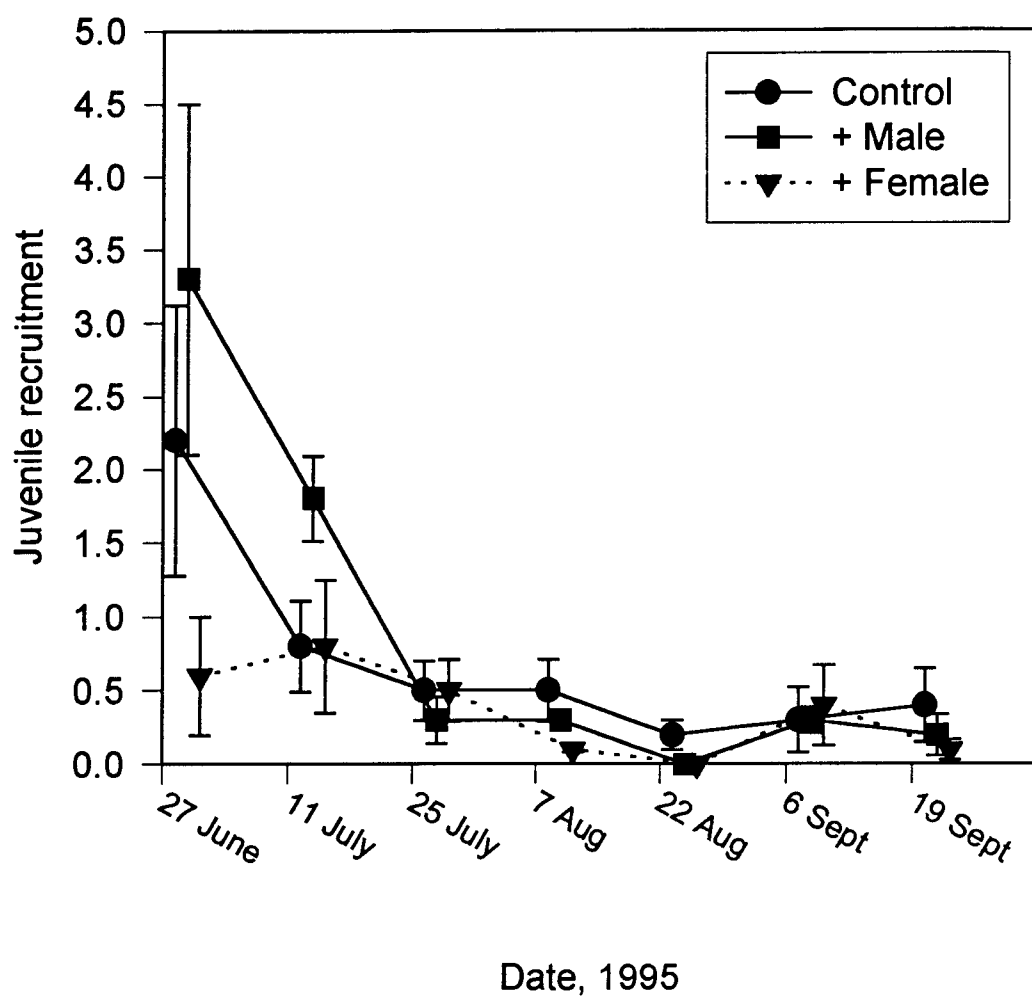


Figure 5. Mean (S.E.) juvenile recruitment, expressed as the number of recruits per adult female four weeks earlier, in control, + male, and + female enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

Infanticide in the laboratory

The incidence of infanticide committed by males on 1–3 day-old pups differed from that of 5–6 day-old ($\chi^2 = 4.05$, $P = 0.04$), 7–9 day old ($\chi^2 = 4.03$, $P = 0.04$), and 14 day-old pups ($\chi^2 = 6.12$, $P = 0.01$); however, the incidence of infanticide did not differ among the latter three age classes (all $\chi^2 \leq 2.39$, $P \geq 0.12$; Table 1). Similarly, females committed infanticide significantly more often against 1–3 day-old pups than 5–6 day-old ($\chi^2 = 4.27$, $P = 0.04$) and 7–9 day-old pups ($\chi^2 = 5.58$, $P = 0.02$). Infanticide by females against 5–6 and 7–9 day-old pups did not differ ($\chi^2 = 1.65$, $P = 0.20$).

DISCUSSION

My results suggest that immigration by unfamiliar males and females into a resident population has no demographic effects on enclosed populations of the gray-tailed vole. Neither rate of reproduction by females nor juvenile recruitment differed among treatments, thus I had no indication that infanticide occurred at a higher rate in treatment than in control populations. Because juvenile recruitment largely determines population size and growth rate, and because survival of individuals was high in all enclosures for all weeks ($> 78\%$), no demographic effects were observed in this study.

The hypothesis that the introduction of unfamiliar individuals would negatively affect resident populations by decreasing juvenile recruitment is not consistent with my results. Similar results were obtained in a study of *M. pennsylvanicus* in which the relatedness of females in a high-density population had no effect on juvenile recruitment or

Table 1. Percent of individuals committing infanticide in laboratory study of gray-tailed voles from enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

	Pup age (Days)			
	1 - 3	5 - 6	7 - 9	14
Males (%)	71.4*	28.6*	30.0*	0.0*
Females (%)	80.0**	30.0**	14.3**	No trials

* 1-3 day-old pups were killed significantly more than 5-6, 7-9, and 14 day-old pups.

** 1-3 day-old pups were killed significantly more than 5-6 and 7-9 day-old pups.

population size (Boonstra and Hogg 1988). However, the negative results from my study contradict data from several other studies, suggesting that relatedness and/or familiarity affects juvenile survival (Ylönen et al. 1990; Lambin and Krebs 1993; Mappes et al. 1996; Wolff and Schaubert 1996). Populations of familiar male and female bank voles, *Clethrionomys glareolus*, showed higher juvenile recruitment than unfamiliar populations, causing densities in familiar populations to become twice as large as those in unfamiliar populations (Ylönen et al. 1990). Another study of bank voles found that not only the presence, but the spacing of unfamiliar females has an additional effect on juvenile recruitment (Mappes et al. 1996). Juvenile recruitment was positively associated with distance between unfamiliar females. Results from a study of gray-tailed voles at the same experimental site as my study suggest that juvenile recruitment decreased as the number of unrelated females sharing a habitat patch increased, whereas the presence of unfamiliar males did not affect juvenile recruitment (Wolff and Schaubert 1996).

The addition of unfamiliar males did not result in lower juvenile recruitment in + male enclosures, indicating that infanticide by males did not occur differentially. Control enclosures from this experiment also were used to determine the effects of corridors on demographic parameters (Davis-Born *in prep* and Chapter 2). Even when presented with dispersal barriers 12.5 m wide, >12% of adult males in control enclosures changed patches. This movement would increase the likelihood of a male being familiar with a given female or a location, which might inhibit a male from committing infanticide after he has copulated (Webster et al. 1981; Wolff and Cicirello 1990; Wolff and Cicirello 1991). If introduced males in the + male treatment moved among patches after introduction, their

familiarity (and copulation) with multiple females may have inhibited them from committing infanticide.

The differences between my study and others may result from several factors. As mentioned previously, Wolff and Schauber (1996) found that survival of juveniles was inversely related to the number of unrelated females sharing a habitat patch, yet mean maximum density in my study (485 voles/ha) was considerably lower than that in the Wolff and Schauber study (2,880 voles/ha). Extremely high densities in the latter study may have resulted in increased competition among females for limited nesting sites, thus infanticide may have occurred more frequently.

Also, my assumption that intruding females would commit infanticide may have been incorrect. Other studies suggest that resident females, rather than immigrating females are more apt to commit infanticide (Hoogland 1985; Wolff and Cicirello 1989). I also assumed that habitat reduction and fragmentation would lead to the formation of kin groups in isolated, high-density habitat patches, particularly by means of female philopatry (Lambin and Krebs 1991, 1993; Wolff 1995). However, results from my study of corridor use showed that natal dispersal by females in control enclosures was greater than expected (Davis-Born *in prep* and Chapter 2). This unexpected dispersal pattern likely resulted in a decreased degree of relatedness among females within a patch, thus familiar groups may not have formed.

