

SOCIAL ORGANIZATION OF A SPECIES OF SINGING MOUSE,  
*Scotinomys xerampelinus*

By

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This thesis is dedicated to my parents, Pierre and Linda, who have supported me in all of my dreams and ambitions throughout my life.

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Abstract of Thesis Presented to the Graduate School  
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*Scotinomys xerampelinus*, a species of singing mouse, is diurnal, insectivorous, and exhibits a complex and unique calling behavior. Little is known about the social structure of this species. This thesis investigated the mating system and spacing patterns exhibited by *S. xerampelinus*. The research consisted of two parts: a field study and a laboratory study.

The field study investigated the spatial organization of a wild Panamanian population of singing mice, with the goal of describing their social and mating system. The field study consisted of mark-recapture live-trapping and radio-tracking in the summers of 2003 and 2004. Our analyses of home range area overlap suggest exclusive space use among females, but not among males. This female exclusive space use could be driven by mutual avoidance, territorial aggression, or some combination of the two. We found patterns of overlap between male and female home ranges, suggesting an absence of intersexual territoriality. Male and female home range areas and body weights

were not significantly different from each other. Males and females each overlapped, on average, with 1.6 individuals of the opposite sex. The spatial and population attributes that we examined were most closely correlated with a promiscuous mating system.

In order to further investigate territorial behavior in *Scotinomys xerampelinus*, a series of resident-intruder laboratory experiments were run on a colony of mice trapped in Panama and their progeny. There was no support for site-specific dominance in either sex. Males were more aggressive than females, and more aggressive towards other males than towards females. Females did not differ in their levels of aggression in response to male and female conspecifics. Females also had more instances of “zero aggression” trials. There was no overall significant difference in out-of-sight behavior for either sex. Based on our field and laboratory findings, we propose that the exclusive area use exhibited by females is driven by mutual avoidance, rather than territorial aggression. Males are intolerant of each other, but do not appear to be territorial, and probably also exhibit a degree of mutual avoidance.

## CHAPTER 1 INTRODUCTION

### **The Singing Mouse**

The singing mice of the genus *Scotinomys* produce a complex sequence of loud vocalizations that project long distances (Hooper & Carleton 1976). The mice typically stand on their hind limbs, angle their snouts upwards, and emit trill-like calls that are audible to humans but also extend into the ultrasonic range (Hooper & Carleton 1976). The function of this call is not known.

The eventual, long-term goal of this research is to understand the function of the complex calling behavior of the singing mice. In other taxa, including mammals and birds, highly vocal behavior has been linked to both territoriality and mate attraction (Poole 1985, Falls 1988, Nowak 1997, Nowicki et al. 1998). This means that one cannot evaluate the function of singing behavior in *Scotinomys* without first knowing their basic social structure, including mating systems and territoriality. Much of the social organization of *Scotinomys* remains largely unknown. Thus, understanding territoriality and mating system in *Scotinomys* is critical to research on the function of calling behavior. We focused on one of the two *Scotinomys* species, *S. xerampelinus*.

In this research, we asked two questions:

1. Does *Scotinomys xerampelinus* have a territorial social system?
2. What is the mating system of *Scotinomys xerampelinus*?

We are following Lott's (1991) definition of a social system: the emergent outcome of a consistent set of social relationships, where social relationships are the result of social interactions between individuals (Hinde 1976, Hinde 1983, Lott 1991).

### **Species Background**

*Scotinomys* is a muroid neotomine rodent (Musser & Carleton 2005), and is most closely related to the genus *Baiomys* (pygmy mice), with the two sister taxa forming the Baiomyini tribe (Bradley et al. 2004, Musser & Carleton 2005). The genus *Scotinomys* consists of two species, *S. teguina* (Alston's brown mouse, or short-tailed singing mouse) and *S. xerampelinus* (Chiriquí brown mouse, or long-tailed singing mouse; Musser & Carleton 2005). Both *Scotinomys* species are native to Central America, with the genus ranging in distribution from Oaxaca, Mexico to Chiriquí, Panama (Hooper 1972). They inhabit cloud forests and high elevation grasslands. The two species exhibit altitudinal and vegetative zone segregation, with *S. teguina* existing at lower elevations. Previous studies have shown that although the two species are for the most part allopatric, there appear to be small areas of sympatry (Hooper & Carleton 1976). Their discontinuous distribution results in mountaintop "islands" of scattered populations. *Scotinomys* are unusual among rodents in that they are highly vocal, are diurnal, and are primarily insectivorous (Hooper & Carleton 1976).

The singing mouse is attractive as a potential model system for research into social behavior and vocal communication. Their calling behavior provides an easily detectable auditory signal that can be manipulated for the purposes of behavioral experiments. The two closely related species are especially appropriate for behavioral ecology studies due to the species' occurrence in both sympatry and allopatry, and their disjunct geographic distribution throughout Central America. This natural variation

allows for the study of the social behavior of the mice in the context of a diversity of ecological and environmental factors. *Scotinomys* research also has conservation implications, since the mice live in fragile, threatened ecosystems. Since singing mice are adversely affected by development and climate change, they are potential indicators of ecosystem health. For this research we focused on a wild population of one species, *Scotinomys xerampelinus*, in Cerro Punta, Panama. This species was particularly conducive to our field and laboratory studies, since it was locally abundant, exhibited a high re-trap success rate, and lives and breeds well in captivity.

*Scotinomys* calls have been observed in various contexts, with males calling more frequently than females, spontaneous calls in both sexes without noticeable external stimulus, calls exhibited by males recently paired with females, and by females in a post-partum estrus (Hooper & Carleton 1976, Blondel pers. obs). In previous descriptions of interspecific dominance involving male-female pairs of both species, the dominant male (which was not always of the same species) called with greater frequency (Hooper & Carleton 1976). Therefore there is anecdotal evidence for both a territorial and a mate attraction or mate contact function for the call. These are not mutually exclusive, and as in avian species, the call may serve different functions in different contexts (Falls 1988). We will return to the question of *Scotinomys* call function in Chapter 4.

### **Territoriality**

In *Scotinomys*, both agonistic behavior in male-male encounters and infrequent encounters of same-sex individuals have been observed anecdotally in a laboratory setting (Hooper & Carleton 1976). The genus is also highly vocal, which is often linked to territoriality in other species (Poole 1985, Falls 1988, Nowak 1997, Nowicki et al. 1998). Thus, **we hypothesized that *S. xerampelinus* exhibits a territorial social**

**system within sexes.** Previous laboratory observations have also shown that males and females can be kept together as breeding pairs even when females are not in estrous, and that males are tolerated by nursing females (Hooper & Carleton 1976). Thus, we **hypothesized that *S. xerampelinus* is not territorial between sexes.**

The territoriality hypotheses were tested by a combination of fieldwork and laboratory experiments. In the field, we determined the home ranges of a wild population of *S. xerampelinus* using radio-tracking and mark-recapture (Chapter 2). We then inferred the population's social system based on the home range patterns.

Since the animals in the field cannot be directly observed, we could not check for agonistic behavior in the presence of a conspecific. Thus, we complemented the field observations with laboratory experiments that allowed us to observe actual avoidance and/or aggressive defense behavior (Chapter 3).

### **Demonstrating Territoriality in Small mammals**

Rodents vary across a spectrum of territorial behavior, from undefended home ranges, such as field mice (*Apodemus*), to solitary asocial individuals that defend against all conspecifics, such as pocket gophers (*Geomys*; Poole 1985, Brown 1997).

Territoriality can also vary within and between the sexes. Rodent territoriality can be quite complex, as in the yellow-bellied marmot (*Marmota*): the males defend harems of females; the females, in turn, are not territorial towards burrow-mates, but are aggressive towards inhabitants of other burrows (Poole 1985).

The most commonly used and oldest definition of territoriality is “defended area” (Maher & Lott 1995). Unfortunately, the concept of territory is not consistently defined among scientists. A survey on the use of the term “territoriality” in the vertebrate literature found that only 50% of studies used the “defended area” definition, with the

remainder using 47 alternative definitions (Maher & Lott 1995). Maher and Lott explain some of this variability by the fact that researchers are often asking different questions. Some may be asking behavioral questions, and therefore they examine direct social interactions and the mechanisms of territory maintenance. Other researchers are more concerned with the consequences of territorial behavior, and are asking ecological questions. Ecological studies may address resource allocation or intensity of predator pressure, for example (Maher & Lott 1995). Additionally, for many species that are difficult to observe behaviorally in the field, consequences of territoriality such as minimal home range overlaps, although considered imperfect proxies of territoriality, are the only evidence of territorial behavior itself (Powell 2000).

Of the 48 total definitions reviewed by Maher and Lott, most were variations on three main conceptual definitions: (1) defended area, (2) site-specific dominance, and (3) exclusive area (Table 1-1). Definitions 1 and 2 are behavioral in nature, while definition 3 is ecological. Some authors in Maher and Lott's review used two- or three-criteria definitions of territoriality, in which all were necessary but none were sufficient alone. In this study, we will define territoriality using three conceptual criteria: site-specific dominance, defended area, and exclusive area use. Each of these criteria measures territoriality in different fundamental aspects and contexts, and none are complete by themselves. This is especially true for exclusive area use, due to its indirect nature.

Territorial behavior is a result of competition for a limiting resource. The primary benefit of territoriality is priority of access to a limited resource, and the primary cost is defense against intruders (Schoener 1983, Fryxell & Lundberg 1998, Vlasman & Fryxell 2002). When the cost of defense is less than the benefit of the resources, territorial

behavior may occur (Carpenter & McMillen 1976, Hixon et al. 1983, Belcher & Darrant 2004).

Two major factors influence territory size: food abundance and intruder pressure (from competitors). Food abundance determines the size necessary for the nutritional requirements of the defender. Competitor density influences the costs of defending a territory, and increasing intruder pressure results in increasing defense costs and decreasing territory size (Yeaton and Cody 1974, Vlasman & Fryxell 2002). The result of these two opposing forces is the optimal territory size that maximizes benefits minus costs. There is considerable debate as to whether food abundance or intruder pressure is the major determinant of territory size (reviewed in Vlasman & Fryxell 2002).

We evaluated whether *S. xerampelinus* occupied an exclusive area by using field observations measuring the degree of overlap between individuals (Chapter 2). The data-collection methods that we used in the field (mark-recapture and radio-tracking) lend themselves to evaluating exclusive use, since territorial displays and interactions that would be observable in larger animals are not easily seen in rodents in the wild. Mark-recapture and radio-tracking are established methods that are used by researchers investigating both rodent social systems and territoriality (Gaulin & Fitzgerald 1988, Batzli & Henttonen 1993, Bubela & Happold 1993, Getz et al. 1993, Kraus et al. 2003).

We evaluated whether *S. xerampelinus* exhibited site-specific dominance and defended an area by using resident-intruder behavioral laboratory experiments (Chapter 3). Demonstrating whether exclusive space use, home area defense and site-specific dominance occurs in *Scotinomys xerampelinus*, using the combination of field and

laboratory studies, will aid greatly in our understanding of the social system of this species.

### **Mating System**

After investigating the general question of territoriality in *Scotinomys*, we turn to their mating system, and investigate more specifically the living arrangement of males and females. Do male and female pairs share use of a territory and/or home range (social monogamy), as occurs in some other muroids, such as *Peromyscus polionotus* (oldfield mouse; Ribble 2003)? Do males overlap several female home ranges (social polygyny), as occurs in the muroid *Microtus xanthognathus* (taiga vole; Wolff 1985)? If so, how many females are overlapped by the male? The three mating systems found in rodents are promiscuity, polygyny, and monogamy. Promiscuity is defined as no exclusivity in reproductive behavior existing between individual males and females after mating has occurred (Clutton-Brock 1989). Polygyny is defined as one male mating with the same group of females in successive mating attempts (Clutton-Brock 1989). Social monogamy is defined as a male-female pair sharing exclusive use of a territory (Reichard 2003). Social monogamy is sometimes (but not always) correlated with sexual monogamy (an observed exclusive sexual relationship within a male-female pair) and genetic monogamy (genetic analysis that confirms exclusive reproduction within a male-female pair; Reichard 2003).

### **Theoretical Bases for Mating System Correlates**

Space use and territoriality patterns among small mammals are thought to be determined by social and ecological factors such as food distribution and predation pressure (Emlen & Oring 1977, Ostfeld 1990). These factors influence female distribution, which in turn determines male distribution (Emlen & Oring 1977, Ostfeld

1990, Hanski et al. 2000, Luque-Larena et al. 2004, Sulok et al. 2004). This results in the different spacing patterns that are characteristic for each mating system (Table 1-2).

Thus, a strong predictor of mating systems is the distribution of resources for a given population (Emlen & Oring 1977), and this is particularly true for small mammal mating systems (Ostfeld 1990).

Female fitness is thought to be highly dependent on food and nesting resources, and thus limited food resources can cause intraspecific competition (Ostfeld 1985a). The “food-defense hypothesis” (Emlen & Oring 1977, Ostfeld 1990, Wolff & Peterson 1998) suggests that certain predictions can be made about female territoriality based on the nature of local food resources. When food resources are sparse, patchy, and slowly renewable, and when population density is low, females are expected to be highly territorial, since resources will be easier to defend. When food resources are abundant, evenly distributed, widespread, and rapidly renewed, and when population is high, females are expected to not be territorial, since the costs of defense would be too high, and the benefits too low. Different combinations of these resource and population attributes would result in intermediate levels of territoriality. An alternative hypothesis to the causes of territoriality in female rodents is the “offspring-defense hypothesis”, which posits that territoriality in females has evolved primarily to prevent infanticide by other females (Wolff & Peterson 1998).

