AN ABSTRACT OF THE THESIS OF

Monica L. Bond for the degree of Master of Science in Wildlife Science presented on October 12, 1998.

Title: Density, Sex Ratio, and Space Use in the Gray-Tailed Vole, *Microtus canicaudus*

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Jerry O. Wolff

Female and male mammals have different behavioral strategies for maximizing their reproductive success. Pregnancy and lactation obligate female mammals to provide greater parental investment than males; thus, females compete with each other for food and space to rear their offspring, while male mammals compete with each other for female mates. Therefore, natural selection should favor any behavior among females that increases their access to food and space to rear successful offspring and any behavior among males that increases their access to females. In two enclosure experiments, the gray-tailed vole, *Microtus canicaudus,* was used as a model species to study (1) the relative influence of male competition versus access to females on space use by males and (2) facultative sex-ratio adjustment at the population level in response to low and high population densities, skewed adult sex ratios, and season.

Home-range sizes of male voles did not appear to expand beyond an overlap with about five members of either sex. Intrasexual competition with 3-4 males and/or overlap with five females appear to set the upper limits to home-range size. Space use by males is influenced by intrasexual competition and by access to females with an upper limit of overlap with either sex. Additionally, facultative sex-ratio adjustment in response to changing population densities and skewing adult sex ratios did not occur, but a seasonal effect was detected with significantly more males produced in autumn than in spring. Under the conditions of this experimental study, I was not able to measure sex ratios of individual

litters, but if any sex-ratio adjustment occurred in response to densities and adult sex ratios, it was not detectable at the population level.

Density, Sex Ratio, and Space Use in the Gray-Tailed Vole, *Microtus canicaudus*

by

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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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Monica L. Bond, Author

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CHAPTER 1

Introduction

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1.1 INTRODUCTION

> One can, in effect, treat the sexes as if they were different species, the opposite sex being a resource relevant to producing maximum surviving offspring. Put this way, female 'species' usually differ from male species in that females compete among themselves for such resources as food but not for members of the opposite sex, whereas males ultimately compete only for members of the opposite sex, all other forms of competition being important only insofar as they affect this ultimate competition.
>
> R. L. Trivers (1972)

Female and male mammals have different behavioral strategies for maximizing their reproductive success. Pregnancy and lactation obligate female mammals to provide greater parental investment than males. Thus, females maximize their fitness by maximizing the survival of their offspring. As a result, females compete with each other for food and space to rear their offspring (Emlen and Oring, 1977; Trivers, 1972). Conversely, male mammals maximize their fitness not by providing paternal care, but by mating with as many females as possible. Thus, males compete with each other for access to reproductive females (Emlen and Oring, 1977; Trivers, 1972). The ultimate factor limiting offspring survival and female fitness is access to food resources and appropriate nesting sites. Access to resources is determined in part by intrinsic factors including population density and sex ratio, as well as by extrinsic factors such as season. The ultimate factor limiting male fitness is the number of females that he can successfully inseminate. Therefore, natural selection should favor any behavior among females that increases their access to food and space to rear offspring successfully and any behavior among males that increases their access to females. Literature on the behavior of small mammals tends to support this paradigm (Ims, 1987; Madison, 1985; Ostfeld, 1985, 1990; Wolff, 1985, 1993).

1.1.1 Determinants of Space Use by Males

In that the main factor that limits a male's reproductive success is the number of females with which it can copulate, extreme competition occurs among males for access to females. This competition may limit the movements of males which influences their space use and the number of females to which they have access. The dispersion or spacing of females will also set a constraint on the time and energy it takes to find and copulate with these females. Thus, dispersion of females and competition with males are two factors that influence how a male utilizes space. Males may defend a group of females (e.g. many ungulates and pinnipeds, Emlen and Oring, 1977) or defend exclusive territories containing food resources to attract females (e.g. pronghorns, *Antilocapra americana*, Byers and Kitchen, 1988; yellow-bellied marmots, *Marmota flaviventris*, Emlen and Oring, 1977; taiga voles, *Microtus xanthognathus*, Wolff, 1980). However, behavioral and/or environmental constraints often make resource or female defense energetically costly (i.e. if females are widely dispersed and territorial). Thus, males may have large and often overlapping home ranges in which they attempt to encompass as many females as possible within that range, as is common among small mammals (reviewed in Madison, 1985 and Wolff, 1985). In the latter case, the relative influences of female dispersion and male competition on an individual male's home-range size and access to females has not been tested experimentally.

1.1.2 Facultative Sex-Ratio Adjustment

Reproductive success is dependent not only on the survival of offspring, but on the offspring's future reproductive success as well. The successful production of "grand-offspring" depends to a great extent on a female's access to space and food resources. In that female mammals are typically philopatric, remaining on or near the natal site, and juvenile males disperse, the reproductive returns on each sex offspring differ depending on the availability of local food and space resources. If females can in some way assess the level of local resource competition, natural selection might favor a facultative sex-ratio adjustment in accordance with these sex differences in behavior and how they relate to resource limitation (Clark, 1978; Clutton-Brock and Iason, 1986; Frank, 1990; Silk, 1983). In fact, a high production of female offspring has been demonstrated in several species of mammals in which daughters had access to local resources (Lambin, 1994; McShea and Madison, 1986; Silk, 1983). Concordantly, a high production of males is associated with intense local resource competition (Clark, 1978; Silk, 1983; van Schaik and Hrdy, 1991; Verme, 1969). In small mammals, such as voles and mice, a greater production of female offspring seems to occur in spring when resources are abundant and females have a higher probability of breeding in their season of birth than do male offspring (Lambin, 1994; McShea and Madison, 1986). Thus, season of birth, probability of early breeding, and access to food and space may all interact to serve as selective forces for a facultative sex-ratio adjustment.

In addition, a biased sex ratio of offspring could also occur if the population were strongly skewed toward one sex. Any female that produced the rarer sex would contribute proportionally more genes to succeeding generations than females that produced the more common sex (Fisher, 1930). Therefore, a strategy of facultative sex-ratio adjustment in which females produced more of one sex offspring might be favored by natural selection in response to population densities and adult sex ratios. Whether females adjust the sex ratio of their offspring in response to skewed adult sex ratios or low and high population densities has not been tested experimentally.

1.1.3 Objectives

I conducted two experiments to determine (1) if male competition or access to females exerts greater influence on space use by males, and (2) if facultative sex-ratio adjustment at a population level occurs in response to low and high population densities and skewed adult sex ratios. I used the gray-tailed vole, *Microtus canicaudus*, a small grassland rodent common in the Willamette Valley in Oregon (Verts and Carraway, 1987), as an experimental model species. Voles are ideal as experimental organisms because they are small and easy to maintain under experimental conditions, are short-lived with rapid generation turnover times, have high reproductive potential, and are easily subjected to manipulation without greatly affecting their social system. In addition, voles represent a typical mammalian social system with females being philopatric and territorial, males having large and overlapping home ranges, and juvenile males dispersing. Thus, results may be cautiously extrapolated for other species with similar life histories.

In my research, I manipulated population densities and population sex ratios of enclosed populations of voles, and observed subsequent home-range sizes of males and sex ratios of recruits. These results describe behavioral patterns involved in adjusting space use and offspring sex ratios in response to changes in absolute and relative numbers of males and females in a population.

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CHAPTER 2

Does Access to Females or Competition among Males Limit Home-Range Size of Males in a Promiscuous Rodent?

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2.1 ABSTRACT

To maximize their fitness, female mammals attempt to maximize offspring survival whereas males attempt to mate with as many females as possible, which results in differential use of space. The relative influence of male competition versus access to females on male space use has not been addressed either theoretically or empirically. I conducted an experiment in which I manipulated total density, density of females and density of males to determine the relative influence of the density of each sex on space use and overlap by male gray-tailed voles, *Microtus canicaudus*. Home-range size correlated inversely with total density and was influenced by each sex. Home-range sizes of males were significantly smaller in high male-low female (HMLF) populations than in low female-high male (LFHM) populations. Males overlapped 4-5 females and 4-5 other males at low and high densities of both sexes. When sex ratios were skewed toward females, males still overlapped 4-5 females but only one other male. When sex ratios were skewed toward males, males overlapped only two females while overlapping three other males. The home-range size of a male does not appear to expand beyond an overlap with about five members of either sex. Thus, intrasexual competition with five males and/or overlap with five females appear to set the upper limits to home-range size of male gray-tailed voles. I conclude that space use by males is influenced by intrasexual competition and by access to females with an upper limit of overlap with either sex.

2.2 INTRODUCTION

Among mammals, females typically provide greater parental investment than do males which results in differential use of space (Emlen and Oring, 1977; Trivers, 1972). Due to the high costs associated with pregnancy and lactation, females tend to compete with each other for food and space to rear offspring, whereas males compete with each other for access to reproductive females (Emlen and Oring, 1977; Trivers, 1972). This pattern of space use has been well-documented in small mammals (e.g. bank voles, *Clethrionomys glareolus*, Bujalska, 1994; grey-sided voles, *C. rufocanus,* Ims, 1987, 1988; meadow voles, *Microtus pennsylvanicus*, Madison, 1980, 1985; California voles, *M. californicus*, Ostfeld, 1985, 1986, 1990; taiga voles, *M. xanthognathus,* Wolff, 1980, 1993). Among small mammals, males generally provide minimal parental investment and thus can maximize their reproductive success by mating with as many females as possible. However, in that all males have this same strategy, considerable competition should occur among males for access to females. Thus, the two main factors that should limit a male's reproductive success are the number of females to which it has access and the number of male competitors with which it interacts.

Male small mammals typically have home ranges that are twice as large as those of females, and their ranges overlap extensively with females and other males (reviewed in Madison, 1985 and Wolff, 1985) but the factors that determine male home-range size and overlap with respect to female density and dispersion are less clear. Ostfeld (1985, 1990) proposed that spacing behavior of male arvicoline rodents is determined by the spatial distribution of females. Ostfeld suggested that males establish territories when females are spatially clumped and can be defended, but overlap home ranges and "share" females when females are evenly distributed. Experiments testing this hypothesis have been equivocal. Ims (1988) found that male grey-sided voles exhibited the greatest spatial overlap when females were clumped. On the contrary, Nelson (1997) found that the spacing behavior of male field voles, *M. agrestis*, was the same irrespective of whether females were clumped or evenly distributed, but was influenced by female densities. Nelson (1997) demonstrated that at high densities of females, males had smaller home ranges with less spatial overlap of other males than at low densities of females. Similarly, Jeppsson (1990) showed that male water voles, *Arvicola terrestris*, with access to females had significantly smaller home ranges than those without access to females. In addition, Nelson (1995) found that male home ranges were larger and more exclusive at low than at high male density but the number of females overlapped by each male did not differ between low and high densities of males. These studies examined space-use responses of males to clumped versus widely dispersed females, low versus high densities of females and low versus high densities of males, but did not test how the number of male competitors *versus* the number of potential female mates in a population influences home-range sizes and spatial overlap of males. The relative influence of male competition versus access to females on the use of space by males has not been experimentally addressed.