If natal dispersal occurred, the potential lack of familiarity among individuals may have resulted in infanticide occurring in all treatments, rather than differentially in the + male and + female enclosures. Juvenile recruitment for nearly all weeks in my study (approximately 0.5 recruits/adult female) was low when compared to past data on

recruitment of the gray-tailed vole in fragmented habitats (>1 recruit/adult female; Wolff et al. *in press*). This difference suggests that pup mortality was high and may have occurred in all treatments, thus limiting my ability to detect treatment differences. Finally, the number of females reproducing was somewhat low when compared to the total number of adult females in all treatments. The proportion of reproductive females was >0.6 in control, + male, and + female enclosures during only one week of my study. This result differs from that of another study of gray-tailed voles, which found that the proportion of reproductive females was > 0.7 until mid-August 1994 (Wolff et al. *in press*). This difference between my study and the Wolff et al. (*in press*) study is likely due to difference in introduction date of animals; in 1994, animals were introduced into enclosures during mid-April and the study was completed in early September, whereas I introduced animals in mid-May 1995 and completed my study in late September. Females exhibited a seasonal decrease in reproduction during a larger portion of my study. Thus, during most of my study, fewer adult females produced young and more adult females remained nonreproductive than were observed early in the summer, translating into fewer recruits per adult female.

Wolff (1995) hypothesized that infanticide committed by males would be greater at low than at high densities, whereas females would commit infanticide more often at high densities. Wolff also suggested that the formation, maintenance, and benefits of kin groups with respect to infanticide should vary with density, however few, if any, data are available to test these hypotheses. Although I attempted to determine how immigrants affected familiar, resident populations in fragmented habitat patches, my study may have lacked the closely related groups necessary to assess these factors. In addition, my low

number of replicates for the introduction enclosures decreased my power to detect significant treatment effects. My results, which suggest that infanticide does not occur differentially by intruding individuals, should be considered with caution due to the limitations and their contradiction with other studies mentioned herein.

CHAPTER 2: INDIVIDUAL- AND POPULATION-LEVEL RESPONSES OF THE GRAY-TAILED VOLE IN FRAGMENTED HABITATS

A major concern in conservation biology is how loss of habitat affects persistence of populations and biodiversity (Gilpin and Soulé 1986; Wilcove et al. 1986). Individuals living in a fragmented habitat often coexist in small patches with a high number of animals, which increases the effects of inter- and intraspecific competition (Lovejoy et al. 1986; Caughley 1994). Several studies have shown that small mammal species living in relatively small patches have reduced movements and small home ranges with considerable overlap among individuals (Yahner 1992; Diffendorfer et al. 1995; Wolff et al. *in press*). A study of the deer mouse, *Peromyscus maniculatus*, the cotton rat, *Sigmodon hispidus*, and the prairie vole, *Microtus ochrogaster*, determined that as fragmentation increased, the proportion of animals changing patches decreased (Diffendorfer et al. 1995). Similarly, a 70% reduction and fragmentation of habitat resulted in greatly decreased movement rates in the gray-tailed vole, *M. canicaudus* (Wolff et al. *in press*). Habitat alteration also resulted in abnormally high vole densities (2,880 animals/ha in fragmented habitat vs. 545 in unfragmented). Fragmentation, which can contribute to high-density environments, may have additional effects on the social composition and demography of fragmented populations such as decreased juvenile recruitment and a breakdown of territoriality (Wolff and Schaubert 1996).

Movement corridors have been shown to facilitate dispersal patterns of individuals living in fragmented habitats (Lorenz and Barrett 1990; LaPolla and Barrett 1993; Bjørnstad et al. *in review*). Habitat fragmentation may increase the risks associated with dispersal over those in unfragmented habitats because dispersers must cross matrices of

lower quality habitat. Several studies have shown greater movement of small mammals (especially males) among patches connected with corridors than isolated patches (e.g., the house mouse, *Mus musculus*, Lorenz and Barrett 1990; the meadow vole, *Microtus pennsylvanicus*, LaPolla and Barrett 1993). As is common among microtines, juvenile dispersal and adult movement patterns are male-biased in meadow voles; without movement corridors, adult males were less apt to follow normal dispersal patterns (LaPolla and Barrett 1993).

Some researchers contend that increased connectivity through movement corridors between fragmented populations will decrease effects such as inbreeding or extinction through normal stochastic demographic processes (Noss 1987; Simberloff et al. 1992). Theoretical models suggest that without corridors, individuals in isolated patches are more likely to mate with relatives, thus inbreeding depression may decrease viability and lead to extinction (Simberloff and Cox 1987; Mills and Smouse 1994). Field data for white-footed mouse, *P. leucopus*, populations support Fahrig and Merriam's (1985) model that suggests isolated populations have lower population growth rates than those in unfragmented habitat. Lower population growth rates were due to high mortality during the winter and a lack of subsequent immigration into open home ranges in the absence of movement corridors. The researchers concluded that isolated populations have a higher probability of extinction than populations connected by corridors.

Beier (1993) applied a population dynamics model to isolated cougar, *Felis concolor*, populations in California and found that one isolated cougar population without access to movement corridors had likely become extinct; another, larger population was at risk of extinction from inbreeding depression if a movement corridor that allowed for gene

flow was destroyed by urbanization. Though somewhat limited in scope, empirical data support theoretical models recommending the maintenance of corridors to facilitate dispersal in fragmented landscapes.

Sex-biased juvenile dispersal is a common feature of mammalian social systems and appears to be a voluntary inbreeding avoidance mechanism (e.g., Getz et al. 1990; Bollinger et al. 1993; *M. townsendii*, Lambin 1994a; *M. oeconomus*, Bjørnstad et al. *in review*). Juvenile dispersal patterns appear to be affected by the proximity of opposite-sex relatives to juveniles that are attempting to establish a territory and secure mates. Among microtines, females are more apt to exhibit natal philopatry than are males (Boonstra et al. 1987; Lambin and Krebs 1991; Lambin 1994a; Wolff 1994a). Because young males are either searching for females with which to mate or are dispersing from the natal area to avoid female relatives, juvenile dispersal in microtines is commonly male-biased (Bollinger et al. 1993; Wolff 1994a; Bjørnstad et al. *in review*). Mating among kin should be more likely to occur in small, isolated environments with no movement corridors to promote dispersal and outbreeding (Simberloff and Cox 1987; Caughley 1994).

Without corridors, individuals are less able to emigrate from their natal site and related individuals remain in proximity to one another as they become adults. Individuals that remain with opposite-sex relatives may be reproductively inhibited, a possible mechanism to prevent inbreeding (McGuire and Getz 1991; Wolff 1992, 1997; Lambin 1994a). Exposure to opposite-sex strangers, however, stimulates sexual maturation, or may reverse reproductive inhibition (Batzli et al. 1977; Schadler 1990; Wolff 1992; Lambin 1994a). The presence of corridors which permit normal dispersal patterns should

reduce the probability that kin would remain together and decrease reproductive inhibition.

Most theoretical, and the few empirical studies that have been conducted, concluded that corridors provide benefits to animal populations. However, contrary to these conclusions, corridors may have short-term negative impacts on semi-isolated populations by increasing the number of aggressive interactions among unfamiliar conspecifics (Hobbs 1992; Wolff 1995). In particular, individuals may commit infanticide when entering an unfamiliar area (Sherman 1981; Wolff and Cicirello 1989). Immigrating females may commit infanticide in response to resource competition in high-density situations when available territory is limited. By killing the offspring of another female, the immigrating female increases her likelihood of obtaining the territory deserted by the victimized female (Hausfater and Hrdy 1984 and references cited therein; Künkele 1992; Wolff 1993*b*). Males kill unrelated young to gain reproductive access to a female. If her offspring die or are killed, a female will come into estrus more quickly than if she is lactating (vom Saal and Howard 1982; Hausfater and Hrdy 1984 and references cited therein; Jeppsson 1986). Males that have copulated within a time frame in which their young would be born and vulnerable to infanticide are inhibited from killing young within their home ranges (Webster 1981; Labov et al. 1985). However, males may be predisposed to killing young when they disperse into an unfamiliar area in which the young they encounter could not be their offspring (Wolff and Cicirello 1989, 1991). Whether corridors facilitate infanticidal behavior is unknown.