Female small mammals invest more energy than males into gestation and parental care, and males invest less into offspring, and more into finding potential mates (Bonaventure et al. 1992). The limiting resource for males is thought to be estrous females or copulations (Ostfeld 1985a), and the distribution of females becomes a strong

influence on male distribution. When females are clumped, they are easy to defend, and males will exhibit territoriality (Emlen & Oring 1977, Ostfeld 1990). The male home range size will maximize their access to fertile females (Shier & Randall 2004). This pattern is characteristic of the polygynous mating system (Table 1-2; Krebs & Davies 1987). When females are dispersed, the defense costs become too high, and males will not exhibit territoriality (Ostfeld 1990). This pattern is characteristic of the promiscuous mating system (Table 1-2; Krebs & Davies 1987). Females are thought to mate multiply in these promiscuous systems in order to confuse paternity, and thus deter male infanticide (Wolff & Peterson 1998), and also to increase the genetic quality of offspring (Neff & Pitcher 2005). The hypothesis that female spatial patterns influence male spacing patterns has been supported by data gathered from extensively studied muroids, such as the microtines (voles; Ostfeld 1990) and the peromyscines (deer mice and white-footed mice; Ribble 2003).

The “females in space” (FIS) hypothesis (Ostfeld 1985a, Ostfeld 1990) is an extension of Emlen & Oring’s (1977) hypothesis. FIS proposes that during the breeding season of a small mammal, relaxed territoriality within one sex is correlated with stricter territoriality in the other. If females are territorial and thus dispersed, males are unlikely to be able to defend multiple females. If females are non-territorial, which usually correlates with females that are clumped around food resources, then males are more likely to be able to defend these groups against other males. In short, when females are territorial, males are not, and when males are territorial, females are not (Ostfeld 1990).

The FIS hypothesis has been supported by both interspecific and intraspecific comparisons. Interspecific comparisons that examine social spacing of rodent species

reveal that territoriality usually occurs in only one sex at a time (Ostfeld 1990).

Intraspecific comparisons have examined changes in food resources and population density among different populations of a particular species. For example, in *Peromyscus leucopus* (white-footed mice), population density increases have been correlated with female shifts from territoriality to overlapping home ranges and with male shifts from overlapping ranges to defended territories (Ostfeld 1990, Wolff & Cicirello 1990).

Although FIS seems to explain promiscuous and polygynous mating patterns, and thus the mating systems of the majority of rodents, FIS is not sufficient to explain the rare occurrences of monogamy and communal breeding in certain species (Ostfeld 1990).

In addition to male and female spacing behavior, another frequently used rodent mating system correlate is sexual dimorphism in size (Table 1-2). Sexual dimorphism is generally present in polygynous systems, but is minimal or absent in promiscuous and monogamous systems. This is because polygynous mating systems involve more intrasexual competition among males than do promiscuous or socially monogamous systems (Heske & Ostfeld 1990). Polygynous males must compete for longer periods of time, and use a more intense “contest” competition. Promiscuous males use a less intense combination of “contest” and “scramble” competition. Thus there is stronger intrasexual selection among polygynous males, resulting in a stronger selection for large size.

Female territoriality is more developed in monogamous and promiscuous species than in polygynous, and large females in promiscuous systems have been correlated with higher reproductive success (Getz et al. 1987, Heske & Ostfeld 1990). This increased intrasexual selection in promiscuous and monogamous females may contribute to the monomorphism observed in these systems (Heske & Ostfeld 1990).

### ***Scotinomys xerampelinus* Mating System**

When studying a species for which the mating system is not known, typically a variety of different factors are examined in order to generate an initial hypothesis. These *a priori* factors usually include mating systems of related taxa, presence or absence of paternal care, occurrence of similar unique behaviors in closely related species (such as calling behavior in the case of *Scotinomys*), sexual dimorphism, and the habitat of the study species.

Social monogamy is rarely found among the neotomines (Nowak 1999, Poor 2005) and is rare even at higher taxonomic levels. For example, social monogamy occurs in only around 5% of mammalian species (Wolff 1985, Clutton-Brock 1989, Ribble 1992). Thus, *S. xerampelinus* would most likely not be monogamous.

Male parental care has historically been used to predict social and mating systems. This is because highly developed mammalian paternal care is closely associated with social monogamy (Dewsbury 1981, Clutton-Brock 1991, Ribble 1992, Getz et al. 1993). However, paternal care is not unique to monogamous systems, and does occur to some extent in promiscuous and polygynous rodent systems (Clutton-Brock 1991, Ribble 2003). Laboratory-observed paternal care has been reported for promiscuous, polygynous and monogamous rodents, and has also been suggested to potentially be a recurring laboratory artifact (Ribble 2003, Wolff 2003, Schradin & Pillay 2005). Moreover, some recent studies have found that paternal care is a poor predictor of social monogamy (Reichard 2003). Thus, although some male parental care has been observed in *S. xerampelinus*, such as huddling over pups (Hooper & Carleton 1976), this behavior is not a strong indicator of social monogamy and does not help infer the mating system of the species.

Comparing the vocal behavior of *S. xerampelinus* to other vocal muroids only slightly helps clarify the mating system. There are very few highly vocal muroids. One other vocal muroid, the grasshopper mouse (*Onychomys*), may be polygynous, although its mating system has not been extensively studied (Nowak 1991, Lautzenheiser 2003).

Looking at the habitat of our study population, we can use the “food-defense” hypothesis” (Emlen & Oring 1977, Ostfeld 1990, Wolff & Peterson 1998) to predict the *S. xerampelinus* mating system. Our study site consisted of an abandoned pasture, dotted with rotting logs, tree stumps and shrubs. The stumps and logs are insect-rich resources for the insectivorous *S. xerampelinus*. Since the insect resources in the study grid follow a patchy distribution, this would suggest a clumped non-territorial female distribution. Clumped distribution of female rodents usually correlates with territorial males, which defend the females against other males, resulting in a mate-defense polygynous mating system (Emlen & Oring 1977, Ostfeld 1990). With all of the above taken together, **we hypothesized that *S. xerampelinus* exhibits a polygynous mating system.**

This hypothesis was tested in the field using mark-recapture and radio-tracking. These methods are frequently used to investigate rodent mating systems (Gaulin & Fitzgerald 1988, Bubela & Happold 1993, Getz et al. 1993, Kraus et al. 2003). The spatial patterns of individuals are directly related to their sexual strategy, and different spacing patterns can be generally associated with specific mating systems (Wolff 1985, Ostfeld 1990, Luque-Larena et al. 2004). We determined the home ranges of a wild population of *S. xerampelinus*, and collected trapping information (such as weight) from the study population. We then made social system inferences based on spatial patterns and sex-specific weights (Chapter 2).

Any inferences that are made based on spacing patterns are limited to a description of the living arrangement of males and females, and are designated by the term “social,” as in “social monogamy,” “social polygyny,” and “social promiscuity”. They do not infer any reproductive interactions or patterns, or genetic relationships (Reichard 2003). Once the social living arrangement is defined, future research (such as genetic analysis) can clarify the genetic and sexual relationships of the study species. However, the male and female spacing patterns and living arrangements of a study population are considered meaningful though indirect measures of reproductive strategy (Shier & Randall 2004).

The field investigations into the *S. xerampelinus* mating system and social system are detailed in Chapter 2. Chapter 3 details the resident-intruder laboratory experiments, and considers the implications of the combined field and laboratory data. In Chapter 4, we will return to the question of the likely function of *Scotinomys* calling behavior, and outline potential avenues for future *Scotinomys* research.

Table 1-1. Definitions of territoriality

Conceptual Definition	Category	Methods
Defended area: Defended area via fighting, self-advertisement, or threat (Mayr 1935; Nice 1937; Lack 1939; Hinde 1956; Brown & Orians 1970)	Behavioral	Observed defense of an area. Includes: agonistic or aggressive behaviour in general (Leighton 1986, Pietz 1987); displays, retreats, chases and fights (Evans 1951, Jarman 1979, Gibson & Bradbury 1987); behavior at boundaries (Young 1956, Carranza et al. 1990).
Site-specific dominance: territory is that part of the animal's home range in which the animal is aggressive and usually dominant to intruders (Emlen 1957, Murray 1969, Leuthold 1977)	Behavioral	Individual A dominates B in area a, but is subordinate to B in area b (Wiens 1976, Desrochers & Hannon 1989); animals reciprocally preventing each other from engaging in certain specific activities in "their" area (Leuthold 1977); overt defense and exclusive use not required (Kaufmann 1983).
Exclusive area: Exclusively occupied area (Pitelka 1959, Schoener 1968, Krebs 1971)	Ecological	Little (non-significant) degree of overlap between individuals or groups (Kolb 1986, Konecny 1987, Sandell 1989); home range overlap that is significantly lower than would be expected by random placement of home ranges in a study grid (Batzli & Henttonen 1993)

Adapted from Maher and Lott 1995

Table 1-2. Characteristics of mammalian mating systems

Mating system	M vs. F HR size	M-M HR overlap	F-F HR overlap	MF pair share HR?	Sexual dimorph	Paternal care	Dispersion of Female
Promiscuity	M>F	Yes	No	No	Minimal	Sometimes	Wide/ Uniform
Polygyny	M>F	No	Sometimes	No	High	Sometimes	Clumped
Social Monogamy	M=F	No	No	Yes	Minimal/ None	Yes	Wide/ Uniform

Correlates of rodent mating systems. M = Male, F = Female, HR = Home Range, dimorph = dimorphism. As reviewed in Ostfeld 1985a, Krebs & Davies 1987, Clutton-Brock 1989, Clutton-Brock 1991, Heske & Ostfeld 1990, Borowski 2003, Reichard 2003, Bergallo & Magnusson 2004, Shier & Randall 2004, Endries & Adler 2005, Schradin & Pillay 2005, Steinmann et al. 2005

CHAPTER 2  
HOME RANGE, TERRITORIALITY, AND  
MATING SYSTEM IN A NATURAL POPULATION OF  
*Scotinomys xerampelinus*  
IN PANAMA

**Introduction**

Space use in rodents is affected by a variety of factors, including resource availability, habitat heterogeneity and suitability, climate (such as moisture regimes and ambient temperature), population density, and predation (Emlen & Oring 1977, Ostfeld 1985a, Ostfeld 1990, Endries & Adler 2005). The distribution of individuals in a population in space and time is also closely associated with the particular mating system and social system of that population (Gaulin & Fitzgerald 1988, Shier & Randall 2004, Steinmann et al. 2005). This is because spatial organization is determined by social processes, which means that the mating system and social system of a population can be inferred from their spatial organization (Shier & Randall 2004). The aim of this field study is to describe the spatial organization and population characteristics of wild-living *Scotinomys xerampelinus* (Rodentia: Cricetidae), and to use this to infer the social system and the mating system of the species.

**Species Background**

*Scotinomys xerampelinus* is known by a variety of common names, including the long-tailed singing mouse, the Chiriquí brown mouse, and the Chiriquí singing mouse. *S. xerampelinus* is a muroid rodent (Myers et al. 2005). The family and subfamily classification of muroids has historically been controversial. The most generally

accepted *Scotinomys* classification until recently had been as family Muridae, subfamily Sigmodontinae (Nowak 1991). However, the latest molecular data have placed the genus in superfamily Muroidea, family Cricetidae, subfamily Neotominae (deermice, woodrats and relatives; Steppan et al. 2004, Musser & Carleton 2005, Poor 2005). Note that in this most recent revision the family Muridae still exists within the superfamily Muroidea; however, *Scotinomys* is no longer designated a murid.

Our long-term research goal is to understand the function of the unique calling behavior of the singing mouse. In avian species, songs are thought to signal territory occupancy, and thus deter potential intruders by announcing the potential for agonistic encounters (Falls 1987, Nowicki et al. 1998). These pre-encounter territorial advertisements minimize defense costs for the resident of a territory, by avoiding some agonistic encounters. For visually inconspicuous birds, a territorial call would become even more important, as it would bring attention to the presence of a possibly unnoticed resident. Since the singing mouse is a highly vocal, small, visually inconspicuous rodent, the *Scotinomys* calling behavior may serve the same function as avian birdcalls. It is therefore critical to assess the *Scotinomys* mating system and social system, and to check for the existence of any territorial behavior. This was accomplished by studying a wild population of *S. xerampelinus*, examining variables that are correlated with different mating systems and presence or absence of territoriality. Specifically, we examined home range spatial patterns, distribution of females, and sexual dimorphism.

### **Home Range**

An animal's home range is "that area traversed by the individual in its normal activities of food gathering, mating, and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered part of the home range

(Burt 1943).” The qualifier “normal” in the above definition is vague, and to this day no consensus exists on whether an animal’s home range should or should not include areas that an animal is familiar with, yet seldom travels (White & Garrott 1990, Powell 2000). One way to define objectively the “normal” movements of an animal is to use a probability level, which specifies the areas where a given animal is most likely to be found (White & Garrott 1990). Depending on the questions being asked, the home range estimator method, the study population and the number of location fixes, the probabilistic definitions of home ranges will vary. In the published literature home range estimators vary from 75% to 95% of the animal’s observed locations within the home range contour (Bubela & Happold 1993, Gliwicz 1997, Hanski et al. 2000, Borowski 2003, Briner et al. 2004, Eccard et al. 2004, Luque-Larena et al. 2004, Endries & Adler 2005). For the purposes of this study, we are defining two types of home range for each individual. The “exhaustive home range” is defined as the 100% minimum convex polygon (MCP) of the location points found for each individual. The “core home range” is defined as the 85% MCP of an animal’s location points, using the recalculated arithmetic mean method (Kenward 2001). This 85% home range includes the majority of location data, without including large areas that are only rarely used by the animal (Bubela & Happold 1993). Home range areas of individuals can overlap with conspecifics, which is referred to in this study as “home range overlap.”

When examining patterns of space use, researchers frequently use as a metric the home range size and overlap of individuals (Shier & Randall 2004). Sex-specific home range patterns, such as the relative sizes and overlap of home ranges between and within sexes, can be interpreted as identifying features of a mating system (Steinmann et al.