The objective of my study was to determine whether space use by males is influenced more by the number of male competitors or by the number of reproductive females in a population. I used the gray-tailed vole, *Microtus canicaudus*, as my behavioral model species. The gray-tailed vole is a typical herbivorous grassland *Microtus* native to the Willamette Valley of western Oregon, USA (Verts and Carraway, 1987). The breeding season extends from early March to late December (Wolff et al., 1994). Previous studies showed that home-range sizes of male gray-tailed voles decrease as total population densities increase (Wolff et al., 1994; Wolff and Schauber, 1996). Similar negative correlations between population density and home-range size of males has been documented in other arvicoline rodents (e.g. prairie voles, *M. ochrogaster*, Abramsky and Tracy, 1980; Gaines and Johnson, 1982; field voles, Erlinge et al., 1990). Whether the decrease in home-range size is due to increased male competition or higher densities of females is not known.

I attempted to discern between two alternative hypotheses to explain home-range size of male voles: (1) if the home-range size of a male were determined by availability of females, then its home-range size would be a function of the number of females to which it has access, or (2) if the home-range size of a male were determined by intrasexual competition, its home-range size would vary directly with the number of male competitors. The first hypothesis proposes that home-range sizes of males should vary with the densities of females more so than with the densities of males, while the second hypothesis predicts that home-range sizes of males should vary with the densities of males more so than the densities of females.

To test these hypotheses, I measured the home-range sizes of male gray-tailed voles with respect to the relative number of male competitors and reproductive females in enclosed populations. Populations were manipulated into four combinations of density and sex ratio: equal sex ratios at low and high densities of both sexes, and sex ratios skewed towards either sex.

2.3 METHODS

2.3.1 Study Site and Experimental Procedures

The experiment was conducted at Oregon State University's Hyslop Farm, 10 km north of Corvallis, Oregon. The experimental units consisted of eight 0.2 ha (45 m by 45 m) enclosures planted with several species of grass. The enclosures are constructed of sheet metal 90 cm high and buried 90 cm deep to contain the voles, and a one-meter strip was mowed bare along the inside of the fences to minimize its use by voles. In each enclosure, nine rows of nine trap stations were spaced 5 m apart for a total of 81 stations, with one Sherman live-trap at each station.

Six adult male and six adult female voles were placed into each of the eight enclosures in the beginning of May 1997 and population densities were allowed to increase until September 1997. Adult sex ratios were about equal throughout the summer, with the lowest sex ratio being 1:1.7 (n = 16) in favor of females. Home-range sizes were calculated at low densities of both sexes (about 10 individuals of each sex) using capture locations from 12 May to 4 July (8 weeks), and for high densities of both sexes (>30 individuals of each sex) using capture locations from 28 July through 19 September (8 weeks). In September, one of two sex-ratio treatments was randomly allocated to each of the eight enclosures, providing four replicates of each treatment, for a completely randomized design with a one-way treatment structure. Sex ratios of populations were skewed towards either a high density of males (25-32) and a low density of females (6-10) (High Males-Low Females = HMLF), or a low density of males (6-10) and a high density of females (25-32) (Low Females-High Males = LMHF). To initiate the experiment, females and males were removed from or added to previous populations such that the study animals were evenly spaced throughout each enclosure. Total population size was 34-52 individuals in each of the eight treatment enclosures. Home-range sizes were calculated using capture locations from 6 October through 28 November (8 weeks). All voles for which home-range sizes were calculated had an initial mass of 30-45 g and were in reproductive condition.

2.3.2 Trapping Procedures

Voles were trapped for 4 consecutive days at 2-week intervals for a total of 7 months (8 weeks per period of home-range estimation). Traps were baited with oats and sunflower seeds and were either set in the evening and checked at sunrise or set before sunrise and checked midday, depending on the ambient temperature. All animals were ear-tagged for identification, and data recorded for each trapped animal included body mass, sex, reproductive condition of females, and trap location. Females were considered in reproductive condition if they were lactating or obviously pregnant. Voles were weighed to the nearest gram using pesola scales. For the sex-ratio treatments, all juveniles were removed from the enclosures to maintain skewed sex ratios and to control densities.

2.3.3 Statistical Analyses

The spacing of animals in the enclosures was determined by mark-recapture trap locations. Home-range sizes were estimated using the minimum-area-convex-polygon method for adult males and females caught $\geq$ seven times in 2 trap weeks, or $\geq$ five times in 3 or 4 trap weeks per period of home-range estimation. A single trap location that was $\geq$ 25 m from all other trap locations was considered either a sallie or a misread eartag and was discarded. To create an index of access to females and intrasexual competition per density and treatment, I calculated the average number of female and male home ranges that each individual male home range overlapped. Two males were considered to have overlapping home ranges if their polygons overlapped or if they were captured at ≥ 2 of the same trap stations. Males were considered to overlap females if their polygons overlapped or if they were caught at ≥ 1 of the same trap stations. Overlap criteria for males was stricter than for females because a male was not likely to compete with another male with whom he had shared only one trap station once, whereas a male was likely have mated with a female with whom he shared one trap station once. Home-range areas were not calculated for animals that did not meet the minimum number of captures, but these animals were included in calculations of overlap. Past studies have shown that female gray-tailed voles maintain exclusive home ranges that are evenly distributed across the enclosures (Wolff et al., 1994; Wolff and Schauber, 1996), therefore I assumed that each male had relatively equal access to females.

I used multivariate analysis of covariance (MANCOVA, PROC GLM; SAS Version 6.12, SAS Institute, Inc., 1996) with enclosures as replicates to compare differences in the mean home-range size of males, the mean number of males overlapped and the mean number of females overlapped by each male per enclosure per treatment. Variation in the number of captures per individual was used as a covariate for home-range size. Home-range data were log-transformed prior to analysis, but back-transformed means are reported here. I also used programs SURGE (Pradel and Lebreton, 1991) and RELEASE (Burnham et al., 1987) to model the survival rates of adult males in the two sex-ratio treatments, combining data from the four replicates within each treatment. These programs evaluate the goodness-of-fit of each model and the number of parameters for survival and capture probabilities. The most parsimonious model was identified using Akaike's Information Criterion (Lebreton et al., 1992). All values are expressed as means and 95% confidence intervals (C.I.).

2.4 RESULTS

The combination of mean male home-range size, mean number of female home ranges overlapped, and mean number of male home ranges overlapped differed among all four combinations of population densities and sex ratios (MANCOVA Wilk's lambda = 30.54, $P = 0.0001$). Thus, univariate analyses were used to compare the individual response variables of home-range size and male and female overlap between treatments.

2.4.1 Home-Range Size

Mean home range sizes of males were 293.08 m^2 (95% CI = 199.77 to 429.98 m^2) at low densities, 60.20 m^2 (95% CI = 50.14 to 72.28 m^2) at high densities, 53.34 m^2 (95% CI = 41.76 to 68.14 m^2) in HMLF populations, and 84.85 m^2 (95% CI = 55.83 to 128.95 m^2) in LMHF populations. Mean home-range sizes of males differed significantly among the four treatments (ANCOVA $F_{3,20} = 30.17$, $P < 0.0001$). Home ranges of males in low-density populations were larger than those of males in high-density populations (ANCOVA $F_{1,14} = 72.98$, $P < 0.0001$), HMLF populations (ANCOVA $F_{1,10} = 97.74$, $P < 0.0001$), and LMHF populations (ANCOVA $F_{1,10} = 58.43$, $P < 0.0001$). As average population size increased by a factor of 3.6, average home range size decreased by a factor of 3.8 (Fig. 1).

Home-range sizes of males in HMLF populations were significantly smaller than those in LMHF populations (ANCOVA $F_{1,6} = 6.54$, $P = 0.043$) but did not differ significantly from those in high-density populations (ANCOVA $F_{1,10} = 3.68$, $P = 0.084$). Males in LMHF populations had home-range sizes that were 78% larger than in HMLF populations (Fig. 1). Home-range sizes of males in high-density populations did not differ from those in LMHF populations (ANCOVA $F_{1,10} = 2.75$, $P = 0.128$).

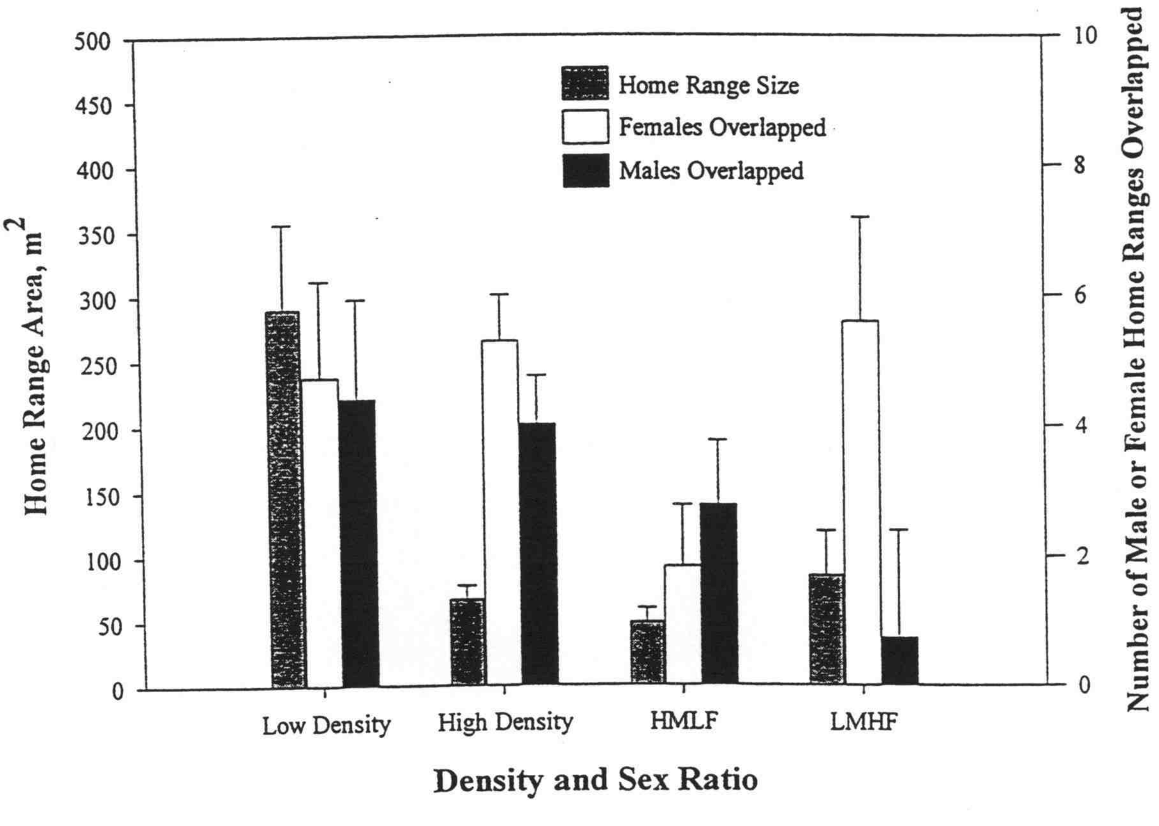

Figure 1. Mean (95% upper confidence limit) home-range area of male gray-tailed voles and mean number of male and female home ranges overlapped by males at all four combinations of density and sex ratio in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997. N = 33 for low density, N = 128 for high density, N = 68 for high male-low female (HMLF), and N = 24 for low male-high female (LMHF).