In this paper, I examine individual- and population-level responses of the gray-tailed vole to fragmented habitats. Experimental vole populations were exposed to two

treatments: isolated patches (control) and isolated patches connected by narrow corridors (treatment). The experiments were conducted in 0.2 ha enclosures. The presence of corridors may have short-term negative effects, but long-term positive effects on population demography, in addition to facilitating normal dispersal patterns. I tested the following hypotheses. 1) More individuals will move among patches in corridor than in control enclosures. 2) Individuals in corridor enclosures will distribute themselves more evenly among patches than those in control enclosures. Corridors should facilitate movement among patches thus individuals can space themselves evenly to avoid high-density situations by colonizing the patches of lowest density. 3) Because of the normal, male-biased dispersal patterns of the gray-tailed vole, more males than females will move among patches in both treatments. 4) Initial juvenile recruitment and population growth rates will be lower in corridor than in control enclosures. This hypothesis assumes that adult males and females that immigrate into a patch may commit infanticide on unfamiliar offspring; infanticide would reduce recruitment and population growth rate. 5) Juveniles in control enclosures should exhibit reproductive inhibition if dispersal is limited and opposite-sex relatives are unable to separate from each other. Juveniles in corridor enclosures should disperse from the natal site, rather than be reproductively inhibited or mate with relatives.

METHODS

Study Species

The gray-tailed vole is the common, grassland, microtine species of the Willamette Valley, Oregon. Gray-tailed voles are similar in appearance, behavior, and ecology to other *Microtus* spp., especially closely related *M. montanus* (Verts and Carraway 1987). Breeding occurs from March through November, gestation time is 21 days, modal litter size is six, juveniles are weaned at 15–18 days, and females can start breeding when they are 18 g (about 18–20 days old). The mating system, like that of most mammals, is polygynous or promiscuous (Wolff et al. 1994). In the field, females have relatively small ($\bar{x} = 56 \text{ m}^2$) home ranges (Wolff et al. 1994); home ranges of males are larger than those of females and overlap those of one or more females. Like many other vole species (e.g. *M. ochrogaster*, Getz et al. 1990; *M. pennsylvanicus*, Bollinger et al. 1993; *M. townsendii*, Lambin 1994a; *M. oeconomus*, Bjørnstad et al. *in review*), juvenile dispersal is male-biased.

Research Facilities

The study was conducted at the vole enclosure research site located at the Hyslop Agronomy Farm of Oregon State University approximately 10 km north of Corvallis, Oregon (Wolff et al. 1994; Edge et al. 1995). The experimental units consisted of eight 0.2 ha (45 x 45 m) enclosures planted with alfalfa (*Medicago sativa*). Each enclosure was constructed of galvanized sheet metal approximately 90 cm high and buried 90 cm deep to

prevent escape or entry by burrowing animals. A 1-m wide strip along the inside of the fence within each plot was kept bare to minimize use by small mammals.

Four replicate enclosures were randomly assigned as control and four as treatment. In late April 1995, alfalfa was killed using RoundUp®, then flail mowed to create four small isolated patches, each 12.5 x 12.5 m (156 m²) in each enclosure (Fig. 6). Each patch was separated from adjacent patches by a 12.5-m wide barren strip to serve as a barrier of unsuitable habitat. The patches within treatment enclosures were connected by 0.7-m wide corridors (LaPolla and Barrett 1993; Andreassen et al. 1996b). Matrices were maintained by herbiciding, mowing, and removal of debris. In late June, the alfalfa was mowed to a height of 20 cm to promote new growth.

Experimental Procedures

Eight male and eight female voles were introduced to each enclosure on 15 May 1995; two animals of each sex were placed in each of four patches for all treatments. All animals were trapped from wild populations in Benton County, Oregon and were unfamiliar with each other. Body mass of introduced animals ranged from 11–52 g for males and 13–42 g for females. Over 90% of the introduced animals weighed >18 g when released into the enclosures.

Trapping Procedures

Nine trap stations were established in each patch with 4 m between traps for a total of 36 trap stations in each enclosure. Two 8 x 9 x 23-cm Sherman live trap (model

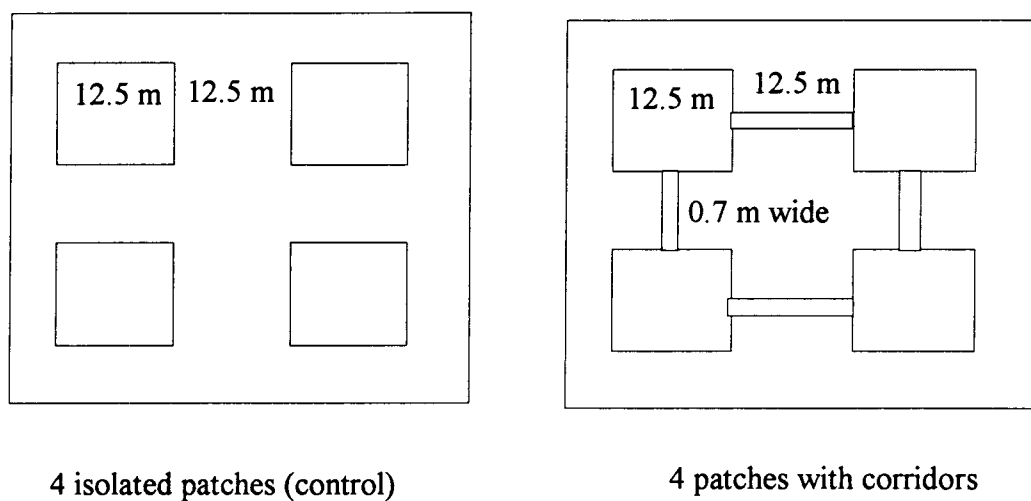


Figure 6. Habitat configurations for control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

LFATG; H.B. Sherman Traps, Inc., Tallahassee, Florida) were placed at each station for a total of 72 traps per enclosure. Animals were trapped for four consecutive nights at two-week intervals (trap period) from late May through September. 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 nontrapping periods. All captured animals were ear-tagged for identification and data on body mass (measured to the nearest 1 g with Pesola spring scales), sex, age, reproductive condition and trap location recorded at first capture each week; trap location was recorded at subsequent captures within the same week.

Reproduction and Recruitment

Animals were considered adults if their body mass was ≥ 30 g. All newly tagged animals were considered recruits born in the enclosures. Females were in reproductive condition if they were lactating, pregnant, or had widely parted pubic symphyses. Because testes of gray-tailed voles cannot be measured externally, the criteria for determining reproductive condition in males is much less conservative than that for females. All males were considered to be reproductive as adults.

Adult and Juvenile Dispersal

I assessed the use of corridors for dispersal of both adults and juveniles. For adults, I compared the number of individuals changing patches between the two treatments. Any individual which changed patches was considered a “disperser”

regardless of the time spent in the new patch. Due to small sample sizes within each enclosure, I pooled all dispersers within the four replicate enclosures of each treatment.

The effect of corridors on juvenile dispersal was determined by comparing individuals in each treatment placed into one of two dispersal categories: 1) residents were recruits that remained in their natal patch, and 2) dispersers were recruits that dispersed on their own volition and remained in another patch for ≥ 2 weeks and did not return to their natal patch. Animals that made excursions to another patch for one week, but returned to their natal patch were considered residents. All animals placed into these categories were first caught in the enclosures between 27 June and 11 August 1995, were < 18 g when initially tagged, and remained for ≥ 6 weeks, long enough to disperse and become reproductive. The specified mass criterion prevents the need for initial body mass to be included as a covariate; only recruits of comparable mass at time of initial tagging were used in this analysis. Similarly, the limited time frame of this criterion accounted for any differences in rate of sexual maturation that might be due to seasonal effects.