2005). However, it is important to remember that spatial patterns alone are not always sufficient to ascertain the actual genetic and reproductive strategy of a population, and sometimes require additional genetic or behavioral information (Reichard 2003). Since home range patterns are so closely tied to an animal's mating and social system, home range information is considered a crucial first step for any investigation into the behavioral ecology of a species (Steinmann et al. 2005).

### **Territoriality**

An animal's territory is not necessarily the entirety of its home range. It is only that part of the home range "which is protected from the individuals of the same species either by fighting or by aggressive gestures (Burt 1943)." As described in Chapter 1, for this *Scotinomys* research, we are using three criteria to measure territoriality: exclusive space use, defended area, and site-specific dominance (Maher & Lott 1995). Each of these criteria involves a different aspect of territoriality, and none of these measures will be considered a complete indicator of territoriality by itself. For the field portion of the study, we are focusing on "exclusive space use," an imperfect but quantifiable proxy for territorial behavior in a natural setting. Exclusive space use has been argued by some as the most fundamental characteristic of territorial behavior (Ostfeld 1990). Overt defense of an area and site-specific dominance were not studied in the field due to the difficulty of observing such behavior in wild-living populations of small rodents. Instead, both defense behavior and site-specific dominance were quantified in the laboratory experiments described in Chapter 3. Small mammal studies have shown that when exclusive home ranges are maintained, these ranges are often actively defended and when substantial home range overlap exists, the ranges are often not actively defended (Ostfeld

1990). Thus, overt defense of an area and exclusive space use are frequently positively correlated and can both be indicators of territoriality (Maher & Lott 1995).

Territoriality can occur both within and between sexes of a particular species. In small mammals, territorial behavior can vary greatly among even closely related species. For example, within the genus *Microtus*, species range from female intrasexual territoriality only, to male intrasexual territoriality only, to family groups that defend against other groups (Ostfeld 1985a). Territoriality can also vary between populations of the same species (Ostfeld 1990). Seasonal cycles in territoriality are well documented and are present in several species of voles. For example, prairie voles (*Microtus ochrogaster*) vary seasonally from male-female pairs to communal groups, and meadow voles (*Microtus pennsylvanicus*) demonstrate a seasonal appearance of male intrasexual territoriality (Turner et al. 1975, McGuire & Getz 1998). Territoriality can also vary among conspecific populations living in different habitats. For example, striped mice (*Rhabdomys pumilio*) vary from simple female intrasexual territoriality in some habitats (females are territorial towards all other females), to complex group living in other habitats (groups composed of one breeding male, multiple breeding females, nonreproducing adult male and female offspring, with each group defending their territory against other groups; Schradin & Pillay 2005). This type of phenotypic plasticity, termed “social flexibility,” is thought to be driven by environmental variability (Lott 1991, Schradin & Pillay 2005).

In previous laboratory observations, *S. xerampelinus* behavior has been anecdotally described as displaying agonistic behavior in male-male encounters, and exhibiting infrequent encounters of same-sex individuals (among both males and females; Hooper &

Carleton 1976). This suggests intrasexual territoriality in both males and females. Previous laboratory observations have also shown that males and females can be kept together as breeding pairs even when females are not in estrous, and that males are tolerated by nursing females (Hooper & Carleton 1976). This suggests an absence of intersexual territoriality. We tested the hypothesis that *S. xerampelinus* exhibits both male and female intrasexual territoriality, but does not exhibit intersexual territoriality.

### **Space Use Patterns**

Once home range data have been collected for a population, we can analyze them for space use patterns and social behavior. A first step is to look at home range area overlap between conspecifics. If we assume that territorial behavior functions to disperse animals throughout space, there should be relatively little overlap between home ranges in the presence of behaviorally-mediated spacing (Wolff et al. 1983). Various methods of quantifying this overlap have been proposed. For example, overlap between home ranges of less than 10% has been proposed as evidence of “exclusive territories” (Belcher & Darrant 2004). However, any percentage cut-off such as this seems arbitrary, and the 10% designation does not have a biologically meaningful rationale.

A preferable, less arbitrary method to quantify territoriality in rodent home range data is the Batzli and Henttonen (1993) method. This involves a null hypothesis that home ranges are located randomly in relation to each other. If home range area overlap is significantly lower than would be expected by random placement of the home ranges within the study grid, then individuals are demonstrating avoidance and/or exclusion of each other, and this meets the “exclusive use” criterion for territoriality (Batzli & Henttonen 1993, Priotto et al. 2002). We used the Batzli and Henttonen method to evaluate home range data.

### Space Use Hypotheses and Predictions

- **Hypothesis 1: *S. xerampelinus* exhibits intrasexual exclusive area use in both males and females.**  
Prediction 1: Home range overlap within sexes is significantly lower than what would result from a random placement. This is consistent with avoidance and/or territorial exclusion.
- **Hypothesis 2: *S. xerampelinus* does not exhibit exclusive area use between sexes.**  
Prediction 2: Home range overlap between sexes is equal to or significantly greater than what would result from a random placement. A random placement would suggest a lack of either exclusion or affiliation. A significantly greater than expected overlap implies aggregation, which could reflect affiliation or a common resource use. Both of these would be consistent with an absence of territorial behavior.

### Mating System Categories

Sex-specific territoriality and spacing patterns are intimately connected with the mating system of the species. Typically, mating systems are associated with behavioral, morphological and spacing characteristics, such that a different combination of characteristics is associated with polygyny, promiscuity, and monogamy. By examining these characteristics in a target population, an inference can be made as to the study animals' mating system. In order to determine the *S. xerampelinus* mating system, we must first examine the patterns that are characteristic of different rodent mating systems as reported in the literature (Table 1-2).

Promiscuity is defined as a lack of fidelity of males for females and vice versa (Clutton-Brock 1989). In promiscuous rodent systems, males tend to be non-territorial (extensive overlapping of home ranges), whereas females are territorial during the breeding season. Males have larger home ranges than females and females are widely distributed. Both paternal and maternal care exists. Promiscuity is also associated with minimal sexual dimorphism.

Polygyny is defined as one male mating with the same group of females in successive mating attempts (Clutton-Brock 1989). In polygynous systems, males tend to be territorial (non-overlapping home ranges), and females may or may not exhibit territoriality. Males have larger home ranges than females and females are clumped in distribution. Typically each male home range will encompass one to several female home ranges (Bubela & Happold 1993). Parental care is limited to the females. Sexual dimorphism is highly developed in polygynous mating systems.

There are similarities in the home range patterns of species with polygynous and promiscuous mating systems, and it is not always possible to differentiate between these two based solely on home range data (Bubela & Happold 1993, Priotto & Steinmann 1999). For example, if male home ranges overlap female home ranges in such a way that several males could have access to a particular female at the same time, the space use patterns would not always distinguish a promiscuous from a polygynous mating system. Access to a female allows the opportunity for reproduction, but does not guarantee it, and therefore a population with extensive intersexual overlapping of home ranges that is actually a genetically polygynous system could be mistaken for a genetically promiscuous system. Some researchers acknowledge these difficulties by using the category “promiscuous-polygynous” instead of differentiating between the two (Steinmann et al. 2005). In all cases, additional information, such as paternity analysis of litters, can be used to clarify the mating system.

Social monogamy is defined as a male-female pair sharing exclusive use of a territory (Reichard 2003). Social monogamy among mammals is rare, but has been reported in around 5% of species, including some peromyscine and arvicoline rodents

(Wolff 1985, Clutton-Brock 1989, Ribble 1992). In socially monogamous systems, male and female home ranges are approximately equal in size and females are widely distributed. Both males and females participate in parental care and sexual dimorphism is minimal.

### **Mating System of *Scotinomys xerampelinus***

One goal of this study is to ascertain the mating system of *S. xerampelinus*. Using data that we collected in the field, we compared *S. xerampelinus* characteristics to the correlates of previously studied rodent mating systems (Table 1-2). We compared relative male and female home range sizes, degree of intrasexual home range overlap, and the spatial distribution of females. We checked whether male and female pairs share a home range and whether sexual dimorphism was present in the study population.

*S. xerampelinus* is classified in the subfamily Neotominae (Steppan et al. 2004, Musser & Carleton 2005, Poor 2005). Promiscuous, polygynous and monogamous mating systems are all represented among the Neotomines, although monogamy is rarely found (Nowak 1999, Poor 2005). Based on the infrequent occurrence of monogamy among Neotomines, the chances are small that *S. xerampelinus* is monogamous.

The most closely related taxon to *Scotinomys* is the genus *Baiomys* (pygmy mice). *Baiomys* and *Scotinomys* comprise the only two genera in the Baiomyini tribe (Bradley et al. 2004). There are two living species of *Baiomys*, and not much is known regarding their social structure and mating system. There is some evidence that they are colonial and breed communally, and they have been reported as “living together peacefully” in a lab environment (Stangle & Kasper 1987, Nowak 1991). The *Peromyscus* genus (deer mice) is also a closely related genus, and consists of 55 species (Nowak 1991). Species of *Peromyscus* are widely variable with respect to mating systems, ranging from

promiscuity to polygyny to social monogamy (Ribble 2003). Examining these close relatives of *Scotinomys*, therefore, does not immediately clarify the *S. xerampelinus* mating system.

### **Mating System Hypotheses for *S. xerampelinus***

Promiscuous, polygynous and socially monogamous mating systems are all represented among the Neotomines, although social monogamy is rarely found (Nowak 1999, Poor 2005). One potential indicator of mating system is the distribution of resources for a given population (Ostfeld 1990). Our study site consisted of an abandoned pasture, dotted with rotting logs, tree stumps and shrubs. The trees and logs are insect-rich resources for the insectivorous *S. xerampelinus*. Since the insect resources in the study grid follow a patchy distribution, this would suggest a clumped non-territorial female distribution. A clumped distribution of female rodents usually correlates with territorial males, which defend the females against other males, resulting in a mate-defense polygynous mating system (Ostfeld 1990).

### **Hypothesis 3: *S. xerampelinus* exhibits a polygynous mating system.**

We predicted that *S. xerampelinus* would follow the polygynous correlates listed in table 1-2, based on field data we collected in the study:

- Prediction 3a: Male home ranges will be larger than female home ranges. This is a pattern observed in most polygynous systems.
- Prediction 3b: Male home ranges will not overlap. This implies that males exhibit the exclusive space use criteria of territoriality.
- Prediction 3c: Males will be larger than females. This implies sexual dimorphism in size, reflecting the intrasexual selection that occurs in polygyny.
- Prediction 3d: Females will follow a clumped distribution. This implies that males are able to defend several females at minimal costs.

- Prediction 3e: Male-female pairs will not share specific home ranges. This rules out the foundational requirement for social monogamy.
- Prediction 3f: Individual male home ranges overlap multiple female home ranges, but individual female home ranges do not overlap multiple male home ranges. This implies that individual males have access to multiple females, but individual females have access to only one male.

We are not making a prediction regarding female intrasexual exclusive space use, since such behavior can be present in all three mammalian mating systems, and as such will not clarify the *S. xerampelinus* mating system (Table 1-2).

## Methods

### Fieldwork

The study site was in Parque Internacional La Amistad in the Cerro Punta region of western Panama. *S. xerampelinus* was observed at this location as early as 1939 by Enders and students (Hooper 1972, Hooper & Carleton 1976). The study extended over two field seasons, 2003 and 2004. All data collection was performed in an abandoned pasture bounded on two sides by a montane forest, on the third side by a small river, and on the fourth side by a deep gully caused by a landslide. Site elevation was 2270 m, and GPS coordinates were N 8° 53.718, W 82° 37.123. Abandoned pastureland has been reported as one of the preferred habitats of *Scotinomys xerampelinus* (Hooper & Carleton 1976), and a recent study that examined the species abundance in five different habitats found the highest *S. xerampelinus* abundance in abandoned pastureland (Van den Bergh & Kappelle 1998). Trapping was also conducted elsewhere in the park, including areas of montane forest.

The abandoned pasture habitat consisted mostly of grass, and was dotted with elephant ears (*Colocasia*), trees such as oak (*Quercus*), shrubs such as scrubby alder (*Alnus*) and *Wercklea* (family Malvaceae), tree stumps and decomposing logs. In 2003,

the grass in the study site was overgrown and extended to approximately 0.75 m high. In 2004, the grass was initially much shorter. Two horses had been put to pasture at the site, and had been grazing (although the site is technically in the Parque). Location of horse manure indicated that the horses had been traversing the entire study site. The horses were removed by their owner at the beginning of the 2004 season. Over the next month, the vegetation gradually grew to a comparable height to 2003.

The home range data collection for the first field season consisted of mark-recapture and radio-tracking over a period of 18 days, from 19 August to 5 September 2003. Home range data collection for the second field season consisted of mark-recapture over a period of 35 days, from 24 May to 27 June 2004. The mountain regions of western Panama have consistent weather throughout the year, and *Scotinomys* reproduce aseasonally (Hooper & Carleton 1976), so there should be minimal biases in the *S. xerampelinus* social system due to seasonality.