2.4.2 Female Home Ranges Overlapped

The mean number of female home ranges that were overlapped by males differed significantly among the four treatments (ANOVA $F_{3,20} = 22.08$, $P < 0.0001$). Males in HMLF populations overlapped fewer female home ranges than did males in low-density (ANOVA $F_{1,10} = 46.97$, $P < 0.0001$), high-density (ANOVA $F_{1,10} = 35.64$, $P < 0.001$) and LMHF (ANOVA $F_{1,6} = 65.50$, $P = 0.0002$) populations. Males overlapped means of about 4-5 females in low-density, high-density and LMHF populations but only about two females in HMLF populations (Fig. 1). The mean number of female home ranges overlapped by males did not differ significantly among any of the other treatments (all ANOVA $F \leq 1.88$, $P \geq 0.20$).

2.4.3 Male Home Ranges Overlapped

The mean number of male home ranges that were overlapped by males in LMHF populations was lower than in HMLF (ANOVA $F_{1,6} = 8.56$, $P = 0.0265$), low-density (ANOVA $F_{1,10} = 28.52$, $P = 0.0003$) and high-density (ANOVA $F_{1,10} = 44.28$, $P = 0.0001$) populations. Males overlapped about 3-5 other males in low-density, high-density and HMLF populations but only about one other male in LMHF populations (Fig. 1). The mean number of male home ranges each male overlapped did not differ significantly among low-density, high-density and HMLF populations (all ANOVA $F \leq 2.85$, $P \geq 0.1224$).

2.4.4 Survivorship

I found no difference in the survival rates of males between the two sex-ratio treatments. Male survivorship in both treatments was 0.930 (95% C.I. = 0.892 to 0.955).

2.5 DISCUSSION

The objective of this experiment was to determine whether access to females or competition with males had the greatest influence on home-range size and space use by male gray-tailed voles. The results suggested that home-range size of males is influenced by a combination of density, access to females, and competition with males. Home-range size of male gray-tailed voles decreased significantly as total population density increased. However, the average number of female and male home ranges each male overlapped did not differ between populations of low and high densities with equal sex ratios. Males overlapped about four other males and about five females by having large home ranges at low densities(293 m^2) and small home ranges at high densities (60 m^2). This result demonstrated that male home-range size correlates negatively with density as predicted, but did not indicate which sex has the greatest influence in this relationship. Male home-range size could have decreased due to increased access to high densities of females (hypothesis 1), or increased competition with high densities of males (hypothesis 2).

The results of the sex-ratio manipulations showed that male home-range sizes were significantly smaller in all populations with high densities of males than in populations with low densities of males. This result suggested that competition with males may limit a male's home-range size. In HMLF populations, each male home range overlapped only about two females while overlapping about three other males. The fact that males did not increase their home-range size after they overlapped about three males (but only two females) supported the hypothesis that male competition may set the upper limit to use of space by males. The number of male competitors with overlapping home ranges was fairly consistent, about 3-4 in low-density populations and in both treatments with 30 males.

If male home-range size and use of space were determined mostly by competition with males, then males in LMHF populations could have overlapped the home ranges of considerably more than five females while overlapping up to about four males. This was not the case. In LMHF populations male home ranges overlapped about five females, the same number as in high and low densities, but only about one male. If male movements are limited by other males, then males in LMHF populations (i.e. little intrasexual competition) could have increased their home-range sizes substantially, thus increasing their overlap of other males to the "upper limit" of about four, and increasing their overlap of females to even greater numbers. However, this did not happen. These data suggested that perhaps once a male gains access to about five females, it may not range farther, such that there may also be an "upper limit" of females that each male attempts to overlap. Thus, the hypothesis that female density influences space use by males was also supported.

Previous studies of small mammals have attempted to determine the effects of female dispersion and density on the use of space by males (e.g. Agrell et al., 1996; Davies, 1991; Ims, 1988; Jeppsson, 1990; Nelson, 1997; Ostfeld, 1986) and the effect of male density on male space use (Nelson, 1995). Nelson (1995, 1997) found that male field voles had smaller and more exclusive home ranges at high than at low densities of females, and that males overlapped fewer other males at low than at high densities of males, in accordance with our results. Similarly, Agrell et al. (1996) found that male field voles overlapped fewer other males at high than low female densities and Jeppsson (1990) demonstrated that male water voles with access to females had smaller home ranges than males without access to females. However, these experiments did not test whether the number of potential mates or the number of male competitors plays a greater role in limiting the use of space by males. While most theory on arvicoline spacing systems predicts male space use to be based on female dispersion and abundance (Bujalska, 1994; Ims, 1987; Madison, 1985; Ostfeld, 1985, 1990; Wolff 1993; but see Fortier and Tamarin, 1998), the results of this study indicate that male intrasexual competition equally influences the movements of males. My findings also demonstrate that there may be an upper limit of both males and females that each male will overlap, which is ultimately reflected in the size of the home range.

According to evolutionary theory males that provide minimal parental investment, as in most small-mammal species, should maximize their reproductive success by mating with as many females as possible (Trivers, 1972). However, attempts to mate with large numbers of females have two major costs, competition with other males and increased risk of predation, both of which limit movements and access to mates. In this study, the maximum number of male home ranges that a given male overlapped was about four, regardless of the number of females. Males apparently adjusted their home-range sizes in response to the number of male competitors, presumably to minimize aggressive interactions (Wolff, 1989). As a result, male survivorship did not vary with density. Thus, spatial overlap and competition with other males may have a high fitness cost and limit male home-range size.

Males are typically more vulnerable to predators than are females (Korpimäki, 1985; Mappes et al., 1993) and males that are more active and/or have larger home ranges (Norrdahl and Korpimäki, 1998) suffer greater mortality than males with smaller home ranges or that are less active. Thus, increased movement, activity, and use of large home ranges may increase predation risk sufficiently to be a selective force for maintaining as small a home range as possible while still providing access to some female mates.

The number of females that a male can effectively monitor and service is not known. Perhaps for a cryptic rodent with high reproductive rates (females in estrus every 21 days) and a 4-day estrous cycle, five females is an appropriate number for a male to monitor on a regular basis. Beyond these five females, male competition and predation risk increase sufficiently that males maintain an optimal home-range size that provides maximum fitness benefits while minimizing the costs of competition and predation. This trade-off between fitness benefits and survival costs should be an evolutionary stable strategy (ESS). Reproductive success of males is maximized by balancing breeding opportunities, reduced competition, and minimized risk of predation.

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CHAPTER 3

Do Population Densities, Adult Sex Ratios, and Season Affect Juvenile Sex Ratios in Gray-tailed Voles?

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3.1 ABSTRACT

Natural selection should favor some mechanism by which parents produce the sex of offspring that will yield the greatest reproductive success if the reproductive returns for each sex offspring are unequal. Four hypotheses that have been proposed to explain how a facultative sex-ratio adjustment could increase individual fitness are: (1) female offspring should be produced in populations with low densities of adult females, (2) male offspring should be produced in populations with high densities; (3) mothers should produce the rarer sex in populations with skewed sex ratios; and (4) more females should be born early in the breeding season and males late in the breeding season. Though some supportive evidence for each of these hypotheses exists based on observational studies, these hypotheses have not been tested experimentally. I conducted a replicated experiment using enclosed populations of gray-tailed voles, *Microtus canicaudus*, to test these four hypotheses for sex-ratio adjustment. I monitored naturally increasing population densities through the spring and summer and manipulated adult sex ratios towards an excess of males or females in the autumn, and measured subsequent sex ratios of recruits. I predicted that (1) female-biased sex ratios would be produced in the spring at low densities, and in populations with an excess of males; and (2) male-biased sex ratios would be produced in summer at high densities, in populations with an excess of females, and in the autumn. Sex ratios did not deviate significantly from 1:1 in any of the spring/low density enclosures, the summer/high density enclosures, or in 7 of the 8 enclosures in the autumn sex-ratio treatments. However, 6 of 8 autumn enclosures produced slightly more males than females, and one enclosure produced significantly higher numbers of males suggestive of a seasonal effect. Thus, I did not observe a facultative sex-ratio adjustment in gray-tailed voles in response to changing population densities and skewing adult sex ratios, but did detect a seasonal effect with significantly more males produced in autumn than in spring. Under the conditions of this experimental study, I was not able to measure sex ratios of individual litters, but if any sex-

ratio adjustment occurred in response to densities and adult sex ratios, it was not detectable at the population level.

3.2 INTRODUCTION

Sex-ratio theory predicts that female mammals can maximize their fitness by investing equally in sons and daughters when the reproductive return of each sex is equal, or by varying the sex ratio of their offspring if the reproductive return of one sex is greater than the other (Clutton-Brock and Iason, 1986; Fisher, 1930; Frank, 1990; but see Karlin and Lessard, 1986). Natural selection should favor some mechanism by which females produce the sex offspring that will in turn produce more of their own offspring than the other sex.