Data Analysis

Population size and growth

Population size was estimated using Minimum Number Alive (MNA), a program in the Statistical Analysis System (SAS Version 6.0; SAS Institute, Inc. 1989). Population growth rates were determined by $\log(MNA_{i+1}) - \log(MNA_i)$. Population density was calculated by dividing population size estimates by the area of alfalfa within each enclosure (624 m^2). Additional cover provided by the narrow movement corridors was not

considered to be habitat area in which voles would establish home ranges. Population size was also determined for each patch within an enclosure and the variance of patch population sizes within the enclosure was calculated.

Survivorship

I calculated sex-specific survival rates (ϕ_i) using derivations of the Cormack-Jolly-Seber mark recapture methodology (Cormack 1964; Jolly 1965; Seber 1965). 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 programs RELEASE (Burnham et al. 1987) and SURGE (Pradel and Lebreton 1991) for survival modeling. Survival rates are expressed as survival/2 weeks.

Statistical analyses

I used the Statistical Analysis System (SAS Version 6.0; SAS Institute, Inc. 1989) to conduct analyses on population size, density, and growth, and the variance of patch population size. Three parameters, population size and density and juvenile recruitment (number of recruits per adult female four weeks before) were ln-transformed to satisfy assumptions of statistical tests. I used univariate repeated-measures analysis of variance

(RMANOVA) to test for effects of treatment and time on demographic parameters, including variance of patch population size within an enclosure (Huynh and Feldt 1970). A Huynh-Feldt-corrected P -value is reported. Back-transformed means and standard errors are presented for transformed data.

Chi-squared analyses were used to assess the effects of treatment on the number of adults changing patches and also when comparing proportions of individuals in the different dispersal categories and habitat treatments. Multivariate ANOVA was used to analyze the demographic data which reflect the effect of corridors on juvenile dispersal and reproductive suppression. Habitat treatment, dispersal category, and sex were included as categorical variables. Longevity was estimated by subtracting the week of first capture from the week of last capture. Statistical significance was assumed when $P \leq 0.05$.

RESULTS

Adult Dispersal

I caught 386 voles 3,769 times between 31 May and 21 September 1995. The number of adults that changed patches differed significantly between control (14 of 57; 24.5%) and corridor (28 of 68; 41%) enclosures for males ($X^2 = 3.83$, $P = 0.05$), but not for females (6 of 67; 9%) and (12 of 67; 18%), respectively ($X^2 = 2.31$, $P = 0.13$). The number of males changing patches was significantly greater than for females in both the control and corridor enclosures ($X^2 = 5.55$, $P = 0.02$ and $X^2 = 8.76$, $P = 0.003$, respectively). The mean number of patch changes did not differ for males in control (2.93,

$S.E. = 1.59$) and corridor ($2.93, S.E. = 1.28$) enclosures ($F = 0.05, P = 0.83$), or for females in controls ($1.67, S.E. = 0.42$) and corridors ($1.92, S.E. = 0.40; F = 0.39, P = 0.54$).

Survival

Due to human-related trap mortality and predation by a feral cat, survival estimates were excluded for one of the control enclosures. Survival rates ranged from 0.789 to 0.953 for control males, 0.522 to 0.953 for corridor males, 0.849 to 0.983 for control females, and 0.713 to 0.932 for corridor females (Fig. 7). Survival rates differed significantly by treatment for males between the weeks of 15 and 31 May, with survival rates for control males higher than those for corridor males. For females, survival rates differed significantly between treatments for all weeks from 15 May to 11 July; survival rates for control females were higher than those for corridor females from 15 May to 12 June, and were lower than corridors from 12 June to 11 July. Survival rates for males in control enclosures were significantly higher than for control females between 12 and 27 June only. In corridor enclosures, survival rates did not differ by sex for any week. Survival rates of both sexes in control and corridor enclosures showed a mowing-related decrease between the weeks of 27 June and 11 July.

Patch Density

Variance of patch population sizes differed over time ($F_{8,40} = 9.94, P = 0.0001$), but not between treatments ($F_{1,5} = 0.76, P = 0.42$). During the week of 31 May–3 June,

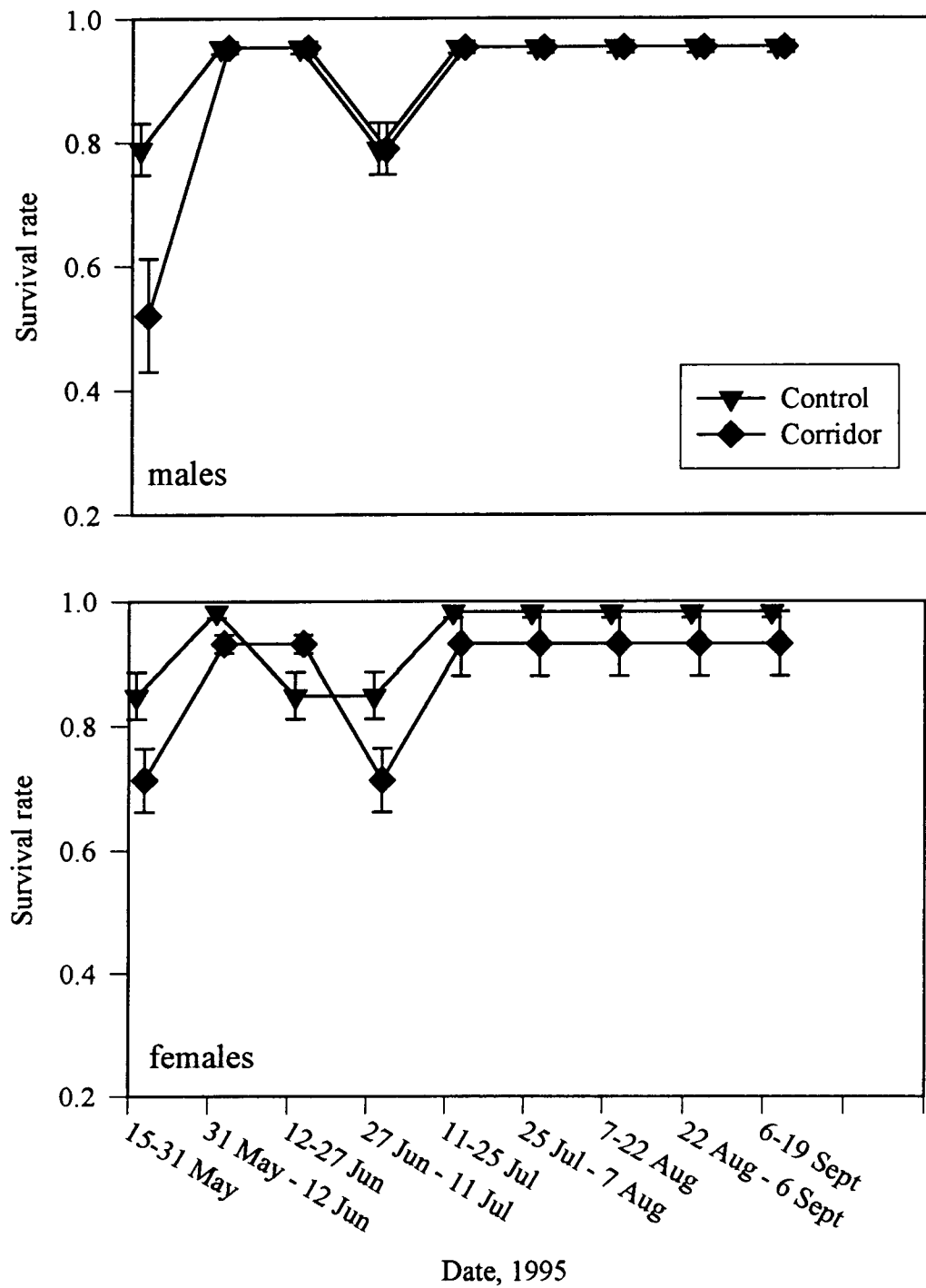


Figure 7. Mean survival rates (\pm S.E.) of male (top) and female (bottom) gray-tailed voles in control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

patch population size within an enclosure ranged from two to five voles in controls and two to six in corridors; during the last week of the study, patch population sizes in control enclosures ranged from three to 16, and four to 13 in corridors. Thus, variance of patch population sizes increased during the study period; this suggests that, even in corridor enclosures, animals did not distribute themselves evenly among patches.