The *Guidelines for the Capture, Handling, and Care of Mammals as Approved by the American Society of Mammalogists* (1998; [www.mammalsociety.org/committees/](http://www.mammalsociety.org/committees/)) was followed throughout the course of this study, and all protocols were approved by the University of Florida Institutional Animal Care and Use Committee. Appropriate research and collecting permits were obtained from the government of Panama. Sherman live-traps were used for all mark-recapture data collection (5 x 6 x 16 cm; [www.shermantraps.com](http://www.shermantraps.com), Tallahassee, FL). In 2003, a 1600 m<sup>2</sup> (40 m X 40 m) grid was laid out in the pasture site, about 30 m from the forest borders. Fifty (50) total traps were placed on the grid. In 2004, a 4200 m<sup>2</sup> (60 m X 70 m) grid was laid out in the same pasture site, with 96 traps. We minimized chances of trapped animals getting wet by

placing a large leaf or handfuls of grass on the top of the trap, covering the hinge holes. Two traps were placed as close as possible to each flagged 10m grid point, in the nearest suitable trapping microhabitat. We defined “suitable microhabitat” as areas where a rodent would reasonably be expected to travel. Rodents, like most small animals that are vulnerable to predation, will generally travel, rest and nest at sites that provide physical protection from predators (Jensen et al. 2005). Rodents generally avoid open spaces, and stay close to peripheral structures. Thus, we placed traps in locations that provided shelter and protection from predators, i.e. next to or in tree trunk hollows, and did not place traps in open areas that had no cover. Upon each animal capture, the grid location was recorded to the nearest 0.5 m, using the ten-meter flagged grid points as guides. We used two traps for each flagged grid point to allow for capture of more than one animal visiting a given location. In 2004, approximately midway through the study (on day 14), the traps were shifted five meters along both the X-axis and Y-axis of the grid, to improve resolution of ranging data.

*Scotinomys* is diurnal and reported to be most active between 7 am and 11 am (Hooper & Carleton 1976). Live-traps were baited with a mixture of peanut butter and oats, and set between 6 and 7 am. They were checked in the early afternoon, and were left unset until the next baiting session. We are confident that all animals in the grid were trapped, due to the lengthy period of trapping and the high recapture of this species. From previous experiences both in the lab and in the field, *S. xerampelinus* do not appear to be trap-shy and will readily enter and re-enter baited live-traps.

Upon first capture trapped mice were weighed, measured, and marked. Sex, age (Juvenile, Sub-Adult, Adult), reproductive state (females: imperforate, perforate, or

pregnant; males: non-scrotal or scrotal), and external parasite load were also recorded (Hooper & Carleton 1976), after which the animal was released. If a marked individual was recaptured, it was weighed, checked for reproductive state and subject ID, and released. Ear-tags have been attempted in the past on *S. teguina*, but failed due to the animals tearing the tag off the ear (Langtimm 1992). Thus, marking was performed using toe clipping (Murray & Fuller 2000). No more than two toes were clipped per animal, and the clips were saved as tissue samples for future genetic analysis. Clipping was done with a pair of clean, sharp dissecting scissors. Lidocaine cream (a topical anesthetic) was used during toe clipping to minimize the animal's discomfort, and a shaving styptic swab (an astringent agent that stops or minimizes external bleeding) was applied to minimize any bleeding.

Concurrently with the live-trapping, in 2003 radio-tracking was performed on all animals caught within the grid. Holohil radio transmitters (www.holohil.com, Ontario, Canada) model BD-2NC were used, which are specifically designed for small mammals, and weigh 0.60 g each. Adult animals trapped at the study grid weighed on average 14.2 g ( $\pm 0.2$  SE), so the transmitters were less than 5% (mean = 4.2%) of the average mouse body mass. Radiocollars have been demonstrated to have no detectable effect on daily energy expenditure of small running mammals (Berteaux et al. 1996).

Transmitters were affixed to individuals using a plastic cable-tie collar (RadioShack brand black indoor/outdoor 9.5 cm cable tie). The transmitters have holes in their housing allowing for a collar to be passed through. The plastic cable-tie was passed through the transmitter housing, and the transmitter antenna was looped around the cable tie, and attached to the cable tie with dental brace bands. In our pilot studies we

found that leaving the antenna extended (not looping it around the collar) initially allowed for a stronger signal reception, but was subsequently gnawed off, resulting in poor or no signal reception. Flexible plastic Tygon tubing (provided by the transmitter manufacturer) was then placed around the cable ties, to prevent abrasion on the animal's neck. The cable tie was closed, leaving a loop large enough for the animal's head to easily pass through. Once the animal's head was through the loop, the cable-tie was tightened. We tightened the loop to the point where the collar was tight, but still loose enough to be turned easily on the animal's neck. Before releasing each collared animal, we placed the animal in a small cage for a period of 2-3 hours, and verified that the collar was not too loose or too tight. If a forelimb was caught in the collar or if the collar fell off, we re-affixed and tightened the collar. If the animal did not exhibit the normal captive behaviors (drinking, eating, running), and appeared to be in discomfort, we replaced the cable-tie. At the end of the study, tagged animals were live-trapped in order to remove their collars.

A Telonics receiver attached to a three-element Yagi antenna was used to locate the animals ([www.telonics.com](http://www.telonics.com), Mesa, Arizona). We located each animal using the homing technique (Mech 1983, White & Garrott 1990). The homing technique is accomplished by repeatedly reducing the receiver gain and rotating the directional antenna, always walking towards the direction where the signal is strongest. We eventually encircle a small area that includes the transmitter. Once we are within a few meters of the transmitter, the exact location of the transmitter can be pinpointed more easily by removing the antenna from the receiver, and using just the dangled receiver cable to localize the signal. The exact location was determined to within 0.5 m. To ensure

accuracy of this homing technique, prior to the study the research team practiced locating hidden radio transmitters within a radius of about 50m. Transmitters were always found, usually within a few minutes.

In order to estimate home ranges, we needed to obtain location fixes for each animal. These location points need to satisfy three criteria. First, there must be enough location points per animal to accurately estimate its home range. Second, for a given animal, each of its location points must be statistically independent (White & Garrot 1990, Kenward 2001). Third, the location points must be obtained throughout the day, so that the entire range of an animal's movements is sampled (Kenward 2001).

To satisfy the first criterion (sufficient location points), we determined the number of fixes sufficient to define each range by plotting a cumulative area curve (Fig. 1). Approximately 80% of the total area was attained by four fixes, and 90% by five fixes. All animals with three or fewer fixes were excluded from the data analysis. Not only were three points too few to estimate the home range, but three or fewer captures over the entire study period did not qualify the animal as a resident of the grid, and these animals were assumed to be on excursions outside of their home range. Residents were defined as having four captures or more over the study period.

The second criterion is statistical independence, which is a prerequisite for home range estimator methods (White & Garrott 1990). Each location data point for a given animal should contribute as much as every other data point, otherwise some consecutive points are autocorrelated, and are not considered independent (White & Garrott 1990, Kenward 2001). A general rule of thumb for obtaining independent data points is that the time interval between consecutive measurements is sufficient for the animal to traverse

its home range (White & Garrott 1990). For the radio-tracking, we gathered data via the point sampling method (Kenward 2001). Each collared animal was localized once per day, with the exception of one day when they were localized twice. The sampling interval was long enough that the data points can be considered statistically independent (Kenward 2001). The animals had ample time to move across the span of their home range between daytime localizations, and on many instances were localized on the opposite side of their range as the previous sampling session. There was one day that the animals were located twice. On this day, five hours were allowed between sampling periods, and several of the animals had traversed their entire range between the sampling intervals. To obtain independent data points it is also important to sample mostly during the active period of the animal's 24-hour cycle. Since *Scotinomys* are diurnal, we sampled mostly during the day and only occasionally at night. Location fixes for each individual did not change within and between nights, indicating minimal nocturnal movement away from their nests. The location fixes collected from the live-trapping mark-recapture did not present an autocorrelation problem, since the traps were only checked once per day.

The third criterion for estimating home ranges is that the location fixes are sampled throughout the day for each individual. Timetabling, or repeated use of particular feeding or resting sites at similar times each day (Kenward 2001), is an issue that can bias results when monitoring animal movements. The problems with timetabling occur if the study animals are only localized at certain times of the day. For example, if an animal tends to always forage in the same area in the early afternoon and forage in a different area in the late afternoon, a study that only samples locations in the early afternoon would not

accurately represent the animal's home range. We minimized timetabling issues by spreading radio-tracking observations for each animal over the entire *Scotinomys* active (daylight) period, and by including some additional sampling at night to check for nest sites. We minimized timetabling in the mark-recapture live-trapping by alternating the order in which we set and checked the traps every day, and varying the time that we checked the traps in the afternoon.

### **Data Analysis**

Home range sizes and overlap were estimated using the minimum convex polygon (MCP) method (Mohr 1947) in the Ranges 6 software program (Kenward et al. 2003). MCP is the most commonly used home range estimator (Powell 2000), and has a long historical use in home range literature, especially in rodent spacing studies (Harris & Leitner 2004, Schradin & Pillay 2005). We chose MCP in part because our data are from both mark-recapture and radio-tracking, and MCP is the only method that is comparable between these different data collection methods; MCP is also the only method that is comparable between studies that use differing grid cell numbers and sizes, making our study more generally accessible to comparisons with other home range studies (Jones & Sherman 1983, Seamon & Adler 1999, Oakwood 2002, Ribble et al. 2002). Another reason that we chose MCP is that we did not have enough data points to use more data-intensive methods such as harmonic means and kernel-density estimators (Ribble et al. 2002, Seamon & Adler 1999). We could have used ellipses such as the Jennrich-Turner estimator or the Dunn estimator, which also require relatively few data points (White & Garrott 1990, Kenward 2001), but these alternative estimators were not detailed enough for our purposes.

We examined primarily 85% MCP (“core home range”), but also looked at outer-edge 100% MCP (“exhaustive home range”). One drawback to outer-edge MCP is that it will greatly overestimate the home range area of an individual, and will include many areas that the individual actually does not use. The outer-edge MCP also will overestimate the home range area overlap between any two individuals. The outer-edge MCP is very sensitive to any unusual or infrequent excursions that extend far from the densest aggregations of an animal’s location points (Kenward 2001). The 85% MCP allows infrequent forays outside of the home range to be excluded from analysis, and is a more accurate estimator of core home range area and overlap (Kenward 2001). The 85% MCP includes only the 85% of the data points closest to the recalculated arithmetic mean of a particular animal’s location fixes. The recalculated arithmetic mean method (Kenward et al. 2003) obtains the area of densest fixes by recalculating the arithmetic mean position after excluding each furthest fix. Our space use analysis depends heavily on an accurate estimate of home range area overlap, and our mating system inferences depend in part on sex-specific home range area estimates and likely areas of contact between sexes. Thus, for most of our analysis we used the 85% MCP. However, we decided to also look at 100% MCP in order to estimate maximal area used, to detect patterns during excursions outside of core home ranges, and in order to examine potential (if infrequent) interactions among individuals.

To calculate home range areas, we used Ranges (Kenward et al. 2003). Some of the radio-tracking fixes were from outside of the grid, but this should not affect the area calculations. We compared male and female home ranges both between and within years, using the Mann-Whitney U test (Statview, Abacus concepts 1996).

We estimated exclusive space use by using a variation of the Batzli and Henttonen method (Batzli & Henttonen 1993). Specifically, we used a null hypothesis of random home range placement throughout the trapping grid. If observed home range overlap is significantly lower than what would result from a random (expected) placement, then the conspecifics are demonstrating avoidance and/or exclusion, and thus meet one criterion for territorial behavior (Batzli & Henttonen 1993, Priotto & Steinmann 1999). If the observed home range area overlap is not significantly different from expected by random placement, then a lack of both affiliation and exclusion is suggested. If the observed home range area overlap is significantly greater than expected by random chance, then aggregation is suggested, which could reflect affiliation or a common resource use.

For the purposes of the overlap analysis, we first excluded any radio-tracking fixes that were exterior to the trapping grid. This is because the Batzli and Henttonen method involves the proportion of the grid used by each animal and thus only points from within the grid could be used. Then, we excluded any unusable habitat in the grid. The null hypothesis assumes that each home range has an equal probability of occurring at any location on the grid (Batzli & Henttonen 1993). Thus, each grid cell should represent usable habitat. In 2003, the vegetation was ungrazed and high enough that each cell was considered usable habitat. In 2004, the vegetation was shorter due to grazing and there were seven grid cells in 2004 where our live-traps did not capture any *Scotinomys* during the entire field season, which included 80 days of trapping (55 days of periodic trapping after the initial 35 days). Three of the grid cells successfully trapped shrews, so it is not known if the *Scotinomys* avoidance represented shrew avoidance or unusable habitat.

The other four grid cells captured no animals over the season. We excluded the seven grid cells from the total grid area, bringing it down from 4200 m<sup>2</sup> to 3500 m<sup>2</sup>.

To generate the overall expected overlap values, we first calculated the expected overlap areas for each pair of animals. For a target animal, we took the proportion of the total grid represented by its within-grid home range area, and multiplied it by the area of the other animal's within-grid home range. For example, take a grid of size 3000 m<sup>2</sup>, animal A with a home range of 300 m<sup>2</sup>, and animal B with a home range of 100 m<sup>2</sup>. The proportion of the total grid of animal A's home range (300/3000, or 10%) is multiplied by animal B's home range area (100 square-meters). The expected overlap of animal A's home range by animal B is 10 m<sup>2</sup>. For each target animal in the grid, we averaged the list of values representing expected home range area overlapped by each other animal. We also computed the same-sex overlap and the opposite-sex overlap for each subject.

To generate the overall observed overlap values, we first calculated the observed overlap areas for each pair of animals, using the software program Ranges 6 (Kenward et al. 2003). For a target animal, we took the proportion of the target animal's home range overlapped by the other animal (estimated by Ranges), and multiplied by the target animal's home range area (estimated by Ranges). For each animal in the grid, we averaged the list of values representing observed home range area overlapped by each other animal. We also computed the same-sex overlap and the opposite-sex overlap for each subject. The male home range areas overlapped by an opposite sex animal are designated as "MF". The female home range areas overlapped by an opposite sex animal are designated as "FM".

For each animal in the grid, we had an average value for “expected overall overlap,” “observed overall overlap,” “expected same-sex overlap,” “observed same-sex overlap,” “expected opposite-sex overlap” and “observed opposite-sex overlap”. Expected and observed data values were compared using the Wilcoxon signed rank test (Statview, Abacus concepts 1996). Data were analyzed within each season (2003 & 2004 separately) and also as a pooled data set (both 2003 & 2004 combined).