While population sex ratios of mammals generally do not vary significantly from one, deviations in offspring sex ratios produced by individual mothers have been observed in numerous natural populations (e.g. yellow-bellied marmots, *Marmota flaviventris*, Armitage, 1987; chimpanzees, *Pan troglodytes*, Boesch, 1997; African galagos, *Galago crassicaudatus*, Clark, 1978; red deer, *Cervus elaphus*, Clutton-Brock et al., 1986; white-footed mice, *Peromyscus leucopus*, Goundie and Vessey, 1986; deer mice, *Peromyscus maniculatus*, Havelka and Millar, 1997; roe deer, *Capreolus capreolus*, Hewison and Gaillard, 1996; Townsend's voles, *Microtus townsendii*, Lambin, 1994; meadow voles, *Microtus pennsylvanicus*, McShea and Madison, 1986; rhesus monkeys, *Macaca mulatta*, Meikle et al., 1984; horses, *Equus caballus*, Monard et al., 1997; African lions, *Panthero leo*, Packer and Pusey, 1987; yellow baboons, *Papio cynocephalus*, Wasser and Norton, 1993; opposums, *Didelphis virginiana*, Wright et al., 1995) as well as in some experimental populations (e.g. root voles, *Microtus oeconomus*, Aars et al., 1995; Ims, 1994; water voles, *Arvicola terrestris*, Bazhan et al., 1996; white-tailed deer, *Odocoileus virginianus*, Verme, 1969). At least five nonmutually exclusive hypotheses have been proposed to explain under what conditions females can benefit by a facultative sex-ratio adjustment (Clark, 1978; Fisher, 1930; Trivers and Willard, 1973; Werren and Charnov, 1978). Factors that can affect the future reproductive success of each sex include population sex ratio (Charnov, 1982, Fisher, 1930), maternal condition (Clutton-Brock et al., 1986; Trivers and Willard, 1973), local resource competition or local resource enhancement (Clark, 1978; Gowaty, 1993; Packer and Pusey, 1987; Silk, 1983) and timing within the breeding season (McShea and Madison, 1986; Werren and Charnov, 1978).

Fisher (1930) noted that the population sex ratio affects individual reproductive success because the rarer sex has a mating advantage. Fisher proposed that females should invest equally in sons and daughters because each sex contributes exactly half the genes to all future generations. If one sex costs less to produce, or if one sex is rarer and thus more reproductively valuable, the profits gained from investing more in that sex would be greater than those gained from investing more in the expensive, or common, sex. This differential investment could induce an individual female to produce a skewed offspring sex ratio that favors the sex least costly to produce at that particular time, thus increasing the overall fitness of the mother and her offspring. For example, a population sex ratio biased towards females makes males more valuable because males have a frequency-dependent mating advantage, and selection favors increased investment in males (Frank, 1990; Hamilton, 1967; Maynard-Smith, 1980). Selection would thus raise the sex ratio until the return on investment in males becomes equal to that of females. The population is always pulled by frequency-dependent selection towards a stability in which total investment in the two sexes is equal (Frank, 1990).

Fisher's hypothesis assumes a linear relationship between parental investment and returns. However, the assumptions for frequency-dependent sex-ratio adjustment are breached when the rate of return is different for sons and daughters (Charnov, 1982; Frank, 1990). For example, biased sex ratios of offspring may evolve when one sex exhibits greater variance in reproductive success than the other sex (Gomendio et al., 1990; Trivers and Willard 1973). Trivers and Willard (1973) proposed that females should adjust the sex ratio of their offspring based on the amount of investment that they can provide for that offspring and how this in turn will contribute to the offspring's fitness, assuming the condition of the young is correlated with the condition of the mother and differences in offspring condition persist into adulthood. Females that are in good condition and/or have high dominance status should produce or invest more in the sex that exhibits the greatest variance in reproductive success because they can invest greater expenditures in their offspring and thus can increase the offspring's fitness (Clutton-Brock et al., 1981, Gomendio et al., 1990). In mammals, males usually have greater variance in reproductive success than do females (Clutton-Brock et al., 1986; Trivers, 1972; Trivers and Willard, 1973); therefore, females in good condition should invest more in sons than in daughters. Conversely, a female in poor condition would benefit most from investing in daughters, because her sons would have a low probability of breeding. Daughters in poor condition are as likely to breed as those in good condition, however, so the fitness of a mother in poor condition is maximized by rearing more daughters than sons. Gosling (1986) noted that if a small litter is produced, the sex ratio should be biased towards sons because mothers can provide maximum investment, while large litter sizes should produce more females because their body size does not determine their ability to breed. Several experimental studies in which food was deprived during pregnancy have demonstrated this phenomenon in some species of rodents (e.g. golden hamsters, *Mesocricetus auratus*, Labov et al., 1986; wood rats, *Neotoma floridana*, McClure, 1981) but not others (water voles, Bazhan et al., 1996; gray-tailed voles, *M. canicaudus*, Goldenberg, 1980; northern grasshopper mice, *Onychomys leucogaster*, Sikes, 1996). Studies of some cervids have produced the opposite results, showing that mothers in poor condition tend to produce male-biased sex ratios (e.g. roe deer, Hewison and Gaillard, 1996; white-tailed deer, Verme, 1969). The observed male-biased sex ratio might arise because a female in poor condition often indicates overexploited habitat, and thus the dispersing sex should be favored to reduce local resource competition (see following hypothesis). Overall, because individual females differ in their ability to invest, the deviations in offspring sex ratios tend to cancel out at the population level (Trivers and Willard, 1973).

The success of offspring recruited into a population depends not only on parental condition and investment, but also on the amount of environmental resources available for survival, establishment of a home range, and reproduction (van Schaik and Hrdy, 1991). Cooperation or competition among kin may cause differential returns in fitness between the sexes and, thus, unequal progeny sex ratios (Clark, 1978; Packer and Pusey, 1987, Silk 1983, van Schaik and Hrdy, 1991). If local resources are abundant, females should produce the sex offspring that enhances the expected reproductive success of the parents and/or siblings (Packer and Pusey, 1987). In most mammal species, females are philopatric and remain on or near the natal site, while males are the dispersing sex. Kin groups often form in which females share food and space to rear offspring (Dalton, 1998; Lambin and Yoccoz, 1998; Mappes et al., 1995; McShea and Madison, 1986; Pusenius et al., 1998). The formation of kin groups is beneficial to females when resource availability is high because cooperative behavior may increase overall fitness (Clutton-Brock and Iason, 1986; Lambin, 1994). In these cases, the production of daughters would be most beneficial to parents. Lambin (1994) found that female-biased litters of Townsend's voles produced in springs of low density yielded twice as many breeding females per litter than unbiased litters produced in springs of high density, indicating a higher reproductive value for females in low-density populations. In some cases, males form alliances with brothers to increase their access to females, thus a mother's fitness is maximized by producing sons (Boesch, 1997; Packer and Pusey, 1987; van Schaik and Hrdy, 1991). Packer and Pusey (1987) found that female African lions bias their litter sex ratios in favor of males when the litter size is above three because sibling males improve each other's reproductive success through cohort alliances. If local resources are limited or scarce, females should produce the dispersing sex or the sex most likely to survive in such conditions (Boesch, 1997; Clark, 1978; Silk, 1978; van Schaik and Hrdy, 1991; Verme, 1969). Clark (1978) suggested that the male-biased offspring sex ratios of African galagos result from heavy competition among female kin for limited local resources. Silk (1983) reviewed available data on several species of baboons and macaques and found that local resource competition may lead to harassment of low-ranking daughters, limiting their access to resources. Thus, mothers produce the sex offspring most likely to survive; i.e. low-ranking females produce more sons and high-ranking females produce more daughters (Gomendio et al., 1990; Silk, 1983; van Schaik and Hrdy, 1991). van Schaik and Hrdy (1991) noted that several models could be operating simultaneously; depending on conditions, one model can overwhelm others and sex ratios can tend in either direction.

Availability of local resources is influenced by seasonal factors. Thus, progeny sex ratios may be affected by the timing of reproduction within the breeding season (Goundie and Vessey, 1986; Lambin, 1994; McShea and Madison, 1986; Werren and Charnov, 1978). Several factors can favor adjusting offspring sex ratios by producing more daughters in spring and more males in autumn. Werren and Charnov (1978) proposed that in spring, females are probably in good health, densities are low, competition for local resources is low, and spring-born females will be able to breed shortly after weaning. Due to competition with adult males, spring-born males often do not breed during their year of birth, or if they do, they breed later than do spring-born females. In autumn, however, densities are high, local resource competition is high, and autumn-born juveniles often will not breed until the following spring. Therefore, mothers might adjust the sex ratio of their offspring to favor daughters in spring and sons in autumn (Werren and Charnov, 1978). Lambin (1994) and McShea and Madison (1986) found that offspring sex ratios of both Townsend's voles and meadow voles, respectively, changed seasonally when vole density was low, with more daughters produced than sons in the spring.

According to these hypotheses, females may over-produce either sex when various factors influence the reproductive value of sons and daughters differentially. The above empirical studies show that sex ratios may vary in response to population density, population sex ratio, season, maternal condition, and social interactions. However, no study has yet been conducted in which an adult population sex ratio has been experimentally manipulated towards an excess of either males or females and the subsequent sex ratio of offspring has been observed. The objective of my study was to determine if facultative sex-ratio adjustment is detectable at a population level in a small-mammal species in response to population densities, adult sex ratios, and timing within the breeding season. I used the gray-tailed vole as a behavioral model species. The gray-tailed vole is a typical small herbivorous grassland rodent native to the Willamette Valley of western Oregon, USA (Verts and Carraway, 1987). The mating system is promiscuous, female gray-tailed voles form matrilineal kin groups, and juvenile males disperse (Dalton, 1998; Wolff et al., 1994). Kin groups potentially increase the reproductive value of producing daughters if the number of females in the population is low and the number of males is high. Philopatric daughters will remain at the natal site and increase the fitness of the group by sharing food and nest sites and cooperatively defending pups against infanticide (Wolff et al., 1994), whereas sons will be forced to compete with a high number of other males for breeding opportunities. Conversely, if the number of males in the population is low and the number of females is high, the reproductive value of sons increases because they will have less competition among each other for access to females, and females will begin to compete for food and space at a local level (Clark, 1978; Fisher, 1930; Lambin, 1994; Silk, 1983; Werren and Charnov, 1978). If numbers of both males and females are equal but relatively dense, local competition for resources is especially high (male home ranges overlap with those of several females). Thus, natural selection should favor the production of daughters at low densities and sons at high densities for the same two reasons: females are philopatric and males disperse.

Fisher's population sex ratio (PSR) hypothesis predicts that if a population sex ratio is skewed towards one sex, female voles should bias their offspring towards the rarer sex. Packer and Pusey's local resource enhancement (LRE) hypothesis proposes that the sex ratio should favor daughters when densities are low and resources are not limited, and Clark's local resource competition (LRC) hypothesis predicts sons should be favored when densities are high and resources are more limited. Werren and Charnov's timing within breeding season (TBS) hypothesis suggests that daughters will be produced in the spring when densities are low and females will be able to breed shortly after weaning, whereas spring-born males may not breed immediately following weaning because they must compete with larger fall-born males. However, fall-born males may have a mating advantage in the spring and thus should be favored at the end of the breeding season. Table 1 shows the predicted sex bias of recruits for each hypothesis or combination of hypotheses.