Juvenile Dispersal

Forty-nine males and 47 females fit the criteria for analyses of the effect of corridors on juvenile dispersal. For all treatment and sex combinations, the frequency of dispersal was not different among enclosures within a treatment (all $F \leq 3.281$, $P \geq 0.06$). A treatment by sex interaction was found for dispersal category ($F_{1,92} = 4.814$, $P = 0.03$; Table 2). More females than males in control enclosures dispersed, while more males than females in corridor enclosures dispersed. Longevity of individuals did not differ between treatment, sex, or dispersal categories (all $F \leq 1.813$, $P \geq 0.18$). Ninety-six percent of male and 94% of female recruits first trapped between 27 June and 11 August were still alive at the end of the study on 21 September. Body mass at time of dispersal differed by sex ($F_{1,28} = 26.849$, $P < 0.001$), but not by treatment ($F_{1,28} = 0.381$, $P = 0.54$). Females in control and corridor enclosures dispersed at a mean body mass of 23.5 and 21.1 g, respectively, and males at a mean body mass of 32.0 and 37.4 g, respectively. No treatment-, sex-, or dispersal-category differences were found for maximum body mass attained (all $F \leq 1.174$, $P \geq 0.28$).

Table 2. Number and attributes (mean, S.D.) of gray-tailed voles by dispersal category in control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

	<u>Control Enclosures</u>		<u>Corridor Enclosures</u>	
	Residents	Dispersers	Residents	Dispersers
N				
males	21	2	15	11
females	14	11	14	8
Longevity in weeks				
males	10.3 (1.20)	11.0 (1.41)	9.1 (1.30)	10.4 (1.08)
females	8.7 (1.22)	10.9 (1.21)	10.1 (1.14)	10.1 (1.14)
Body mass (g) at time of dispersal				
males	-	32.0 (14.14)	-	37.4 (5.09)
females	-	23.5 (4.78)	-	21.1 (3.80)
Maximum body mass (g)				
males	41.9 (3.22)	37.5 (3.18)	44.1 (4.12)	45.4 (2.28)
females	39.5 (4.24)	42.5 (3.86)	40.4 (4.73)	38.1 (2.99)
Percent reproductively active (%)				
males	95.2 (N = 20)	100 (N = 2)	93.3 (N = 14)	100 (N = 11)
females	71.4 (N = 10)	72.7 (N = 8)	71.4 (N = 10)	87.5 (N = 7)
Number of weeks to sexual maturation				
males	4.8 (1.36)	6.0 (0)	4.0 (0.78)	4.0 (0.89)
females	6.4 (2.50)	7.8 (2.25)	6.0 (1.33)	6.0 (1.16)

Demography

Population size increased from the initial 16 animals in May to means of 22 in control and 29 in corridor enclosures (Fig. 8). Mean peak densities estimates, based on the amount of habitat available (0.0625 ha for both treatments) were 358 animals/ha in control and 457 animals/ha in corridor enclosures (Fig. 8). Population-size and density estimates differed over time (both $F_{9,54} = 6.62$, $P = 0.01$), but not between treatments (both $F_{1,6} = 0.10$, $P = 0.77$); population estimates were lower early in the study and gradually increased as animals became established within the enclosures and began to reproduce. Correspondingly, population growth rates differed over time ($F_{8,48} = 12.28$, $P = 0.0001$), but not between treatments ($F_{1,6} = 0.27$, $P = 0.62$; Fig. 9).

Juvenile recruitment measured by the number of recruits per adult female 4 weeks prior differed over time ($F_{6,36} = 3.08$, $P = 0.02$), but did not differ by treatment ($F_{1,6} = 3.09$, $P = 0.13$; Fig. 10). Juvenile recruitment was high in both treatments during the first week of recruitment (27–30 June), then decreased substantially. The number of recruits per adult female continued to decrease gradually throughout the summer until the last week of the study (19–21 September), when I observed a slight increase in all enclosures.

Reproductive Inhibition

The number of males becoming reproductive did not differ by treatment ($F_{1,43} = 0.12$, $P = 0.91$) or dispersal category ($F_{1,43} = 0.44$, $P = 0.51$); this was also true for females ($F_{1,43} = 0.30$, $P = 0.59$ and $F_{1,43} = 0.41$, $P = 0.52$, respectively; Table 2). Because the criteria for defining sexual maturity is much more conservative for females than for males,

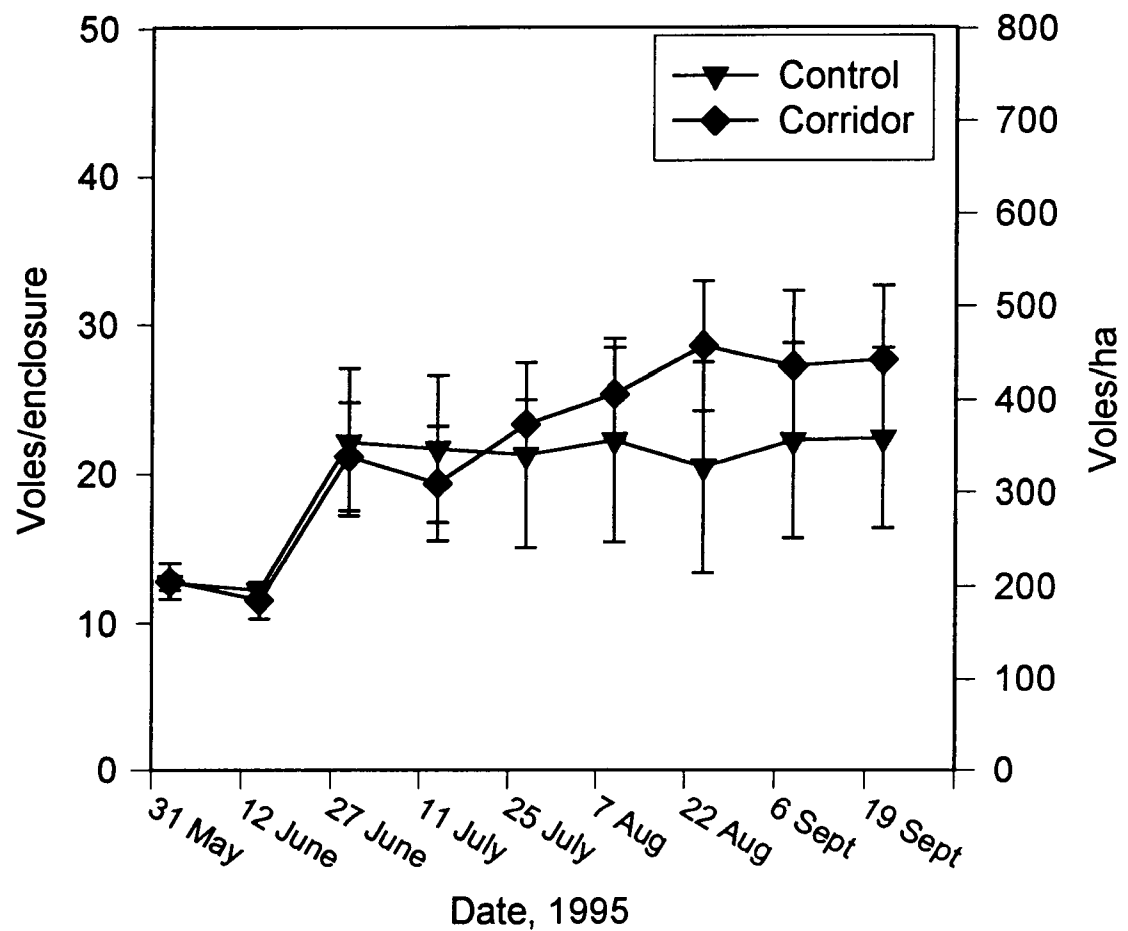


Figure 8. Mean (S.E.) population size (left) and density (right) of gray-tailed voles in control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995. Population density refers to number of animals per total area of alfalfa habitat.