All descriptive results will be presented as mean  $\pm$  standard error.

### **Results**

In 2003, 24 adults were trapped on the study grid (9 males and 15 females, a sex ratio of 0.6:1). In 2004, 20 adults were trapped on the study grid (9 males and 11 females, a sex ratio of 0.8:1). In 2003, six females were found to be pregnant and/or lactating, seven females were perforate, and two females were imperforate. Pregnant females were dispersed throughout the 2003 field season, with pregnancies and/or lactating conditions detected in August and September 2003. June and July pilot trapping sessions at the site also revealed pregnant females. In 2004, three females were found to be pregnant and/or lactating, seven females were perforate, and one female was imperforate. Pregnant females were dispersed throughout the 2004 field season, with pregnancies and/or lactating conditions detected in May and June 2004. Post-study trapping at the site in July and August 2004 also revealed pregnant females. All nine 2003 males were scrotal. One 2004 male was found to be non-scrotal, and the other eight males were scrotal. The ratio of females that were perforate, pregnant or lactating to males that were scrotal in 2003 was nine males to 13 females (0.7:1), and in 2004 was eight males to ten females (0.8:1). The average adult weight was  $14.2 \text{ g} \pm 0.2$ . Male and female mean weights were not significantly different from each other (unpaired t-test;

males: 14.4 g mean  $\pm$  0.3, N = 43; females: 14.0 g mean  $\pm$  0.3, N = 39; t-value = -0.919, p = 0.361). The density of resident animals in the study grid in 2003 was 62 mice/hectare, and in 2004 it was 28 mice/hectare. The total number of location fixes for 2003 (mark-recapture and radio-tracking combined) was 158 and in 2004 (mark-recapture only) was 104.

During the 2003 field season, 24 animals were trapped over 19 days, and subsequently radio-tracked. Ten of these animals had 4 or more location fixes within the grid. The other 14 animals had 3 or fewer location fixes each. The ten animals that were used in the analysis consisted of 5 males and 5 females. Data used from the 2003 field season consist of both trapping and radio-tracking data. During the 2004 field season, 19 animals were trapped over 35 days mark-recapture study. Ten animals in 2004 had four or more fixes within the grid. These animals consisted of 5 males and 5 females. Despite the differences in grid size between the two field seasons, we coincidentally had identical numbers of male and female residents in the grid for each field season. Data used from the 2004 season consist of only live-trapping data, as the animals were not radio-tracked during the 35-day trapping period. Mean number of fixes for grid residents over the two field seasons was  $7.7 \pm 0.7$ , ranging from 4 to 13 per animal.

In addition to the cumulative area curve described in the Methods section (Figure 2-1), we further verified that we had obtained sufficient fixes to determine home range in two ways. First we checked for a correlation between number of fixes and home range area. There was no significant correlation between home range area and number of location fixes for the individuals included in home range analysis. This was checked for each field season separately and for the two field seasons pooled together (2003: r =

0.225,  $r^2 = 0.050$ ,  $p = 0.533$ ,  $N = 10$ ; 2004:  $r = 0.320$ ,  $r^2 = 0.103$ ,  $p = 0.367$ ,  $N = 10$ ; pooled:  $r = 0.307$ ,  $r^2 = 0.094$ ,  $p = 0.188$ ,  $N = 20$ ). Second, we also verified in the published rodent literature that similar numbers of fixes per animal have been considered sufficient and have been used to estimate home range sizes (Batzli & Henttonen 1993, Adler et al. 1997, Seamon & Adler 1999, Priotto et al. 2002, Ribble et al. 2002, Bergallo & Magnusson 2004, Tchabovsky et al. 2004).

Because the home range area calculations were not restricted to the grid, in 2003 we included an additional two males and two females that had the majority of their locations outside of the grid. We also included radio-tracking fixes for grid residents that had gone outside of the grid. In 2003 the average number of fixes used for home range area calculation was  $9.8 \pm 1.4$ . Male home range areas were not significantly different than female home range areas in either year (85% MCP, Table 2-1, Figure 2-6; Mann-Whitney U test; 2003: Z-value = -0.192,  $p = 0.848$ ,  $N_1 = 7$ ,  $N_2 = 7$ ; 2004: Tied Z-value = -0.940, Tied-p = 0.347,  $N_1 = 5$ ,  $N_2 = 5$ ). Home range areas for each sex did not change significantly between years (85% MCP, Table 2-1, Figure 2-6; Mann-Whitney U test; females: Z-value = -1.056,  $p = 0.2912$ ,  $N_1 = 7$ ,  $N_2 = 5$ ; males: Z-value = -0.893,  $p = 0.372$ ,  $N_1 = 7$ ,  $N_2 = 5$ ). There was a small but non-significant trend for male home ranges to be larger than female home ranges in both years, and for the home ranges to decrease in area from 2003 to 2004 in both sexes (Figure 2-6).

For 85% MCP home ranges, each home range was overlapped on average by 2.2 other animals (Figures 2-2 & 2-4). Males overlapped with 1.0 other males (range: 0-2), and females overlapped with 0.2 other females (range: 0-1). Mice of both sexes overlapped on average with 1.6 opposite-sexed animals (range: 0-4).

In 2004, two resident individuals were not caught after day 12 of the 35-day study. These animals are identified in Figure 2-4 (IDs 44 and 48). It is possible that they were dispersing or died. However, we decided not to exclude them from the analysis. Other animals were trapped several times in the same grid cells as ID 44 and 48 both on the same day and within one day before or after trapping 44 and 48, and thus would not adversely affect our overlap measures.

Home range area overlaps (according to the Batzli and Henttonen 1993 method) revealed both significant and near-significant patterns (Tables 2-2, 2-3 and 2-4). The 2003 observed average home range overlap of males by other males was significantly less than males overlapped by females for 85% MCP (Figure 2-7; Wilcoxon signed rank test; 85% MCP: Z-value = -2.023,  $p = 0.043$ ,  $N = 5$ ). The 2004 observed average 85% MCP home range overlap of females by other females was less than females overlapped by males; this approached significance (Figure 2-7; Wilcoxon signed rank test; Z-value = -1.826,  $p = 0.068$ ,  $N = 5$ ).

The overall population of animals in the grid had less observed 85% MCP overlap in 2004 than would be expected by random chance, approaching significance (Wilcoxon signed rank test; Z-value = -1.886,  $p = 0.059$ ,  $N = 10$ ). Both the pooled data and the 2003 data had greater observed 100% MCP overlap than would be expected by random chance; this difference approached significance in the pooled data, and was significant for the 2003 data (Wilcoxon signed rank test; pooled: Z-value = -1.886,  $p = 0.059$ ,  $N = 20$ ; 2003: Z-value = -2.293,  $p = 0.022$ ,  $N = 10$ ).

The male-male 100% MCP home range overlap was greater than expected by random chance; this was significant in the pooled data, and approached significance in

2003 (Wilcoxon signed rank test; pooled: Z-value = -1.988,  $p = 0.047$ ,  $N = 10$ ; 2003: Z-value = -1.753,  $p = 0.080$ ,  $N = 5$ ). Male-female home range overlap was greater than expected by random chance in 2003, at both 85% and 100% MCP; this difference approached significance (Wilcoxon signed rank test; 85% MCP: Z-value = -1.753,  $p = 0.080$ ;  $N = 5$ ; 100% MCP: Z-value = -1.753,  $p = 0.080$ ,  $N = 5$ ).

The female-female 85% MCP home range overlap was less than expected by random chance; this was significant in the pooled data and in 2004, and approached significance in 2003 (Wilcoxon signed rank test; pooled: Z-value = -2.701,  $p = 0.007$ ,  $N = 10$ ; 2003: Z-value = -1.753,  $p = 0.080$ ,  $N = 5$ ; 2004: Z-value = -2.023,  $p = 0.043$ ,  $N = 5$ ). Female-female 100% MCP home range overlap was less than expected by random chance in the pooled data and in 2004; this approached significance in the pooled data, and was significant in 2004 (Wilcoxon signed rank test; pooled: Z-value = -1.886,  $p = 0.059$ ,  $N = 10$ ; 2004: Z-value = -2.023,  $p = 0.043$ ,  $N = 5$ ). Female-male 100% MCP overlap was greater than expected by random chance in 2003, approaching significance (Wilcoxon signed rank test; Z-value = -1.753,  $p = 0.080$ ,  $N = 5$ ).

## **Discussion**

### **Territoriality**

Our results suggest that *S. xerampelinus* females exhibit exclusive space use, because 85% MCP overlap between females is significantly less than expected by chance (Tables 2-2, 2-3, 2-4, Figures 2-2 & 2-4; Hyp. 1, prediction 1). This is one of the criteria for territoriality, although the pattern could also be driven by mutual avoidance. We did not find support for male intrasexual exclusive space use, since 85% MCP overlap between males is not significantly different than would be expected by chance. None of the intrasexual 85% MCP analyses revealed more overlap than expected by chance,

which would have indicated that same-sex mice actively affiliate with each other, or aggregate around common resources, as would be found in a colonial or communal breeding system, for example.

We have no evidence that *S. xerampelinus* exhibits intersexual exclusive space use, because 85% MCP overlap between males and females is not significantly less than would be expected by chance (Tables 2-2, 2-3, 2-4, Figures 2-2 & 2-4; Hyp. 2, prediction 2). In some cases the male-female overlap is significantly greater than would be expected by chance, and in some cases it is not significantly different than would be expected by chance. This suggests that males and females do not exclude each other from their home ranges, and in some cases aggregate, as a result of either active affiliation or utilization of a common resource.

We also examined the 100% MCP home ranges, in order to detect patterns during excursions outside of core home ranges, and in order to examine potential (if infrequent) access among individuals. By looking at the polygon outer boundary angle points (Figures 2-3 & 2-5), it seems that the mice will occasionally venture outside of their core home ranges and overlap a considerable distance into other ranges. In 2003 it appears that the 100% MCP home ranges tend to converge on specific points (Figure 2-3). Unfortunately we do not have a map of the vegetation in 2003, but we suggest that these points are logs, tree stumps and shrubs. The convergence is less in 2004, but we have a vegetation map for that year, and will perform an overlay analysis for further verification. The resource distribution for these insectivores in the study grid was patchy, with the resource-rich insect habitats such as rotten logs and tree stumps dotting the pasture. We propose that the mice exhibit exclusive space use among females, but will tolerate

infrequent female intrasexual overlap at resource-rich “hot spots” (which are also overlapped by males). In these cases, the benefits for the intruder of using these resources outweigh the costs of agonistic same-sex interactions. Additionally, the increased intruder-pressure at these resource points will make them harder to defend. An alternative, but not mutually exclusive, adaptive benefit of the infrequent wide-ranging excursions, evidenced by the extensive overlap at the 100% MCP level, is the increased opportunity for male and estrous female encounters, especially at highly visited resource areas.

### **Mating System**

Our results suggest that *S. xerampelinus* likely exhibits a promiscuous mating system, because we found that the attributes of the *S. xerampelinus* social system was more consistent with rodent promiscuous systems than with polygynous or monogamous systems (Table 1-2; Hyp. 3). Our original hypothesis and predictions had been that *S. xerampelinus* exhibits a polygynous mating system. However, home range areas (Figure 2-6) were not significantly different between males and females, which is consistent with social monogamy (inconsistent with prediction 3a). Male home ranges did overlap, which is consistent with promiscuity (inconsistent with prediction 3b). Males were not significantly heavier than females, and this absence of sexual dimorphism is consistent with promiscuity and social monogamy (inconsistent with prediction 3c). Females were widely distributed, which is consistent with promiscuity and social monogamy (inconsistent with prediction 3d). Male-female pairs did not share specific home ranges, which is consistent with promiscuity and polygyny but directly contradicts social monogamy (consistent with prediction 3e). Additionally, males had on average access to several (1.6) females, and females had on average access to several (1.6) males, which is

also consistent with promiscuity (inconsistent with prediction 3f). Taken together, the results of this study suggest that that this population of *S. xerampelinus* exhibits a promiscuous mating system. Our initial hypothesis and predictions of a polygynous system were not supported. A definitive assessment of mating system will require assessing patterns of genetic parentage in a natural population.

Finally, regarding male-male home range area overlap, we should note the fact that five males exhibited nearly totally exclusive core home ranges with respect to other males, while five other males had extensive male-male core home range overlap (Figures 2-2 & 2-4). The two evenly mixed space use patterns suggest the possibility of alternative strategies among males. Such behavior has been observed in other rodents. For example, male prairie voles (*Microtus ochrogaster*) exhibit alternative strategies, with some males adopting a territorial behavior, and others adopting a non-territorial wandering behavior (Pizzuto & Getz 1998). If a similar phenomenon were occurring in *S. xerampelinus*, it would be difficult to detect population-level patterns of male space use due to underlying heterogeneity. Further research and the resulting increased sample sizes would allow us to investigate this possibility.

## **Conclusion**

The population density in the abandoned pasture decreased between the two field seasons (from 62 mice/hectare in 2003 down to 28 individuals/hectare in 2004). This may be due to changes in environmental conditions between the two field seasons. There were two major environmental changes between 2003 and 2004. In 2004 there was decreased vegetation due to grazing and increased disturbance due to two horses living in the pasture. Although the grazing would not have affected the major insect-rich resources such as rotting logs and tree stumps, the decreased vegetation may have

lowered somewhat the standing insect population of the pasture. The shorter grassy vegetation also would have decreased the habitat quality by rendering animals more vulnerable to predation. Finally, the grazing horses themselves would have provided some disturbance. The increased disturbance and more predator-vulnerable habitat in 2004 may have resulted in a decrease in the quality of habitat in the pasture, which in turn could have resulted in a decreased population density.