To test these hypotheses, I monitored naturally increasing population densities and experimentally manipulated adult sex ratios in enclosed populations of gray-tailed voles and measured subsequent sex ratios of recruits. Populations were manipulated into four combinations of density and sex ratio: equal sex ratios at low and high densities of both sexes, and sex ratios skewed towards either sex.

3.3 METHODS

3.3.1 Study Site and Experimental Procedures

The experiment was conducted at Oregon State University's Hyslop Agronomy Farm, 10 km north of Corvallis, Oregon. The experimental units consisted of eight 0.2 ha (45 m by 45 m) enclosures planted with several species of grass. The enclosures are constructed of sheet metal 90 cm high and buried 90 cm deep to contain the voles, and a one-meter strip was mowed bare along the inside of the fences to minimize its use by voles. In each enclosure, nine rows of nine trap stations were spaced 5 m apart for a total of 81 stations, with one Sherman live-trap at each station.

Six adult male and six adult female voles were placed into each of the eight enclosures in the beginning of May 1997 and population densities were allowed to increase until September 1997 (18 weeks). Sex ratios of adults and recruits were calculated in each enclosure for low-density populations (< 30 adults) using captures from 26 May through 4 July, weeks 2-8, and for high density populations (> 50 adults) using captures from 11 August through 19 September, weeks 12-18. In late September, one of two sex-ratio

Table 1. Predicted recruit sex ratio based on four hypotheses: Population Sex Ratio (PSR), Local Resource Enhancement (LRE), Local Resource Competition (LRC), and Timing within the Breeding Season (TBS).

Explanatory Variable	Predicted Recruit Sex Ratio
Population Density	
Low (< 30 adults), spring	Female (LRE, TBS)
High (> 50 adults), summer	Male (LRC)
Population Sex Ratio	
Male-skewed (30M:10F), autumn	Female (PSR, LRE)
Female-skewed (10M:30F), autumn	Male (PSR, LRC)
Season	
Spring	Female (TBS)
Autumn	Male (TBS)

treatments was randomly allocated to each of the eight enclosures, providing four replicates of each treatment, for a completely randomized design with a one-way treatment structure. Population sex ratios were manipulated towards either high densities of adult males (25-32) and low densities of adult females (6-10) (High Males-Low Females = HMLF) or low densities of adult males (6-10) and high densities of adult females (25-32) (Low Males-High Females = LMHF). Total population size was 34-52 adults in each of the eight enclosures during the sex-ratio treatment. Sex ratios of adults and recruits were calculated for each enclosure using captures from 6 October through 23 December. Thus, sex ratios were measured for three separate time periods throughout the study (Table 1). Logistical constraints prevented me from conducting all four combinations of density and sex ratio at the same time period. Therefore, some hypotheses are confounded with each other, such as spring/low density and LMHF/local resource competition (Table 1). However, both spring and LRE hypotheses predict female-biased offspring sex ratios, and both LMHF and LRC hypotheses predict male-biased offspring sex ratios. In addition, the autumn and LRE hypotheses are confounded but both predict male-biased offspring sex ratios.

Any newly captured, untagged animals were considered recruits born into the population. All newly captured animals were ear-tagged and left in the enclosures throughout the summer to allow population densities to increase, but were removed from the sex-ratio treatment enclosures to maintain skewed sex ratios and to control densities.

3.3.2 Trapping Procedures

Vole populations were monitored using standard mark-recapture techniques. Voles were trapped for 4 consecutive days at 2-week intervals from early May until late December (8 months total). Traps were baited with oats and sunflowers seeds and were either set in the evening and checked at sunrise or set before sunrise and checked midday, depending on the ambient temperature. All animals were ear-tagged for identification, and data recorded for each trapped animal included body mass, sex, reproductive condition of females, and trap location. Females were considered reproductive if they were pregnant or lactating. Voles were classified as juveniles (< 30 g) or adults (≥ 30 g), and all untagged animals were considered recruits. Voles were weighed to the nearest gram using pesola scales.

3.3.3 Statistical Analyses

Sex ratios were estimated in two ways: (1) from the number of animals captured during any given trap week, and (2) from all animals trapped or recruited into the populations over an extended time period (Myers and Krebs, 1971). The numbers of males and females per enclosure were counted at 2-week intervals, and an average adult and recruit sex ratio per enclosure was estimated for low-density, high-density, HMLF, and LMHF populations. Recruits produced at low densities were calculated by counting juveniles trapped during weeks 4-8, and at high densities by counting juveniles trapped during weeks 14-18. Sex ratio is expressed as the percentage of males in each enclosure. The probable date of conception was estimated for each recruit in the sex-ratio treatments, assuming juveniles gain about one gram per day, gestation period is 21 days, and pups are weaned at 15 days, to determine whether each recruit was conceived before or after the treatment.

Enclosures were considered the independent experimental units (N = 8 for low densities, N = 8 for high densities, N = 4 for each sex-ratio treatment). To assess the relative levels of local resource competition and availability of space for female offspring in the density and sex-ratio treatments, I determined the space use and degree of home-range overlap among adult females. I calculated the average number of female home ranges that each individual female home range overlapped and the average proportion of shared trap stations. I estimated home-range sizes using the minimum-area-convex-polygon method for adult females caught ≥ seven times in 2 trap weeks, or ≥ five times in 3 or 4 trap weeks per treatment. Two females were considered to have overlapping home ranges if their polygons overlapped or if they were captured at ≥ 1 of the same trap stations. To calculate the proportion of shared trap stations (i.e. overlapping territory), I divided the total number of trap stations within each female's home-range area by the number of trap stations that all other female home ranges shared with that female. Home-range areas were not calculated for animals that did not meet the minimum number of captures, but these animals were included in calculations of overlap. To assess the degree of competition among males for access to females in HMLF and LMHF populations, I calculated the numbers of male and female home ranges that each male home range overlapped. I estimated male home-range sizes and overlap using the same methods as with females, with different overlap criteria: two males were considered to have overlapping home ranges if their polygons overlapped or if they were captured at ≥ 2 of the same trap stations. I used multivariate analysis of covariance (MANCOVA, PROC GLM; SAS Version 6.12, SAS Institute, Inc., 1996) to compare differences in the mean home-range sizes of females, the mean number of females overlapped by each female, and the mean number of trap stations overlapped by females among densities and treatments, using variation in the number of captures per individual as a covariate for home-range size. Similarly, I used MANCOVA to compare differences in the mean home range-sizes of males, the mean number of males overlapped, and the mean number of females overlapped by each male. Home-range data were log-transformed, proportions of shared trap stations were arcsine square-root transformed, and counts of male and female overlap were square-root transformed prior to analyses to stabilize variances and meet assumptions of normality.

I performed chi-square analyses for each enclosure at low densities, high densities, HMLF, and LMHF to calculate the probabilities that the observed sex ratios of adults and recruits were sampled from a population with a 1:1 ratio (i.e. is the proportion of male adults and male recruits within each enclosure different than an expected 0.5). I tested adult sex ratios to confirm that no significant difference in sex ratio from 0.5 occurred in low and high densities but did occur in the sex-ratio treatments.

ANOVA (PROC GLM; SAS Version 6.12, SAS Institute, Inc., 1996) of the proportion of male recruits/enclosure/ treatment was used to determine whether the mean sex ratio of recruits differed between low and high densities and between HMLF and LMHF populations. The proportional data were arcsine square-root transformed prior to analysis to meet assumptions of ANOVA.

To determine whether recruitment rates differed between low and high densities or between HMLF and LMHF populations, I used a Kruskall-Wallis test to compare the overall number of male or female recruits/pregnancy/enclosure among all treatments, and a Wilcoxon rank-sum test with a 0.5 continuity correction factor to compare each density and sex ratio to each other (2-sample). I used non-parametric tests because the data were normally distributed but no transformation was able to equalize variances. Recruits per pregnancy were calculated by dividing recruits by (1) the number of females pregnant or lactating at week 2 and/or lactating at weeks 4 and 6 for low-density populations, (2) the number of females pregnant at week 10, or pregnant or lactating at week 12 and/or lactating at weeks 14 and 16 for high-density populations, and (3) the number of times each female was pregnant and/or lactating within each sex-ratio treatment.

Finally, I used ANOVA of the proportion of male recruits/enclosure/season (spring or autumn) to determine whether sex ratios of recruits differed between spring and autumn. I combined the recruit sex ratios for all enclosures in the autumn for a mean sex ratio ($N = 8$) after determining no PSR treatment effect on recruit sex ratio. The proportional data were arcsine square-root transformed prior to analysis to meet ANOVA assumptions. All values are represented as means ± standard deviation, or as means and 95% upper confidence limits for back-transformed logarithms of home-range size.

3.4 RESULTS

3.4.1 Sex Ratios of Adults

To confirm my sex-ratio effect, I examined sex ratios of adults in each enclosure at low densities, high densities, HMLF, and LMHF. Sex ratios of adults did not differ from 1:1 within any of the eight enclosures at low density (all $X^2 \leq 1.3$, $P \geq 0.25$) or at high density (all $X^2 \leq 3.35$, $P \geq 0.05$). The most skewed sex ratio was 1:1.7 (n = 16) in favor of females (38% male) in one of the enclosures at low density. Sex ratios of adults were biased towards males in all four of the HMLF enclosures (all $X^2 \geq 4.24$, $P \leq 0.05$) and towards females in all four of the LMHF enclosures (all $X^2 \geq 10.76$, $P \leq 0.001$). Thus, adult sex ratios were relatively even at low and high densities and skewed towards males in the HMLF treatment and towards females in the LMHF treatment.

3.4.2 Evidence for Local Resource Competition and Male Intrasexual Competition

The combination of mean female home-range size, mean number of female home ranges overlapped, and proportion of shared trap stations differed among all four combinations of population densities and sex ratios (MANCOVA Wilk's lambda = 11.12, $P < 0.0001$). Thus, univariate analyses were used to compare the individual response variables of home-range size, female overlap, and shared trap stations between densities and treatments.