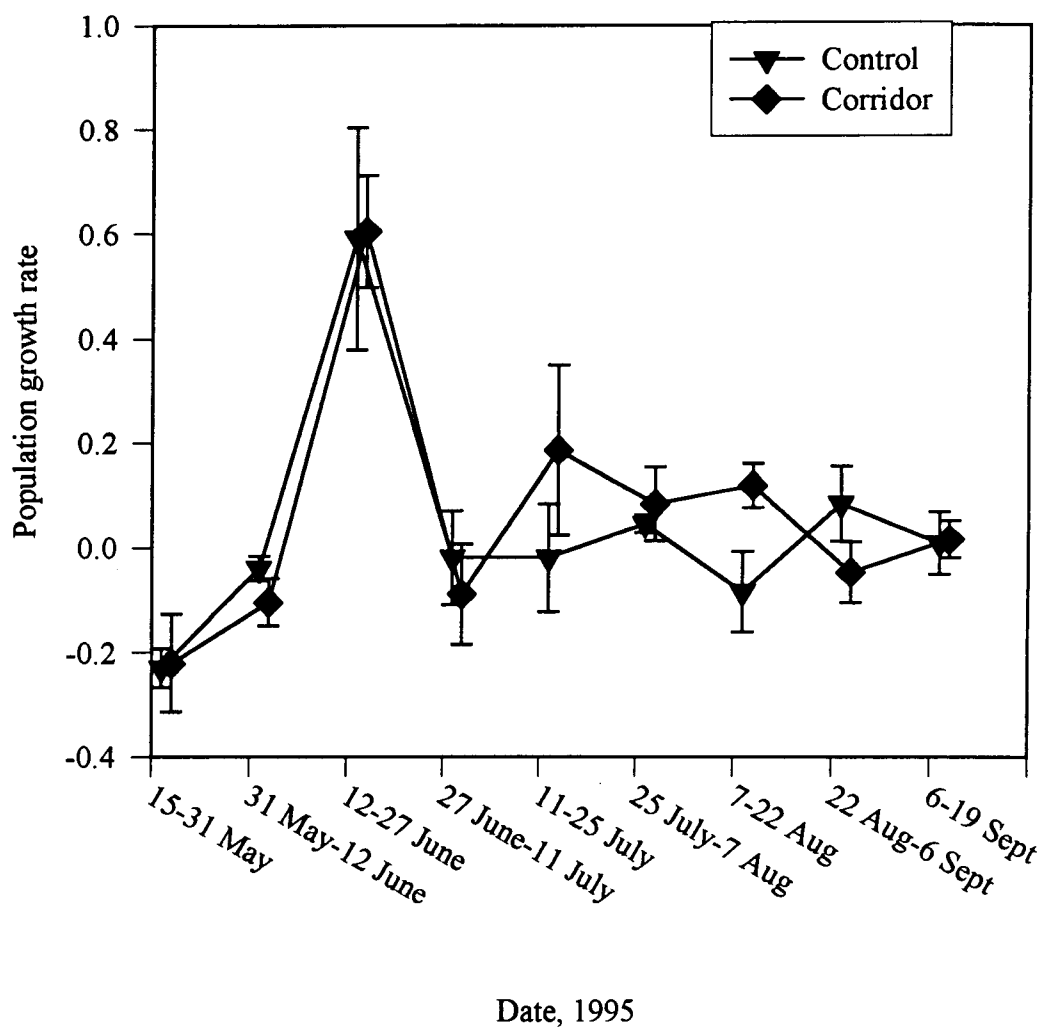


Figure 9. Mean (S.E.) population growth rates of gray-tailed vole populations in control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

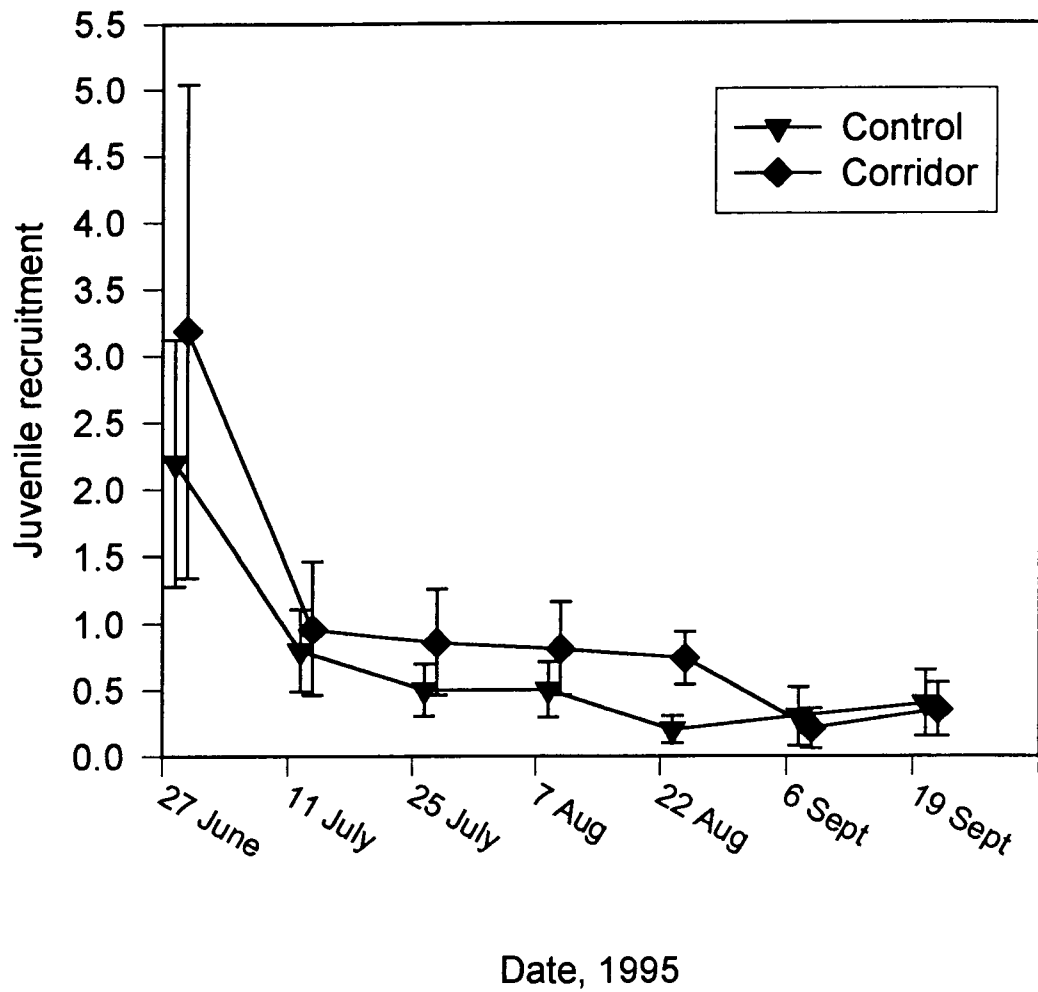


Figure 10. Mean (S.E.) juvenile recruitment, expressed as the number of recruits per adult female four weeks earlier, in control and corridor enclosures at Hyslop Agronomy Farm, Benton County, Oregon, 1995.