The spatial patterns that we observed in the field are consistent with the prevailing models for space use and territoriality among small mammals. Female rodent distribution is thought to be determined primarily by food and nest resources, or infanticide-prevention, and male distribution is determined primarily by estrous female distribution (Emlen & Oring 1977, Ostfeld 1990, Wolff & Peterson 1998). This results in the different spacing patterns that are characteristic for each rodent mating system (Table 1-2). When females are territorial and dispersed, the defense costs for males are expected to become high enough that males will not exhibit territoriality. Thus, when females are territorial, males are not, and when males are territorial, females are not (Ostfeld 1985a, Ostfeld 1990). Our field data appear to support this hypothesis, at least with regard to the exclusive space use criterion of territoriality.

Future research on the spacing patterns of *S. xerampelinus* would benefit from an increase in the number of animals monitored, and an increase in the number of fixes per animals. This would allow for application of and comparison between a wider set of home range estimator methods, and a more detailed examination of home range intensity of use, home range area, and home range overlap. Populations should also be monitored

at different times of the year, to support our assertion that there are no major seasonal changes in the social organization.

*S. xerampelinus* in the laboratory environment exhibits a degree of social behavior. It is able to live in monogamous breeding pairs, exhibits allo-grooming behavior, and some paternal care (Hooper & Carleton 1976, Blondel pers. obs.). However, in this particular population of *S. xerampelinus*, our data are consistent with a promiscuous mating system. Our data suggest that the function of the calling behavior could play a role in agonistic interactions, mate attraction, and possibly territoriality. Future research can clarify this function through manipulative experiments.

Our field data indicate female exclusive space use, and thus satisfy one of our criteria for territorial behavior in females, but there was no support for exclusive space use among males and in intersexual interactions. Our other criteria for territoriality were investigated in a laboratory setting. We used a series of behavioral experiments to test whether *S. xerampelinus* exhibits overt defense and site-specific dominance towards conspecifics. This is detailed in Chapter 3.

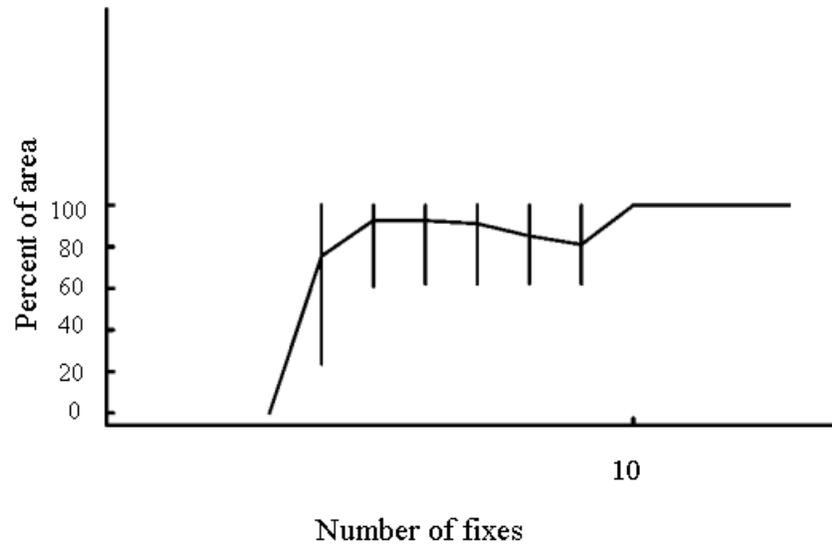


Figure 2-1. Cumulative area plot for *S. xerampelinus* using 100% minimum convex polygons, from 2003 trapping data. Curves represent mean areas, and vertical bars represent the range of values. N = 10 animals.

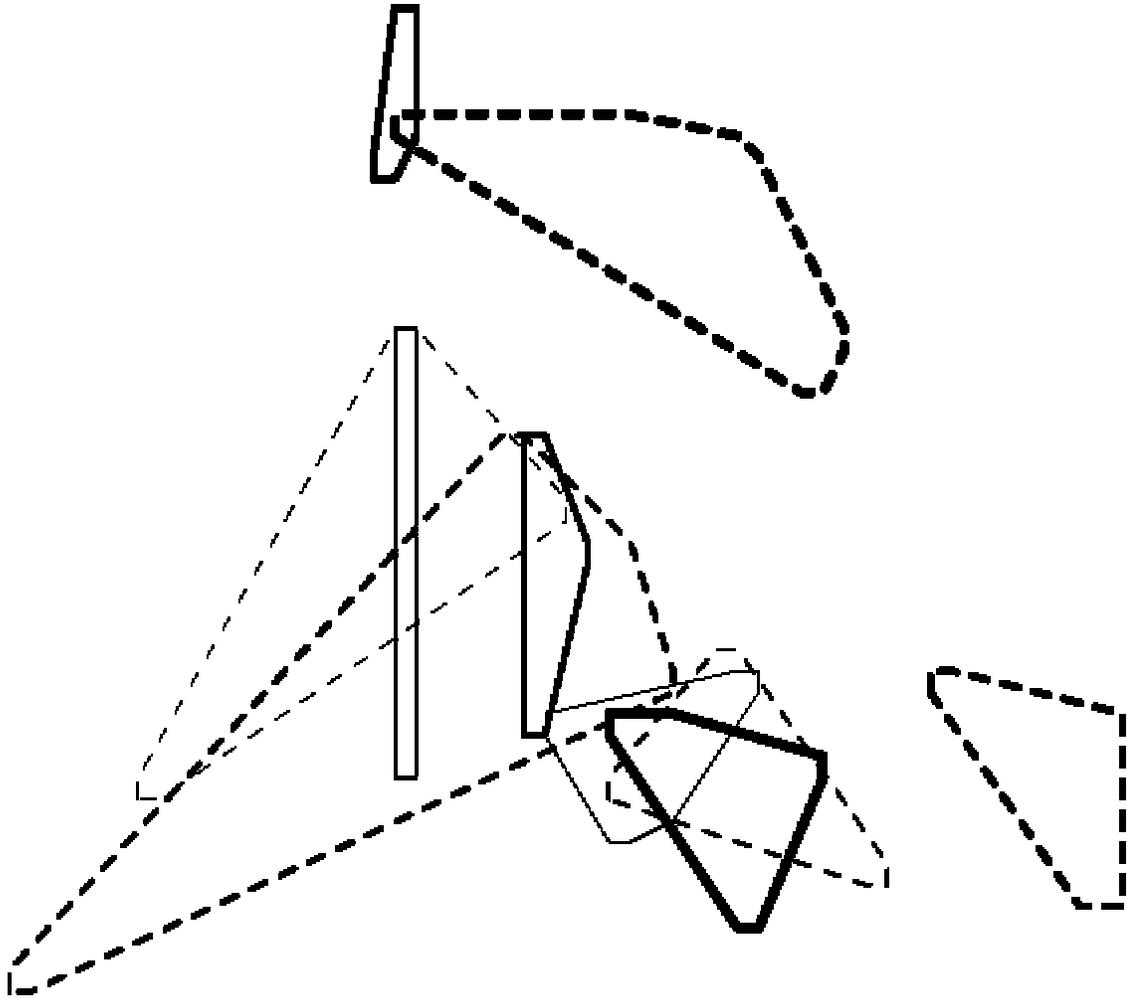


Figure 2-2. 2003 Home ranges for all animals with four or more location fixes. 85% minimum convex polygon, recalculated arithmetic mean method. Male home ranges are depicted in solid lines; female home ranges are depicted in dashed lines. Different individuals are depicted by different line widths.

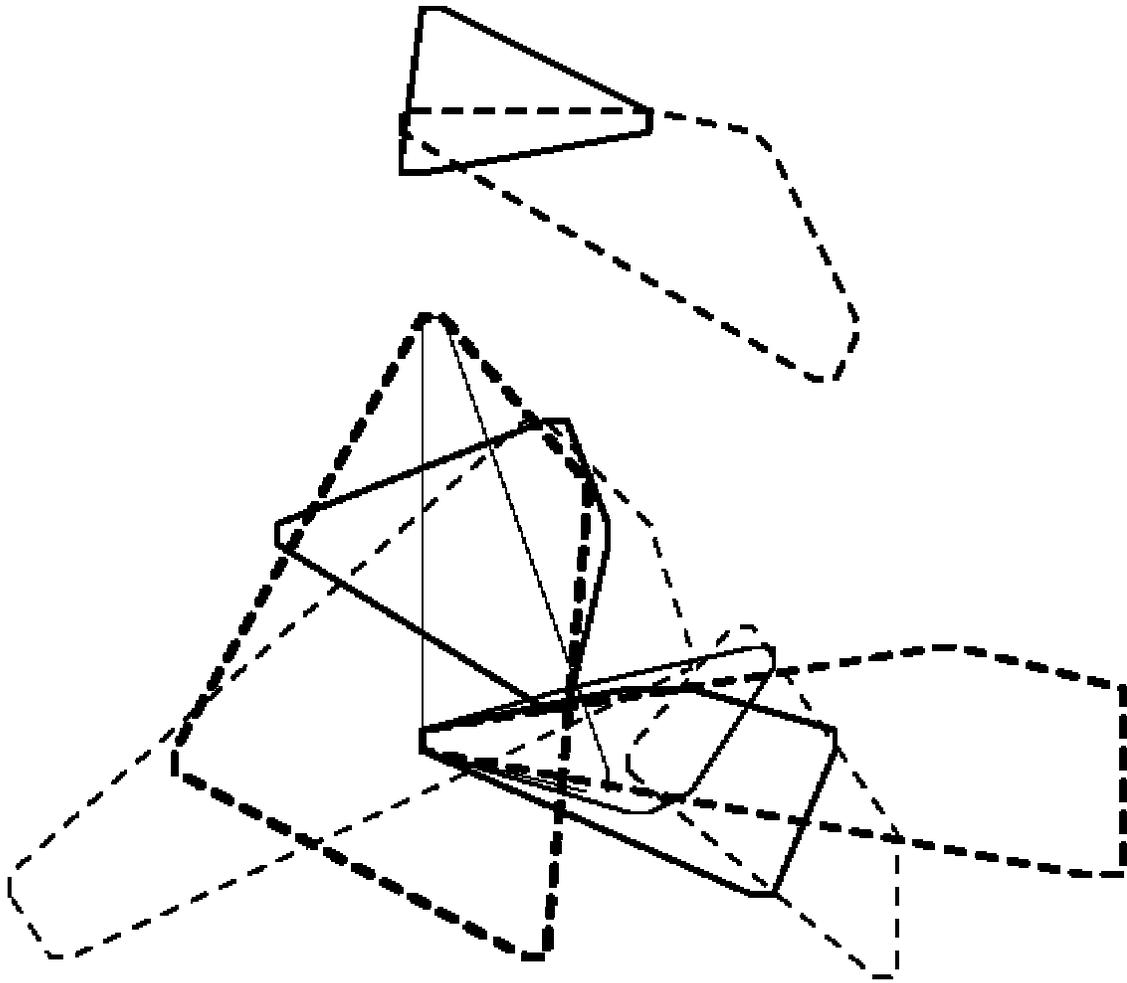


Figure 2-3. 2003 Home ranges for all animals with four or more location fixes. 100% minimum convex polygon. Male home ranges are depicted in solid lines, female home ranges are depicted in dashed lines. Different individuals are depicted by different line widths.

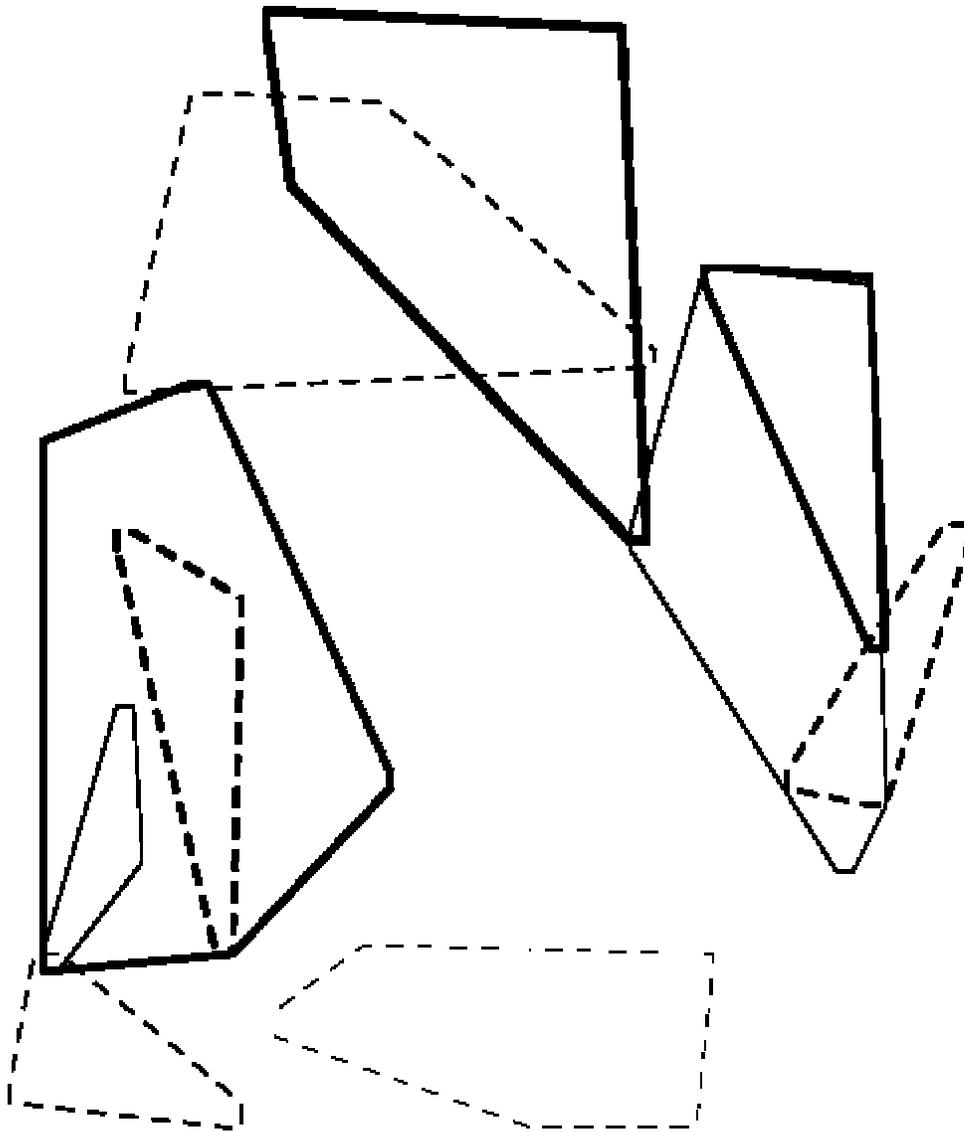


Figure 2-4. 2004 Home ranges for all animals with four or more location fixes. 85% minimum convex polygon, recalculated arithmetic mean method. Male home ranges are depicted in solid lines, female home ranges are depicted in dashed lines. Different individuals are depicted by different line widths. Individuals 44 & 48 are identified on their boundary lines.