The mean home-range size of females differed significantly among low-density, high-density, HMLF, and LMHF populations (ANCOVA $F_{3,20} = 26.99$, $P < 0.0001$). Home-range areas were significantly larger at low densities than at high densities, HMLF, and LMHF (all ANCOVA $F \geq 30.5$, $P \leq 0.0002$). Home range areas did not differ between high densities and either LMHF (ANCOVA $F_{1,10} = 1.26$, $P = 0.29$) or HMLF (ANCOVA $F_{1,10} = 0.13$, $P = 0.73$) populations, but were smaller in LMHF than in HMLF populations (ANCOVA $F_{1,6} = 10.03$, $P = 0.02$). Home ranges were largest at low densities (91.83 m^2, 95% C.I. = 69.00 to 122.18 m^2) and smallest at high densities and in LMHF populations (*high density*: 29.05 m^2, 95% C.I. = 23.52 to 35.87 m^2; *LMHF*: 25.51 m^2, 95% C.I. = 20.24 to 32.15 m^2). Home-range sizes in HMLF populations were slightly larger than at high densities (40.73 m^2, 95% C.I. = 29.94 to 55.40 m^2). Female home ranges at low densities were about 2.3 times larger than those in HMLF populations and about 3.6 times larger than those in high density and LMHF populations. Home ranges were about 1.5 times larger in HMLF populations than those in high density and LMHF populations.

The mean number of female home ranges overlapped by each female differed significantly among the four treatments (ANOVA $F_{3,20} = 5.39$, $P < 0.007$). Numbers of females overlapped did not differ between high density and LMHF populations (ANOVA $F_{1,10} = 0.28$, $P = 0.61$), but did differ significantly among all other densities and sex ratios (all ANOVA $F \geq 5.42$, $P \leq 0.035$). Females overlapped the greatest number of other females at high densities and LMHF, and the fewest at HMLF (Fig. 2). In addition, the proportion of trap stations overlapped did not differ between low densities and HMLF (ANOVA $F_{1,10} = 0.26$, $P = 0.62$) or between high densities and LMHF (ANOVA $F_{1,10} = 1.30$, $P = 0.28$) but differed among all other densities and sex ratios (all ANOVA $F \geq 7.21$, $P \leq 0.0002$). Trap station overlap was greatest at high densities and LMHF and smallest at low densities and HMLF (Fig. 2). Thus, the most amount of space for future female offspring was available at low densities of females (low density and HMLF), and the least amount of space at high densities of females (LMHF and high density; Fig. 2).

Male home-range sizes in HMLF populations were significantly smaller than those in LMHF populations ($F_{1,6} = 6.54$, $P = 0.043$). Males in LMHF populations had home-range sizes that were 78% larger than in HMLF populations (*HMLF*: 48.98 m^2, 95% C.I. = 37.86 – 60.26 m^2; *LMHF*: 85.11 m^2, 95% C.I. = 50.20 – 120.23 m^2). Males in HMLF populations overlapped fewer female home ranges than did males in LMHF populations (ANCOVA $F_{1,10} = 65.50$, $P = 0.0002$). Males overlapped about five females in LMHF populations but only about two females in HMLF populations (Fig. 3). The mean number of male home ranges

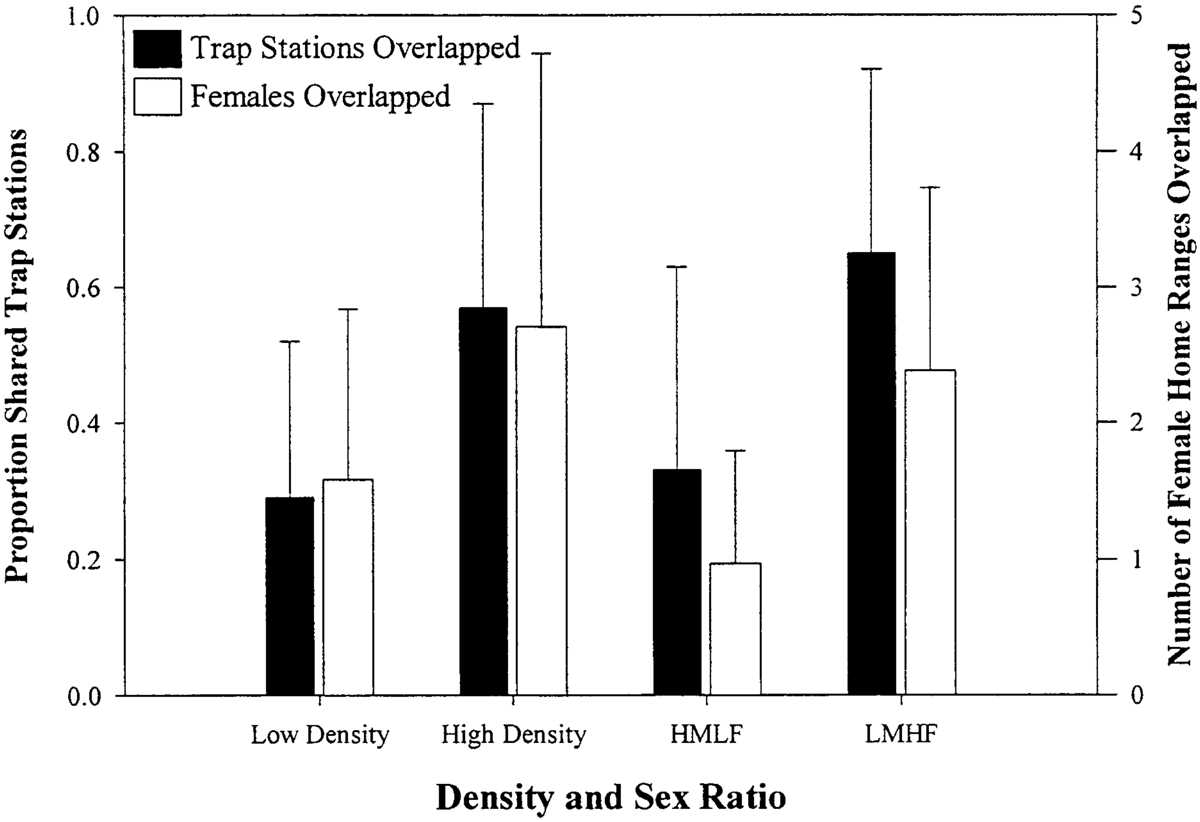

Figure 2. Mean (standard deviation) proportion of shared trap stations and number of female home ranges overlapped by adult female gray-tailed voles for each density and sex ratio treatment in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997.

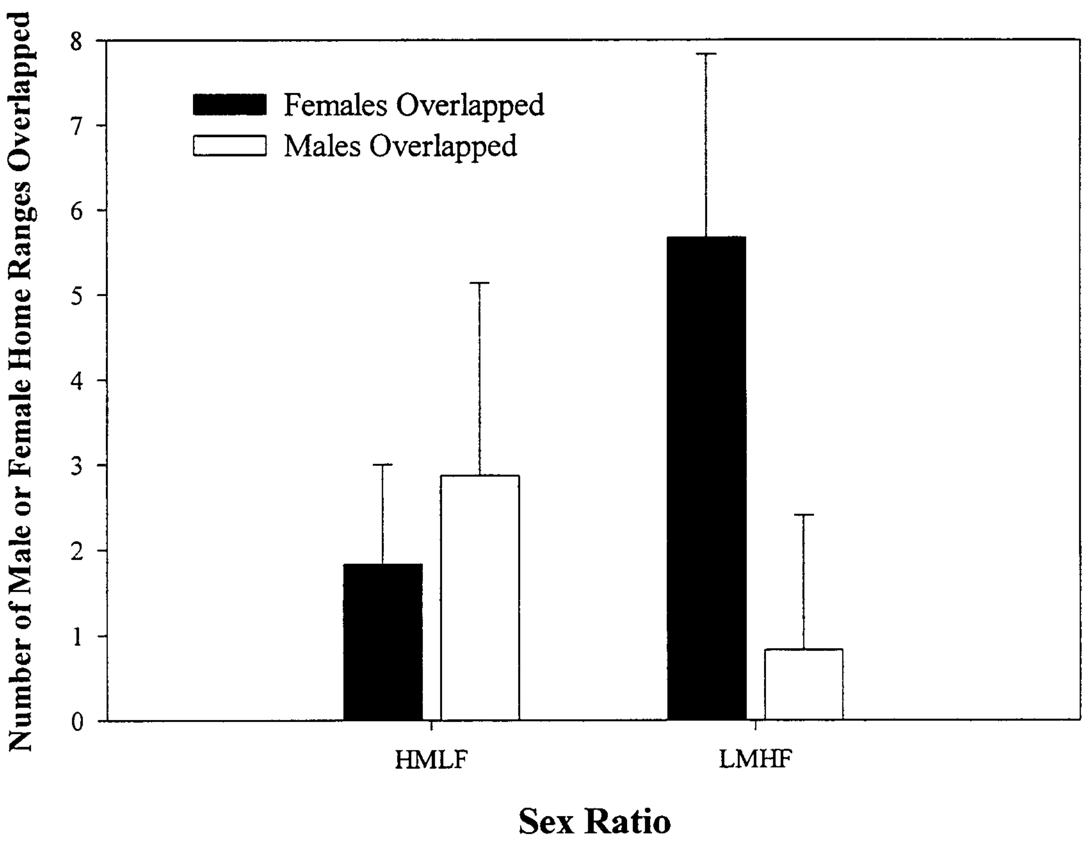

Figure 3. Mean (standard deviation) number of female and male home ranges overlapped by adult male gray-tailed voles in two sex-ratio treatments in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997.

that were overlapped by males in LMHF populations was lower than in HMLF populations (ANCOVA $F_{1,10} = 8.56$, $P = 0.0265$). Males overlapped about three other males HMLF populations but only about one other male in LMHF populations (Fig. 3). Thus, males faced greater competition for females in HMLF than in LMHF populations. In addition, males had a frequency-dependent mating advantage in LMHF populations and females had a frequency-dependent mating advantage in HMLF populations.

3.4.3 Sex Ratios of Recruits

I captured 250 recruits conceived in low-density populations (16-29 total adults), 229 in high-density populations (50-97 total adults), 300 in HMLF, and 255 in LMHF for a total of 1,034 recruits. Sex ratios of recruits did not deviate significantly from an expected 1:1 within any of the eight enclosures at low densities (all $X^2 \leq 3.33$, $P \geq 0.05$), high densities (all $X^2 \leq 3.6$, $P \geq 0.05$) or in the four enclosures in the HMLF treatment (all $X^2 \leq 2.17$, $P \geq 0.05$; Table 2). A greater proportion of males than females was caught in 3 of 8 enclosures at both low and high densities, and in 3 of 4 HMLF enclosures, but none of these sex-ratio biases deviated significantly from expected (54% - 61% male; Table 2). Sex ratios of recruits were male-biased in all four of the LMHF enclosures (58% - 71% males) but this bias was significant in only 1 of 4 enclosures (71%, $X^2 = 5.76$ $P < 0.02$; Table 2).