I did not compare differences in reproductive maturation rates between sexes. For the 47 males that became reproductive, the number of weeks to sexual maturity differed by treatment ($F_{1,43} = 9.24$, $P = 0.004$), with males in control enclosures maturing more slowly than males in corridor enclosures. The number of weeks to sexual maturity did not differ by dispersal category for males ($F_{1,43} = 1.70$, $P = 0.20$; Table 2). For the 35 reproductive females, the number of weeks to sexual maturity did not differ by treatment ($F_{1,32} = 2.55$, $P = 0.12$) or dispersal category ($F_{1,32} = 1.10$, $P = 0.30$; Table 2).

DISCUSSION

Data on dispersal allow rejection of the null hypothesis that corridors would not affect dispersal. For males and females, the number of individuals changing patches was nearly doubled from control to corridor enclosures. My results are consistent with those from several other studies of small mammals in which individuals of both sexes were more apt to move among patches when movement corridors were present than when they were absent. Chipmunks, *Tamias striatus*, (Henderson et al. 1985) and white-footed mice (Merriam and Lanoue 1990) moved among habitat patches more when corridors were present than when confronted with barren matrices, and root voles, *M. oeconomus*, (Bjørnstad et al. *in review*) used corridors to move between more widely spaced habitat patches than when corridors were absent. Use of corridors by house mice depended on the type of movement corridors; mice used corridors composed of split-rail fences surrounded by unmowed grass more than those composed of only unmowed grass (Lorenz and Barrett 1990). Contrary to my findings, female meadow voles showed no

treatment effect for frequency of movement between habitat patches in the presence of corridors (LaPolla and Barrett 1993). This discrepancy could be explained by differences in experimental design: habitat patches in LaPolla and Barrett's study were larger and closer together than those used in my study. In addition, population densities within each of their patches were considerably lower than for my study (approx. 100 voles/ha vs. 300–400 voles/ha). Competition among females for resources may have been lower in their study, resulting in less movement among patches by females searching for a “better” home range. I did not determine if food was limiting in this study. However, flail mowing, which occurred during the middle of the study, stimulated new growth of alfalfa. In addition, the density of voles in this study are much lower than those observed during other studies at the same site (Wolff et al. *in press*), suggesting that food may not have been limiting. Complex burrow systems existed prior to introduction of animals into the enclosures, thus burrow sites were already excavated and should not have been limiting. My results, in conjunction with several other studies, suggest that corridors, which probably provide additional protection from predators, are used by voles when crossing barren matrices.

The results regarding patch density did not support my hypothesis that voles in corridor enclosures would distribute themselves more evenly among patches than individuals in control enclosures. This hypothesis assumed that resource competition would drive adult movement patterns (Krebs et al. 1969; Waser 1985; Anderson 1989). If resource competition for food is the driving force for adult movements, at high densities individuals should move to areas of lower total conspecific density such that fewer individuals would be competing for the same food source (Waser 1985). I found no

treatment effect on variance in patch densities; in fact, variance increased over time in control and corridor enclosures. In a study of meadow voles, two components of vegetative cover, biomass of standing crop and litter, were associated positively with population density and negatively with dispersal (Peles and Barrett 1996). When moving among habitat patches, cotton rats and prairie voles of both sexes, and male deer mice were more apt to move to larger patches, suggesting that either resource competition or edge effect may have driven their movements (Differdorfer et al. 1995). However, patches in all enclosures during my study appeared to be homogenous with respect to vegetative cover and quality, thus differential patch densities cannot be attributed to resource differences. Other studies of microtine rodents have suggested that increased densities do not affect the dispersal frequency of individuals, thus resource competition for food probably does not drive adult movements (Beacham 1980; Tamarin et al. 1984; Verner and Getz 1985; Sandell et al. 1991). Meadow voles, prairie voles, and field voles did not increase emigration rates during times of increasing population growth rates (Verner and Getz 1985; Sandell et al. 1991). These results suggest that alternative proximate and ultimate causes may drive adult movement patterns in the gray-tailed vole. These causes might include mate competition, kin groups, and inbreeding avoidance, among others, and could be determined by analyzing sex-specific patch composition and relatedness of individuals inhabiting the patch (Dobson 1982; Bollinger et al. 1993; Salvioni and Lidicker 1995). Because individuals did not colonize available patches of lower total density, I conclude that resource competition did not drive adult movement patterns in this study.

My third hypothesis that males would move among patches more than would females was supported by the results. Males in control and corridor enclosures moved among patches more than did females, as has been observed in this and other small mammal species (Lorenz and Barrett 1990; Bollinger et al. 1993; Wolff et al. *in press*). Regardless of patch size, male cotton rats, deer mice, and prairie voles moved among habitat patches more frequently than did females (Bollinger et al. 1993); this result also was observed in house mice (Lorenz and Barrett 1990). Eight times as many male house mice dispersed in the presence of split-rail fence corridors as did females, although sample sizes were small (Lorenz and Barrett 1990). In a previous study of the gray-tailed vole, 15% of males moved among small patches, while 6% of females did (Wolff et al. *in press*). Even when risk of predation exists, adult males apparently will move across barren matrices. Male root voles commonly crossed barren matrices 4 m wide, and have been observed crossing matrices up to 15 m wide (Ims et al. 1993; Andreassen et al. 1996a). As discussed above, competition for food does not appear to be the driving forces for movement patterns in my study. Movements of males may be affected by sexual competition (Krebs et al. 1969; Anderson 1989). Empirical data on sexual competition in small mammals has been somewhat contradictory, thus the role of competition in driving male movement patterns is largely unknown (Dobson 1982; Wolff 1985; Ribble 1992). Alternatively, the frequency and distance of adult male movements may be determined by the spacing of females (Emlen and Oring 1977; Ostfeld 1985; Ims 1988; Kawata 1989). Theoretical models and empirical data suggest that females commonly establish kin groups, or clusters of overlapping home ranges of relatives (Lambin and Krebs 1991; Salvioni and Lidicker 1995). Thus, males must move among patches to search for females

with which to mate, and/or to avoid having a home range that overlaps that of a philopatric daughter (Bollinger et al. 1993; Andr  n 1994; Salvioni and Lidicker 1995). While males crossed barren matrices in control enclosures, the presence of corridors facilitated the normal, male-biased adult dispersal pattern.

An unexpected result in my study was that in control enclosures, more juvenile females than males emigrated and they emigrated at a lower body mass than control males. This dispersal pattern deviates significantly from the normal, male-biased emigration in juvenile microtine rodents (Boonstra et al. 1987; Lambin 1994a; Wolff et al. 1994). One explanation for this reversed dispersal pattern is that females may have dispersed to avoid their male relatives who were not leaving their natal patches. Females can breed at a younger age than can males (~ 18 g for females compared to > 30 g for males; Hagen and Forslund 1979). Thus, if males were remaining in their natal site until they reached sexual maturity, females may have emigrated to avoid male relatives and to search for unrelated males with which to mate. Wolff (1992) found that young female white-footed mice did not become sexually mature if they remained in the presence of their opposite-sex relatives. Similar patterns of reproductive inhibition occur in other mammals when females remain with male relatives such as the prairie vole, Townsend's vole, *M. townsendii*, and muskrat, *Ondatra zibethicus* (Batzli et al. 1977; Carter et al. 1986; Caley 1987; McGuire and Getz 1991; Lambin 1994a). When dispersal is not inhibited by social and physical barriers, sexual maturation is not delayed and inbreeding seems to be avoided. K  nkele and Von Holst (1996) found that 100% of opposite-sex siblings in a population of European wild rabbits, *Oryctolagus cuniculus*, occupied non-overlapping territories by the time of first mating. In prairie voles, opposite-sex siblings often

established home ranges near each other, but were not observed in the same social group and did not form mating pairs (Getz et al. 1994). For male Townsend's voles, presence of the female parent when a male reached sexual maturity resulted in nearly a 30% increase in dispersal distance from the natal site (Lambin 1994a). In my study, females that emigrated from their natal site tended to reach sexual maturity earlier than nonemigrating females, though this difference was not significant. Thus, emigration from the natal patch and exposure to opposite-sex individuals may enhance reproductive development and reduce the chances of reproductive inhibition that can occur in natal groups (Wolff 1993a, 1994a).