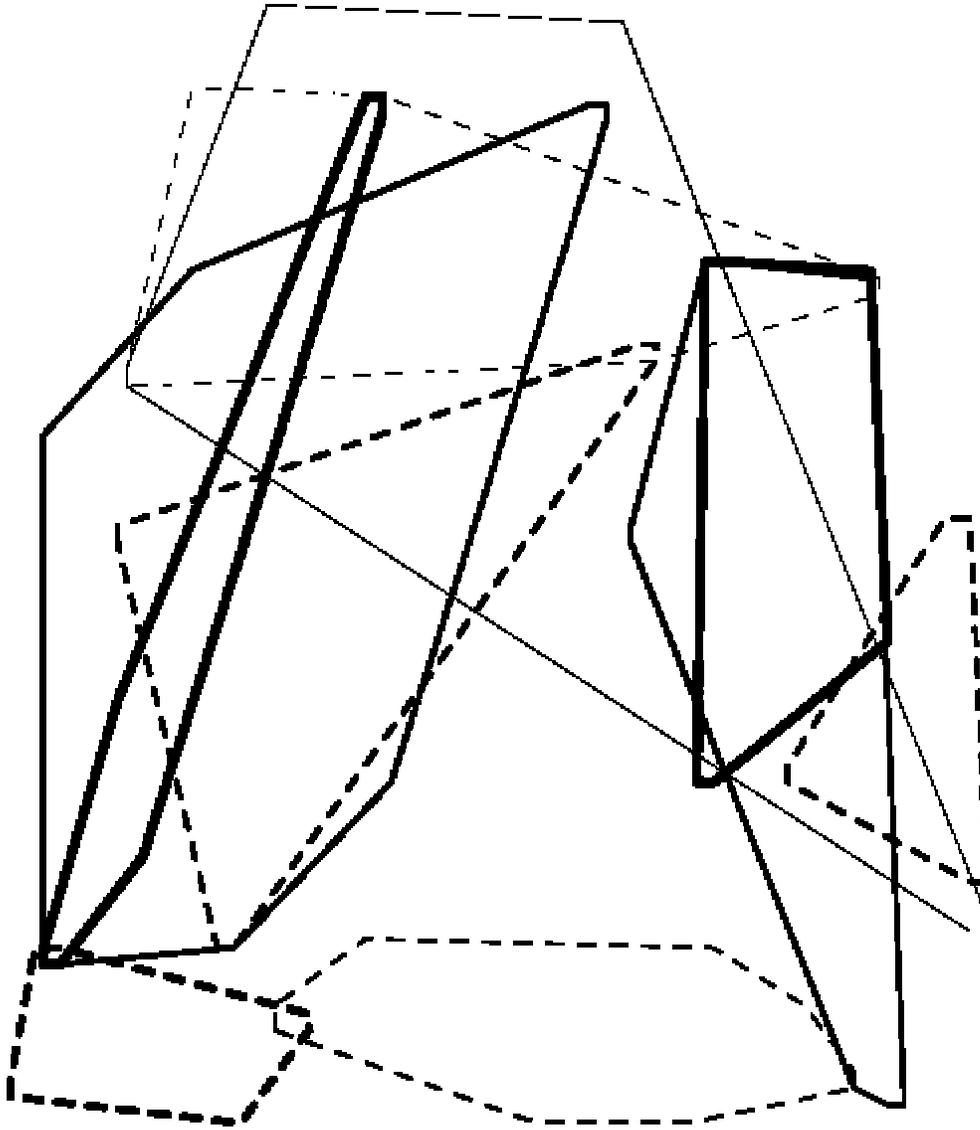


Figure 2-5. 2004 Home ranges for all animals with four or more location fixes. 100% minimum convex polygon. Male home ranges are depicted in solid lines, female home ranges are depicted in dashed lines. Different individuals are depicted by different line widths.

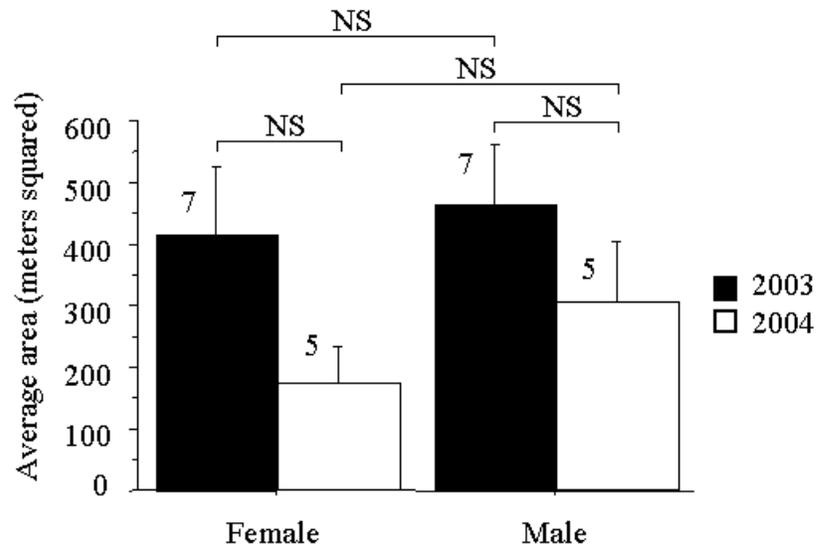


Figure 2-6. Home range mean area comparisons across seasons, 85% minimum convex polygon, recalculated arithmetic mean method. Error bars indicate mean  $\pm$  1 standard error. Sample sizes are indicated above bars. NS: nonsignificant.

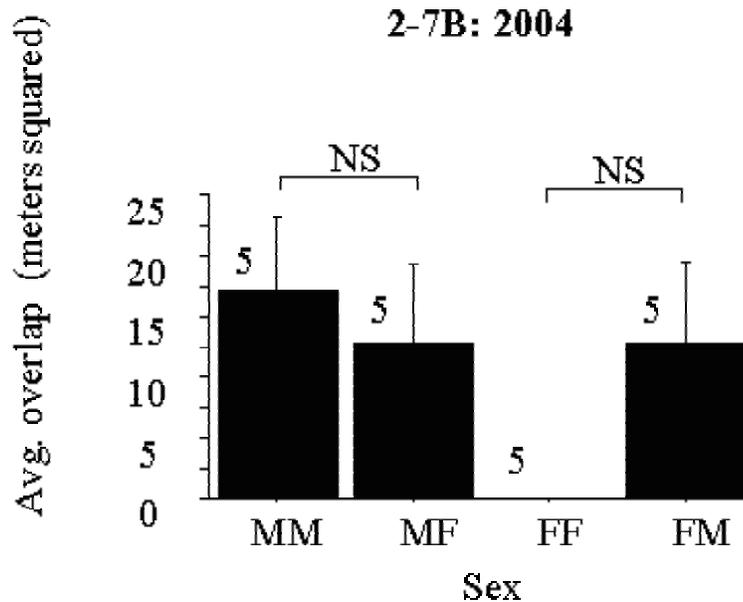
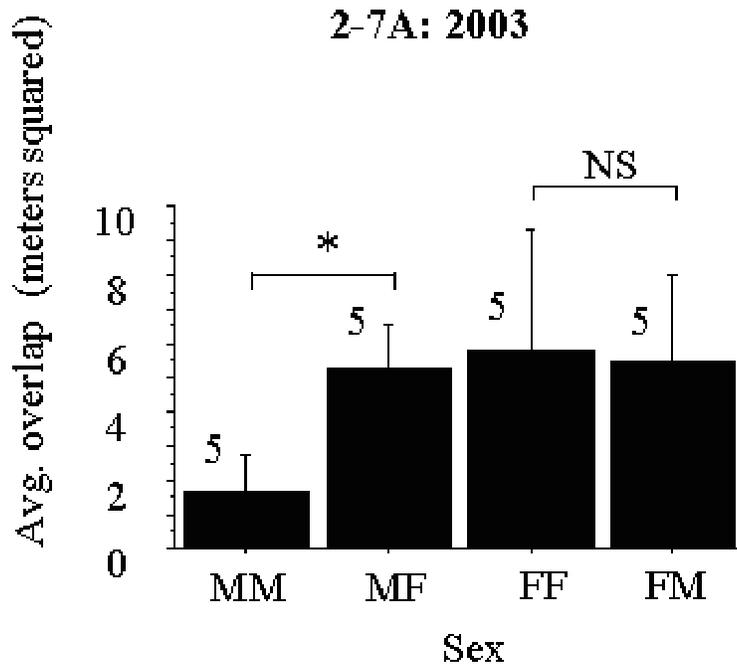


Figure 2-7. Mean area of home range overlap, 85% minimum convex polygon, recalculated arithmetic mean method. (A): 2003, (B): 2004. MM indicates male overlapped by male, MF indicates male overlapped by female, FF indicates female overlapped by female, FM indicates female overlapped by male. NS: nonsignificant; \*  $P < 0.05$ . Error bars indicate mean  $\pm$  1 standard error. Sample sizes are indicated above bars.

Table 2-1. Average home range areas for *S. xerampelinus*

Sex	Year	85% MCP (m <sup>2</sup> )
Male	2003	462 ± 102
	2004	307
	Pooled	398 ± 72
Female	2003	417 ± 109
	2004	174
	Pooled	316 ± 75

MCP = minimum convex polygon, recalculated arithmetic mean method. 2003 and 2004 data were combined to calculate the pooled areas. Calculated by Ranges 6 (Kenward et al. 2003).

Table 2-2. Pooled home range overlap data, comparison of observed vs. random.  
 Comparison of observed versus random home range overlap, pooled over both field seasons.

POOLED DATA	MCP	Sig Diff?	P value	Result
Overall, Obs. vs. Random	85	NO	ns	
	100	Approaches	0.052	<b>Obs &gt; Random</b>
Male-male, Obs vs. Random	85	NO	ns	
	100	YES	0.047	<b>Obs &gt; Random</b>
Male-female, Obs vs. Random	85	NO	ns	
	100	NO	ns	
Male-male obs Vs. male-female obs	85	NO	ns	
	100	NO	ns	
Female-female, Obs vs. Random	85	YES	0.007	<b>Obs &lt; Random</b>
	100	Approaches	0.059	<b>Obs &lt; Random</b>
Female-Male, Obs vs. Random	85	NO	ns	
	100	NO	ns	
Female-female obs Vs. Female-male obs	85	NO	ns	
	100	NO	ns	

MCP = minimum convex polygon, recalculated arithmetic mean method. Obs = observed home range area overlap in study grid. Random = home range area overlap due to a null hypothesis of random placement of home ranges in study grid. Batzli and Henttonen (1993) method.

Table 2-3. Comparison of observed versus random home range overlap, for 2003 field season

2003	MCP	Sig Diff?	P value	Result
Overall, Obs. vs. Random	85	NO	ns	
	100	YES	0.022	<b>Obs &gt; Random</b>
Male-male, Obs vs. Random	85	NO	ns	
	100	Approaches	0.080	<b>Obs &gt; Random</b>
Male-female, Obs vs. Random	85	Approaches	0.080	<b>Obs &gt; Random</b>
	100	Approaches	0.080	<b>Obs &gt; Random</b>
Male-male obs Vs. male-female obs	85	YES	0.043	<b>MM &lt; MF</b>
	100	YES	0.043	<b>MM &lt; MF</b>
Female-female, Obs vs. Random	85	Approaches	0.080	<b>Obs &lt; Random</b>
	100	NO	ns	
Female-Male, Obs vs. Random	85	NO	ns	
	100	Approaches	0.080	<b>Obs &gt; Random</b>
Female-female obs Vs. Female-male obs	85	NO	ns	
	100	NO	ns	

MCP = minimum convex polygon, recalculated arithmetic mean method. Obs = observed home range area overlap in study grid. Random = home range area overlap due to a null hypothesis of random placement of home ranges in study grid. Batzli and Henttonen (1993) method.