Mean sex ratios of recruits (percent males) did not differ between low and high densities (ANOVA $F_{1,14} = 0.72$, $P = 0.41$) or between HMLF and LMHF (ANOVA $F_{1,6} = 2.74$, $P = 0.15$; Fig.4). However, the mean sex ratio of recruits differed significantly between spring and autumn (ANOVA $F_{1,14} = 6.31$, $P = 0.02$). Populations in the spring recruited an average of 47% (± 10%) males whereas populations in the autumn recruited an average of 58% (± = 7%) males.

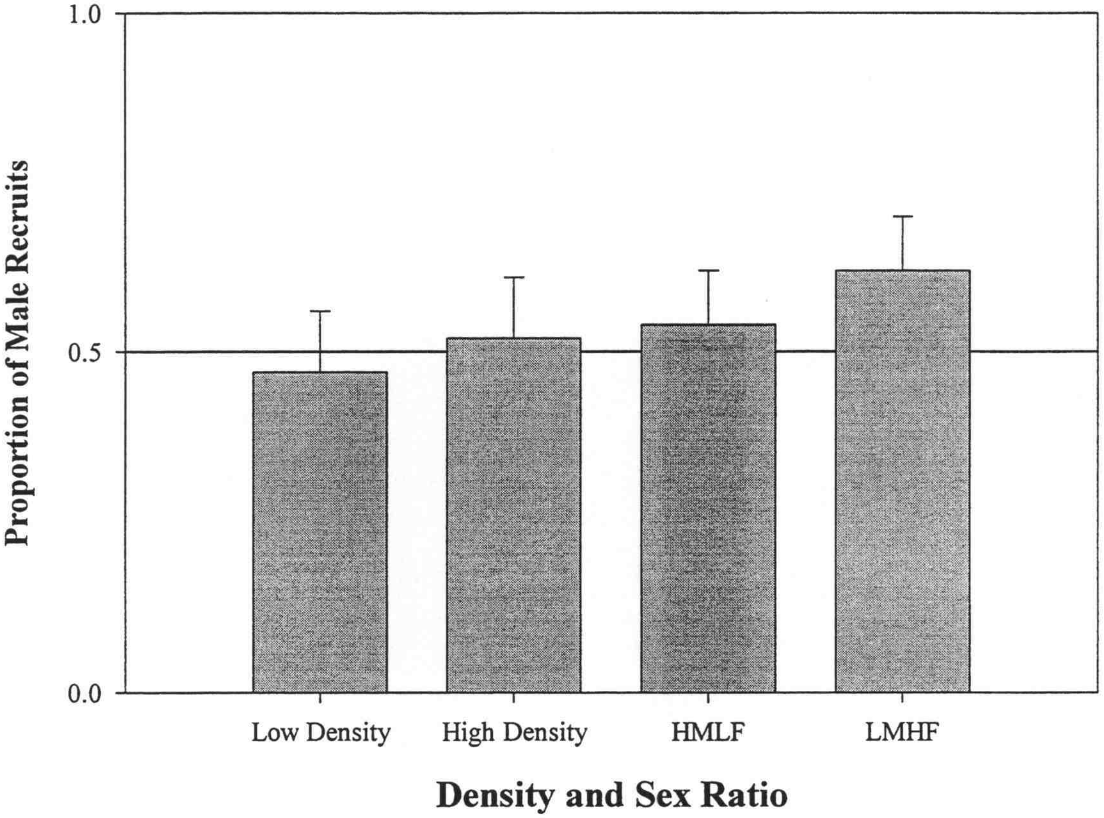

Figure 4. Mean (standard deviation) proportion of male gray-tailed vole recruits for each density and sex-ratio treatment in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997.

Table 2. Sex ratios (percent males) of adult and recruit gray-tailed voles per enclosure at low density, high density, HMLF and LMHF in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997. Numbers in parentheses express sample size and X^2 value testing the null hypothesis that the percent males in each enclosure does not differ significantly from 50%. N/A refers to data not applicable.

	Low Density		**High Density**		**HMLF**		**LMHF**	
Encl.	Adult	Recruit	Adult	Recruit	Adult	Recruit	Adult	Recruit
1	59% (27,0.78)	55% (38,0.42)	39% (67,3.35)	50% (32,0.0)	N/A	N/A	25% (40,20)*	62% (46,2.08)
2	45% (20,0.2)	33% (30,3.33)	44% (97,1.25)	47% (47,0.19)	68% (34,4.24)*	61% (46,2.17)	N/A	N/A
3	59% (29,0.86)	62% (42,2.38)	50% (66,0.0)	36% (22,1.64)	N/A	N/A	17% (52,22.2)*	71% (34,5.76)*
4	46% (24,0.15)	41% (46,1.39)	47% (94,0.38)	51% (47,0.02)	N/A	N/A	24% (41,10.8)*	58% (43,1.14)
5	59% (22,0.62)	48% (31,0.03)	53% (62,0.26)	43% (21,0.43)	68% (40,4.0)*	57% (96,2.04)	N/A	N/A
6	38% (16,1.3)	36% (14,1.14)	53% (62,0.26)	71% (28,3.6)	71% (35,6.43)*	54% (101,0.8)	N/A	N/A
7	59% (22,0.62)	55% (31,0.29)	41% (68,2.12)	44% (18,0.22)	N/A	N/A	20% (40,14.4)*	58% (132,3.03)
8	60% (25,1.0)	44% (18,0.22)	53% (50,0.18)	71% (14,2.57)	69% (39,5.77)*	44% (57,0.86)	N/A	N/A

* = $P < 0.05$

Table 3. Mean number of male and female recruits/pregnancy/enclosure/treatment in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997. N/A refers to data not applicable.

Enclosure	**Low Density**		**High Density**		**HMLF**		**LMHF**	
	Males	Females	Males	Females	Males	Females	Males	Females
1	3.50	2.80	0.76	0.76	N/A		0.57	0.36
2	1.11	2.20	1. 00	1.14	2.62	1.95	N/A	
3	6.50	4.00	0.50	0.88	N/A		0.53	0.34
4	3.17	4.50	0.96	0.92	N/A		0.47	0.20
5	2.50	2.67	0.53	0.71	2.12	1.77	N/A	
6	1.00	1.80	1.67	0.67	4.22	3.11	N/A	
7	3.40	2.80	0.67	0.83	N/A		0.47	0.34
8	2.67	3.30	1.00	0.40	1.19	1.52	N/A	

The mean number of male and female recruits per pregnancy was significantly different among all four combinations of density and sex ratio (*male* = Kruskall-Wallis X_3^2 = 17.62, $P < 0.0005$, *female* = Kruskall-Wallis $X_3^2 = 20.48$, $P < 0.0001$; Table 3). Both male and female recruitment rates differed significantly between each density and sex-ratio treatment (all two-tailed Wilcoxon $Z > \pm 2.12$, $P < 0.03$) with the exception of male recruitment rates between low density and HMLF populations (Wilcoxon $Z = -0.93$, P = 0.37; Table 3). Recruitment rates for both males and females were greater in populations with low densities of females than in populations with high densities of females (Fig. 5).

3.5 DISCUSSION

The objective of my research was to determine if facultative sex-ratio adjustment is detectable at a population level in a small-mammal species in response to population densities, adult sex ratios, and timing within the breeding season. My results did not support the hypothesis that female recruits should be favored in low-density populations (LRE hypothesis). When population densities are low with little competition for food and space to rear offspring, as is most often the case in the spring, females are likely to begin forming matrilineal kin groups (Dalton, 1998; Lambin and Yoccoz, 1998; McShea and Madison, 1986). With only 6-8 females per enclosure (~ 35 females/ha), adequate space was available for females to maintain mutually exclusive home ranges with little overlap with neighbors in the spring/low density period of my study. Home-range sizes of females averaged 91.83 m^2, each female's home range overlapped 1.58 (± 1.26) home ranges of neighboring females, and 29% (± 23%) of each female's home range was overlapped by other females. Thus, a considerable amount of vacant space was available for daughters to colonize, and daughters likely occupied space near their natal sites (Fig. 2). However, although I found a trend

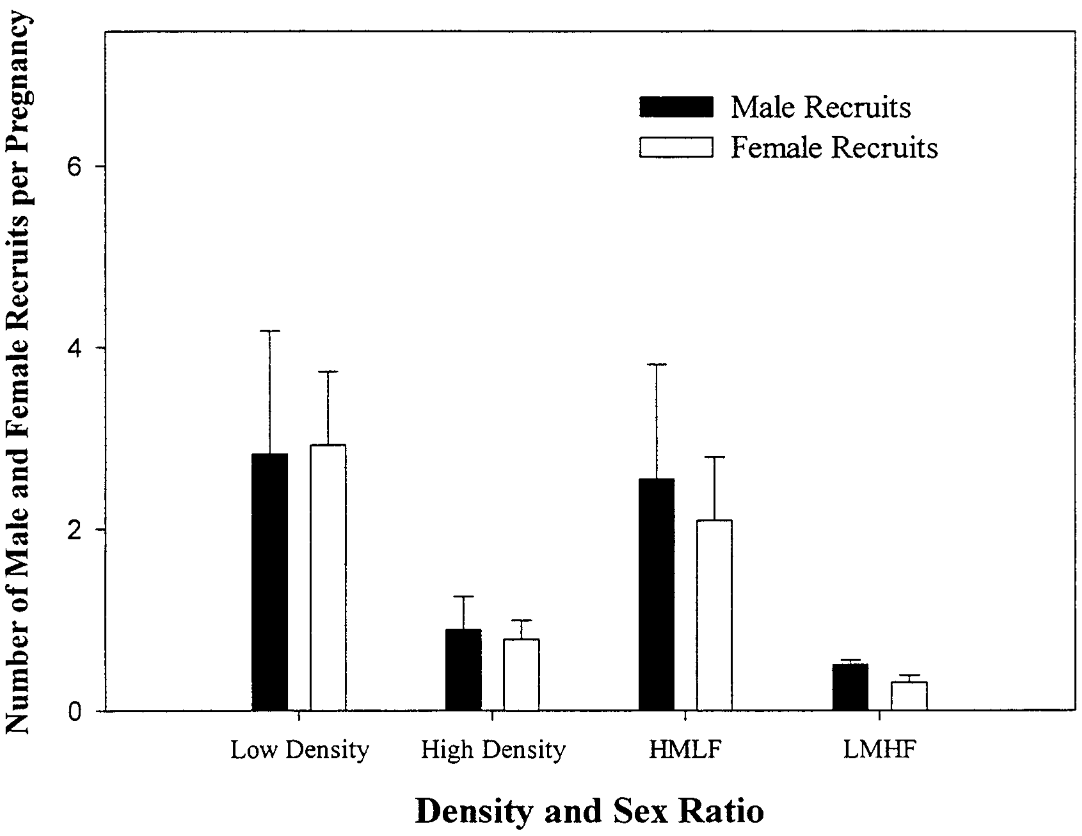

Figure 5. Mean (standard deviation) number of male and female gray-tailed vole recruits per pregnancy for each density and sex-ratio treatment in eight enclosures at Hyslop Farm, Benton County, Oregon, 1997.

towards more female recruits (47 % male), this result was not conclusive. In a recent study using gray-tailed voles, Dalton (1998) found that females did form kin groups at low densities, but they had no measurable effect on fitness of members in the group. Individual benefits to remaining in kin groups has been shown for Townsend's voles (Lambin and Yoccoz, 1998), field voles, *M. agrestis* (Pusenius et al., 1998), and bank voles, *Clethrionomys glareolus* (Mappes et al., 1995), but I was unable to demonstrate that this benefit was sufficient to induce a sex-ratio adjustment favoring daughters at low densities in gray-tailed voles.