My fourth hypothesis that initial juvenile recruitment and population growth rates would be lower in corridor than control enclosures was rejected based on the results. In fact, juvenile recruitment rates were slightly, though not statistically, higher in corridor than in control enclosures. These are not the results expected if intrusion of strangers disrupts reproduction and/or results in infanticide. Because juvenile recruitment rates were comparable in treatment and control enclosures, I have no evidence of differential infanticide or reduction in recruitment. Survivorship of individuals within each of the treatments could confound these results in that differences in the survival rates of reproductive individuals may make comparisons of juvenile recruitment between treatments inappropriate. Survival rates for females in corridor enclosures were lower than those for control females for much of the study. However, the statistical significance of this relationship may not be biologically meaningful because survival rates in control and corridor enclosures were very high when compared to other studies at the same site (Edge et al. 1995; Wolff et al. *in press*). In a study to determine the effects of density and

mowing on the gray-tailed vole, Edge et al. (1995) found that female survival rates ranged from 0.72 to 0.96. A similar range for female survivorship, 0.71 to 0.94, was found when the gray-tailed vole was exposed to habitat loss and fragmentation (Wolff et al. *in press*). While aggressive interactions may occur when strange individuals immigrate into resident populations, male survivorship differed between treatments during the first week of the experiment only, and should have no confounding effect on the demography of the populations (Simberloff and Cox 1987; Wolff 1995, 1997). Juvenile recruitment (< 1 recruit per adult female from a median litter size of 6) was low in all enclosures for six of the seven weeks of my study when compared to a previous study at the same site (Wolff et al. *in press*). In that study, juvenile recruitment ranged from 0.4 to 3.75 recruits per adult female, with means of 1–2 recruits per adult female for control and fragmented treatments (Wolff et al. *in press*). Low juvenile recruitment in both control and corridor enclosures suggests that high mortality occurred between birth and recruitment and did not differ by treatment. I had no measure of infanticide, but the mortality factor(s) affecting early pup survival were not treatment-related.

A viable hypothesis for the lack of treatment effect on juvenile recruitment is inhibition of infanticidal behavior in males. In that males are inhibited from committing infanticide within their home ranges for a period of time after they copulate (Jeppsson 1986; Soroker and Terkel 1988; Wolff and Cicirello 1990), infanticide in male voles may be less common than proposed for some other groups of mammals (e.g., lions, *Panthera leo*, Packer and Pusey 1984; langurs, *Presbytis entellus*, Hrdy 1979; red howler monkeys, *Alouatta seniculus*, Crockett and Sekulic 1984). Evidence suggests that *Microtus* females mate promiscuously, which would confuse paternity, and thus reduce the chance of

infanticide (Dewsbury and Baumgardner 1981; Xia and Millar 1991; Boonstra et al. 1993). If all, or the majority of all, males in both treatments in my study had mated, they may have been inhibited from committing infanticide in general, thus access to new areas via corridors did not result in increased mortality of pups by infanticide.

My final hypothesis, which predicted that juveniles in control enclosures would be reproductively suppressed because of a lack of exposure to opposite-sex strangers, was also consistent with the results for males in control enclosures. When considering reproductive condition throughout the 6-week time period required for my analyses, no treatment differences in the number of individuals of either sex becoming reproductive were observed. The number of individuals moving among patches in control enclosures may have been adequate to ensure exposure of some young females to opposite-sex strangers during the 6 weeks; nearly 25% of adult males in controls changed patches, even without the additional cover provided by corridors. Thus, most juvenile females were likely to have access to an unrelated male with which to mate. Also, as discussed earlier, juveniles showed a sex-reversed dispersal pattern possibly caused by females dispersing to avoid male relatives who were not leaving their natal patches (Boonstra et al. 1987; Lambin 1994a; Wolff et al. 1994). By dispersing, females may have avoided reproductive inhibition and inbreeding depression by accessing unrelated males, while at the same time limiting the incidence of reproductive inhibition in males by providing males with access to unrelated females.

The number of weeks to sexual maturity was higher for control males than for corridor males, consistent with the hypothesis of reproductive inhibition of young individuals in the presence of opposite-sex relatives not exposed to unrelated potential

mates. Several studies have demonstrated that opposite-sex relatives do not breed in overlapping territories (Wolff et al. 1988; Getz et al. 1994; Künkele and Von Holst 1996) and that sex-biased dispersal reduces the incidence of reproductive inhibition (Wolff 1992; McGuire and Getz 1991; Lambin 1994a). The difference in rate of sexual maturation may be due to differences in movements of females. In this study, twice as many adult females in corridor enclosures changed patches as females in control enclosures. The movement of a female parent in corridor enclosures may have resulted in a shorter period of reproductive inhibition for males in corridors than in controls. I did not observe a similar trend in delayed rate of sexual maturation for females in either control or corridor enclosures. In my study, juvenile females were more likely to disperse than males and were not reproductively inhibited.

Theoretical models suggest that by facilitating movement, corridors in fragmented habitats will reduce extinction resulting from demographic stochasticity and inbreeding depression by facilitating movement (Fahrig and Merriam 1985; Simberloff and Cox 1987; Stamps et al. 1987). Under the conditions of my study, corridors facilitated normal dispersal patterns of adults. Individuals did not use corridors to distribute themselves evenly among habitat patches, and juveniles in a patchy environment exhibited a sex-reversed natal dispersal pattern. These results suggest that innate age- and sex-specific behavioral patterns of a species must be taken into consideration when assessing demographic effects of habitat fragmentation and connectivity to a population. My study suggests that, for the gray-tailed vole, corridors do not promote infanticide (Webster et al. 1981; Ylönen et al. 1990; Wolff 1995). Conducting similar studies over a longer period of time, with increased sample size, patch size, and distance between patches, in conjunction

with genetic analyses to determine the relatedness of individuals will help further elucidate the role of fragmentation with and without corridors in altering the social environment of a population.

CONCLUSIONS

Infanticide has been observed in laboratory and field studies of several species of small mammals (vom Saal and Howard 1982; Labov et al. 1985; Wolff and Cicirello 1991; Lambin 1994*b*). I conducted laboratory trials and determined that male and female gray-tailed voles will commit or attempt to commit infanticide, particularly when presented with 1–3-day-old pups. I then conducted field experiments to determine if infanticide was committed by immigrants invading familiar kin groups in habitat patches by 1) translocating individuals among patches and 2) by creating movement corridors by which individuals could disperse. I did not observe decreased juvenile recruitment, population size, or population growth rate in introduction or corridor treatments. Based on these results, I suggest that infanticide did not occur differently among treatments in my study. However, I make this statement with caution for two reasons. First, I did not measure infanticide directly, but used population-level measurements to determine if infanticide occurred. Also, because in this experimental design sample sizes were small ($n \leq 4$) for all treatments, statistical power for detection of significant differences among treatments was low.

Results from my study may aid in evaluation of landscape design in a fragmented environment. Corridors were used by both sexes to move among habitat patches, thus promoting gene flow. Density of individuals in a patch did not appear to be affected by the presence of corridors. Social factors, such as inbreeding avoidance, may be more important at these population densities in determining spacing of individuals relative to conspecifics. In this study, juvenile dispersal in a patchy environment did not follow the

common, male-biased pattern observed in most species of small mammals. Instead, juvenile females were more apt to disperse from their natal site than males, possibly as an inbreeding avoidance mechanism or to avoid reproductive inhibition in the presence of opposite-sex relatives. Although infanticide was not observed in this study, I recommend that behavioral factors, which may affect individual dispersal or reproductive patterns, be considered in landscape planning. For example, fragmentation of habitat may limit dispersal, leading to inbreeding. In this study, landscape alterations seemed to alter the common dispersal pattern of the gray-tailed vole, possibly because of behavioral responses of the voles to avoid inbreeding.

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