Similarly, my results did not support the hypothesis that male-biased recruit sex ratios should be produced at high densities to reduce pressure on local resources (LRC hypothesis). Densities at the end of the summer reached 23-54 adults of each sex (~ 400 adults/ha). These densities approach or exceed peak densities for microtine rodents (Taitt and Krebs, 1985). At these high densities, mean home-range sizes of both males and females were significantly smaller than those at low densities, overlap by females increased to 2.71 (± 2.01) home ranges of other females, and the amount of home range overlap increased to 57% (± 30%). Thus, space was more limited at high than at low densities, but I did not find a measurable bias in the sex ratios of recruits (52% male). While space was more limited at high densities than at low (Fig. 2), the enclosures did not appear to be limited in food resources at the end of the summer, though I did not quantify food availability. Thus, local resource competition may never have been great enough to induce male-biased sex ratios at high densities. However, overall juvenile recruitment was lower at high densities (< 1 recruit/pregnancy) than at low densities (≥ 4 recruits/pregnancy). Similarly, Wolff and Shauber (1996) found that the number of recruits per pregnancy correlated inversely with the number of adult female gray-tailed voles, but pregnancy rates did not diminish despite population densities approaching 3,000 voles/ha. My result suggested some mortality factor that limited offspring survival.

The results of my study also provided no support for Fisher's hypothesis that sex ratios would be adjusted to increase the frequency of the rarer sex in the population (PSR hypothesis). More males were recruited in all of the four LMHF populations, as predicted by the PSR hypothesis; however, more females were recruited in only one of the four HMLF populations. Two explanations can be offered to explain the lack of support for the PSR hypothesis in my study: (1) the experimental skew in population sex ratios was conducted in the autumn; therefore, the effects of the timing within breeding season may have overwhelmed the effects of a skewed adult sex ratio and (2) a biased sex ratio of offspring might have occurred at the pre- or post-partum level, but was not reflected in the population recruitment sex ratio. Manipulations of offspring sex ratios could result from differential parental investment in the sexes either at conception or after birth (Trivers and Willard, 1973). McShea and Madison (1986) found that embryo sex ratios of meadow voles were 1:1, but due to differential maternal investment, recruitment rates were higher for females than males. Differential maternal investment in the sexes has also been demonstrated in several laboratory experiments (Bazhan et al., 1996; Labov et al., 1986; McClure, 1981). I was not able to determine birth sex ratios in my study, but sex ratios at the time of recruitment could be confounded by differential selection by sex prior to recruitment.

My study also may not have been conducted over a long enough time period or through enough generations to test the PSR hypothesis. According to Fisher (1930), the rarer sex should contribute proportionally more genes to succeeding generations than the more common sex. Therefore, selection should eventually favor that lineage that produced more of the rarer sex. In that I removed offspring during the sex-ratio treatments, I was unable to test this aspect of Fisher's hypothesis.

The results of my study are partially consistent with the TBS hypothesis that recruit sex ratios should be female-biased in spring and male-biased in autumn. Competition between spring-born males and larger, autumn-born males for access to females should give a reproductive advantage to mothers that produce daughters in the spring and sons in the autumn. When I combined the autumn data and tested differences in sex ratios between spring and autumn, I found male-biased recruit sex ratios in 7 of 8 enclosures and an overall average of 58% male recruits (Table 2). Thus, even with a confounding treatment designed to produce more females, a male bias prevailed. However, my results did not show a strong female bias in juvenile recruitment in spring, with female-biased recruit sex ratios in 5 of 8 enclosures and an overall average of 53% female recruits.

According to Werren and Charnov (1978), spring-born females should be able to breed shortly after weaning, whereas spring-born males may not breed immediately following weaning because they must compete with larger autumn-born males for access to mates. My results did not show a significant female bias in spring populations. These results differed from those of Lambin (1994) and McShea and Madison (1986), who observed female-biased recruit sex ratios in Townsend's voles and meadow voles, respectively, in the spring. However, in gray-tailed voles, spring-born females may not have a reproductive advantage over spring-born males because female kin groups do not provide any fitness benefits to group members (Dalton, 1998).

While I found no significant female bias in recruit sex ratios in the spring, the results of my study showed a male-biased recruit sex ratio in the autumn (Fig. 4). Similarly, McShea and Madison (1986) found male-biased sex ratios in autumn litters of meadow voles. McShea and Madison examined the primary (embryo) and secondary (birth) sex ratios, whereas I observed the tertiary (recruit) sex ratios. Thus, male-biased birth sex ratios in the autumn appear to persist into the post-weaning recruitment period. I finished trapping for recruits on 23 December, the end of the breeding season (Wolff et al., 1994) and was still observing a male bias in juvenile recruitment. Boonstra (1989) found that juvenile male meadow voles had the highest probability of entering the breeding population if they were born late in the year and delayed maturing until the following spring, whereas females had the highest probability of entering the breeding population if they matured in their year of birth. Also, in a study of the overwinter demography of gray-tailed voles in these enclosures, Brunkal (1996) found that male survivorship was higher than that of females (*males* = 73% - 88%; *females* = 58% - 88%). While survivorship declined for both sexes from autumn into winter, survival rates for male voles never declined below 73% while female survival rates declined dramatically, rebounded and then declined again in February (Brunkal, 1996). Similarly, Madison et al. (1984) noted that juvenile male meadow voles may have a higher overwinter survival rate than females because males are more tolerated within winter communal groups. Therefore, the reproductive benefits of producing the sex with higher overwinter survivorship and greater probability of breeding the next spring may have induced the production of male-biased sex ratios in the autumn in my study.

Clutton-Brock and Iason (1986) and Frank (1990) reviewed available literature on facultative sex-ratio adjustment and found that while population sex ratios generally do not deviate significantly from 1:1, at any given time offspring sex ratios can fluctuate in response to a variety of related extrinsic (season, availability of local resources) and intrinsic (densities, adult sex ratios, maternal condition, competition or cooperation among siblings, sex differences in energy requirements during early growth) factors. I found that timing within the breeding season appeared to affect the sex ratio of gray-tailed vole recruits with more males produced in the autumn, but no sex biases occurred in any of the other treatments. Under the conditions of this experimental study, I was not able to measure sex ratios of individual litters. However, if differential mortality or production of one sex were occurring at the fetal or litter level, these selective factors were not detectable at the population level. The recruitment sex ratio in this study did not deviate from 1:1 under four different experimental treatments suggesting that the ultimate benefits of producing sons and daughters over a range of environmental and social conditions may balance each other resulting in populations with equal numbers of males and females.

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CHAPTER 4

Conclusions

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4.1 CONCLUSIONS

The gray-tailed vole was used as a model species to test hypotheses on spacing behavior and facultative sex ratio adjustment. Specifically, the influences of female dispersion and intrasexual competition on male home range size and the influences of population density, adult sex ratio, and season on sex ratios of offspring were studied in two experiments conducted in enclosed populations.

In general, female small mammals compete with each other for food and space to rear offspring while males compete with each other for access to reproductive females (Emlen and Oring, 1977; Trivers, 1972). Chapter 2 describes male space-use responses to manipulations of the densities of females and males. In general, responses were similar to those reported in other small mammal studies (e.g., Agrell et al., 1996; Jeppsson, 1990; Nelson, 1995, 1997). However, no other study examined the relative influences of access to females and male competition. I found that both competition and access to females influence the home-range size of males, with an upper limit of overlap with either sex. Attempting to mate with large numbers of females have two major costs, competition with other males and increased risk of predation, both of which limit movements and access to mates. In this study, the maximum number of male home ranges that a given male overlapped was about four, regardless of the number of females. Thus, spatial overlap and competition with other males may have a high fitness cost and limit home- range size. Additionally, the maximum number of female home ranges that a given male overlapped was about five. Beyond five females, male competition and predation risk may increase sufficiently such that males maintain an optimal home-range size that provides maximum fitness benefits while minimizing the costs of competition and predation. Reproductive success of males is maximized by balancing breeding opportunities, reduced competition, and minimized risk of predation.

Mammalian population sex ratios generally do not deviate from 1:1, but variations in offspring sex ratios have been observed in numerous natural and experimental populations. Sex ratio theory predicts that natural selection should favor the production of that sex offspring which provides the greatest reproductive return to the parents if the return for one sex is different than the other. Chapter 3 describes the sex ratio of recruits in response to season, population densities, and skewed adult sex ratios. None of the populations in my study contained either female-biased recruit sex ratios at low densities of females or male-biased sex ratios at high densities of males and/or both sexes as predicted by Packer and Pusey's (1987) local resource enhancement, Clark's (1978) local resource competition and Fisher's (1930) population sex ratio hypotheses. My study design did not allow me to determine litter sex ratios, thus, facultative sex-ratio adjustment may have occurred at the fetal or litter level in response to manipulations of density and sex ratio (McShea and Madison, 1986; Trivers and Willard, 1973), but it was not detectable at the population level. However, significantly more males than females were produced in the autumn than in the spring, suggestive of a seasonal effect on recruit sex ratios (Werren and Charnov 1978). A recent study of gray-tailed voles showed higher overwinter survivorship of males than females. Therefore, the reproductive benefits of producing males in the autumn may have been sufficiently high as to induce a facultative sex-ratio adjustment at the end of the breeding season. The ultimate benefits of producing sons and daughters over a range of environmental conditions may balance each other resulting in populations with equal numbers of males and females.

Hopefully, my research will contribute to our understanding of spacing systems and population dynamics of voles and of species with similar behavioral patterns.

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