Table 2-4. Comparison of observed versus random home range overlap, for 2004 field season

2004	MCP	Sig Diff?	P value	Result
Overall, Obs. vs. Random	85	Approaches	0.059	<b>Obs &lt; Random</b>
	100	NO	ns	
Male-male, Obs vs. Random	85	NO	ns	
	100	NO	ns	
Male-female, Obs vs. Random	85	NO	ns	
	100	NO	ns	
Male-male obs Vs. male-female obs	85	NO	ns	
	100	YES	0.043	<b>MM &gt; MF</b>
Female-female, Obs vs. Random	85	YES	0.043	<b>Obs &lt; Random</b>
	100	YES	0.043	<b>Obs &lt; Random</b>
Female-Male, Obs vs. Random	85	NO	ns	
	100	NO	ns	
Female-female obs Vs. Female-male obs	85	Approaches	0.068	<b>FF &lt; FM</b>
	100	NO	ns	

MCP = minimum convex polygon, recalculated arithmetic mean method. Obs = observed home range area overlap in study grid. Random = home range area overlap due to a null hypothesis of random placement of home ranges in study grid. Batzli and Henttonen (1993) method.

CHAPTER 3  
AGONISTIC BEHAVIOR IN THE SINGING MOUSE:  
A RESIDENT-INTRUDER STUDY

**Introduction**

Little is known about the social structure of *Scotinomys xerampelinus*. One of the goals of this thesis is to define the *S. xerampelinus* social system. The experiment described in this chapter asks the question: is *S. xerampelinus* territorial? In previous laboratory observations, *S. xerampelinus* behavior has been anecdotally described as displaying agonistic behavior in male-male encounters, and mutual avoidance during same-sex encounters among both males and females (Hooper & Carleton 1976). Same-sex pairings cannot be maintained in the laboratory, with the exception of some same-sex sibling groups. This could be interpreted as evidence for intrasexual territoriality. Previous laboratory observations have also shown that males and females can be kept together as breeding pairs even when females are not in estrous, and that males are tolerated by nursing females (Hooper & Carleton 1976). This suggests an absence of intersexual territoriality in this species.

Chapter 2 described a live-trapping and radio-tracking field study on a population of *S. xerampelinus*. In the field we observed home range spacing patterns and detected exclusive area use by females, which is often a consequence of territorial behavior, and has been used as a criterion of territoriality (Ferron & Ouellet 1989, Sandell 1989, Hellgren & Vaughan 1990, Ylonen 1990, Maher & Lott 1995). We did not find any significant evidence of male-male exclusive space use in our field study. However, the

results were somewhat inconclusive, because 50% of males in the study grid (five males) exhibited nearly total non-overlap of home ranges with other males at the 85% contour of their home ranges, while the other 50% of males exhibited extensive male-male home range overlap at the 85% contour. The field results also showed evidence of intersexual home range overlap, especially for males overlapped by females, which suggests that there is no or minimal intersexual exclusive space use.

Defended area and exclusive area have been shown to be positively correlated in small mammal studies (reviewed in Ostfeld 1990). Research on other small mammals has shown that exclusive home ranges are correlated with site-specific dominance, defense behavior, and sometimes avoidance behavior (Stickel 1968, Harper & Batzli 1997). *Peromyscus* species that maintain mostly exclusive home ranges also display site-specific dominance and defense behavior in resident-intruder trials (Stickel 1968, Wolff et al. 1983). Our fieldwork conclusions of female intrasexual exclusive space use suggest possible territoriality, and this would be further supported if we could also show overt defense behavior of an area and site-specific dominance, which, with exclusive area use, are the three most commonly used criteria of territoriality (Chapter 1; Maher & Lott 1995). Detailed behavioral observations were not possible with this species in the field, but they are possible in staged-encounter laboratory experiments.

We examined *S. xerampelinus* behavior in a series of resident-intruder experiments, which can be used to measure territorial aggression in small mammals (Bester-Meredith & Marler 2001). Resident-intruder tests consist of presenting a resident with an intruder individual and scoring the resulting aggressive and avoidance behaviors. In doing so, we

hope to inform our understanding of space-use patterns described in the preceding chapter.

**Hypothesis (based on field observations in Chapter 2): *S. xerampelinus* exhibit female intrasexual territoriality, as defined by defended area and site-specific dominance, but do not exhibit male intrasexual territoriality, and do not exhibit intersexual territoriality.**

- Prediction A (defended area): Female-female encounters in resident-intruder experiments will result in significantly more aggressive behavior than opposite-sex encounters. Aggressive behavior in male-male resident-intruder experiments will not be significantly different than opposite-sex encounters.
- Prediction B (defended area and exclusive space use): Female same-sex encounters in resident-intruder experiments will result in more time spent hidden out-of-sight by the intruder as compared with opposite-sex encounters and controls (only one animal in arena). Male same-sex encounters in resident-intruder experiments will result in less or equal time spent hidden out-of-sight by intruder as compared with opposite-sex encounters and controls (only one animal in arena). We predict avoidance behavior resulting from female intrasexual territoriality, as defined by exclusive space use and defended area.
- Prediction C (site-specific dominance): In female same-sex resident-intruder experiments, residents will display more aggressive behavior than intruders. In male same-sex resident-intruder experiments, resident and intruder aggressive behavior will not be significantly different. This will fulfill the site-specific dominance criterion of territoriality for females, but not for males.

## Methods

### Experimental Design

Fourteen breeding pairs were created for the experiment, consisting of 17 wild-caught mice and 11 of their lab-reared offspring. A breeding pair was defined as a male and female pair that has been in a cage together for at least 7 days. A closely related species, *S. teguina*, has an estrous cycle of 4-6 days (Dewsbury et al. 1976), and therefore, we felt that 7 days was enough time for copulations to occur. Most of the breeding pairs produced litters close to 1 month after pairing; since *S. xerampelinus*

females have gestations of approximately one month, this indicates that copulations occurred within the first week of cohabitation.

Each animal in the experiment was tested six times, once in each of six treatments:

1. Opposite-sexed intruder (focal animal serves as resident)
2. Same-sexed intruder (focal animal serves as resident)
3. No-intruder control (focal animal serves as resident)
4. Opposite-sexed resident (focal animal serves as intruder)
5. Same-sexed resident (focal animal serves as intruder)
6. No-resident control (focal animal serves as intruder)

This experiment used a round robin design, such that over the course of the 9-week experiment (April to July 2005), each member of each breeding pair was tested as a resident three times (treatments 1-3) and also tested as an intruder three times (treatments 4-6). Each animal was tested with no more than one treatment per day and was used in no more than one of each treatment. Treatments were chosen in a randomized order for each focal animal, and the identity of each resident and each intruder in a given trial was randomized. Resident/intruder matchups for a given trial were never genetically related, to the best of our knowledge. For simplicity we assumed that wild-caught individuals were unrelated. Residents/intruder matchups for a given trial had also never been cage-mates.

### **Procedure**

For a given trial, the resident's home cage was used. We defined "resident" as an animal that had occupied its cage, with no changes of bedding, for a minimum of two days. Prior to the trial, the resident's food and water bowls were removed, as well as all moss. The resident's mate and any pups were removed for the duration of the trial. Fifteen minutes were allowed after removal of cage-mates, in order for the resident to acclimate to their absence. Males and females (including lactating females with pups)

forage on their own in the field, and on the one occasion that a male and female were found nesting together, they frequently were observed foraging separately (Blondel, unpublished data). Thus, the temporary separation of cage-mates is not an unusual context for the resident subject. For breeding pairs that had pups, trials were delayed until pups were mobile with open eyes, to minimize stress to both residents and pups. Additionally, one parent (the mate of the trial subject) was always with the pups.

The resident's PVC log remained in the cage. An extra PVC log was placed into the cage to provide the intruder with a hiding place. The intruder animal was removed from its home cage (and thus from its mate) and placed for a 15-minute acclimation period in a temporary holding aquarium. This allowed the intruder some time to adjust to the absence of its mate.

One of the two mice in each trial was randomly selected to be marked with a spot of fluorescent powder on its back, to allow for identification during scoring. The other mouse was "marked" with a blank utensil to control for the effect of handling and marking. The intruder was then placed in the resident's cage, in an acclimation chamber (an 8 cm-diameter vertically-placed open-bottomed PVC pipe) for 5 minutes.

*S. xerampelinus* are most active from 8 to 11 AM, but their activity patterns also show a small increase in activity shortly before dawn and shortly after dusk (Hooper & Carleton 1976). Our pilot laboratory studies revealed that the mice exhibit a "freezing" behavior and do not move when placed in an unfamiliar environment with full overhead lights, even when allowed to acclimate for several hours. The mice will only start to move when the lights are turned off. Therefore, the experiments were run during the active part of the *S. xerampelinus* cycle (between 8 AM and 8 PM), but the overhead

lights were turned off during each trial. A red light was used so that behavior could be scored. In pilot studies, the mice were active in the dark, and did not exhibit any signs of settling down for the “night”.

Each trial was begun by the removal of the vertical open-bottomed acclimation chamber, allowing the resident and the intruder to interact. Each trial lasted 20 minutes, and was scored real-time using JWatcher (Blumstein et al. 2000) in 30-second scan samples (Altmann 1974, Martin & Bateson 1993). Behaviors were scored using the ethogram given in the Appendix. In addition to the scan samples, we scored certain behaviors by “all-occurrence sampling,” also known as “conspicuous behavior recording” (Martin & Bateson 1993). These were infrequent yet significant behaviors that may have been missed if only scan sampling was used. The behaviors scored by all-occurrence sampling were lunges, fights, calls and chitters (Appendix). The three behaviors analyzed in this report are lunges, fights, and out-of-sight. Our definition of “lunge” is “one animal moves suddenly towards other animal with open mouth.” Our definition of “fight” is “two animals in contact (usually ventral-ventral), rolling around together, with mouths open; movement is more rapid than during allo-grooming, both animals are moving, and biting is attempted.” Our definition of “out-of-sight” is “hidden under log“. Trials were videotaped for future analysis.

We attempted to minimize the stress of the encounters and prevent injury to the mice in several ways. The two PVC logs provided shelters and a defensible retreat. If the fight lasted longer than 10 seconds or seemed especially intense, we interrupted it by separating the mice by gently touching them with a small stick or capped pen. This was

always enough to stop the fight and separate the mice. Upon completion of the trials, each participant was examined and no injuries were found.

During the study, on two separate occasions one of the cage mates in a breeding pair died (no wounds or injuries were visible, so the mortalities did not seem to be related to the experiments). On another occasion, a breeding pair had to be separated due to aggressive behavior between cage mates. In each of these instances, we paired the surviving/remaining individuals with a new unrelated mate, so that the round-robin trial design could be continued.

### **Subjects**

We used a colony of wild-caught *Scotinomys xerampelinus* and lab-reared first filial (F1) progeny. The mice were live-trapped in Cerro Punta, Panama in August 2004, on the site of our field study and on nearby transects (see Chapter 2 for trapping methods and study site details). Appropriate collection and export permits for the animals were obtained from the government of Panama, and appropriate entry and import permits were obtained from the United States Fish and Wildlife Service and the United States Department of Homeland Security. The animals were maintained in the lab under a 12L:12D light cycle, with lights turning on at 08:00 AM. The mice were fed *ad libitum* kitten chow, mixed with peanuts, sunflower seeds, and various beans and peas, as well as regular allotments of mealworms. They were housed in 38-liter aquaria (50.8 cm X 25.4 cm X 30.5 cm), and in addition to cage bedding their environment was enriched with moss and opaque PVC pipe “logs”. Twice daily water-misting was performed to increase humidity to levels approximating those in the animals’ native cloud forest habitat. All protocols were approved by and all animals were maintained under the guidance of the University of Florida Institutional Animal Care and Use Committee.

## Data Analysis

Aggressive behaviors (fights and lunges) and out-of-sight (OOS)-alone behaviors were analyzed across the trial treatments. OOS was given the qualifier “total” and “alone”. “OOS-alone” signifies that the animal is alone under a log. “OOS-total” signifies all the instances that an animal was scan-sampled under a log, including both alone and with another mouse. In the context of a resident-intruder paradigm, when OOS-alone levels for a particular treatment are significantly higher than for the control treatment they can be interpreted as avoidance behavior. We checked for a treatment effect within each sex, for sex differences in behavior, and for differences between residents and intruders.

Aggressive behaviors were analyzed using the Wilcoxon Signed Rank test for all paired data (two treatments for one individual, resident versus intruder in a given trial), and the Mann-Whitney U test for all unpaired data (male versus female). Avoidance behaviors were analyzed using the Friedman test for all related data (three treatments for one individual), and using the Kruskal-Wallis test for all unrelated independent data (male average versus female average). Multiple comparisons for Friedman and Kruskal-Wallis tests were performed using the Conover method (Conover & Inman 1981). Analysis was performed using the StatView and Statsdirect statistical software packages (Abacus concepts 1996, StatsDirect 2002).

Many factors other than treatment and subject sex could potentially affect agonistic behavior, such as time of day, number of days since cage was changed, or order of treatment. We controlled for such factors via the randomized experimental design. However, there were three factors that we felt should be analyzed separately, because of their potential influence on behavior. These factors were: presence/absence of current

litter (“current litter”), pregnant state of female (“fourth week of pregnancy”), and “rearing environment”.

“Current litter” refers to the male or female individual currently having a litter of unweaned pups (although they are not in the cage at the time of the trial). “Fourth week of pregnancy” only applies to females, and indicates that the female was less than 8 days from her next litter-birth, as calculated post-hoc by litter records. “Rearing environment” indicates whether the animal is wild-caught or lab-reared.

These factors could all affect agonistic behavior. An individual with dependent offspring may behave dramatically different than an individual without a current litter. Thus, subjects that are pregnant or that have a current litter may exhibit differing levels of territoriality and agonistic behavior than individuals that are not associated with dependent offspring. For example, lactating female *Peromyscus* species are more aggressive than males and nonbreeding females (Wolff 1989). Additionally, rearing environment may affect behavior. Lab-reared animals have had a different environmental experience than wild-caught animals, with the lab-reared individuals only encountering their parents, siblings, and eventually an opposite-sexed mate. Wild-caught individuals have had the opportunity to encounter novel adults in a natural context. On the other hand, lab-reared animals have always and only experienced the laboratory environment, so they may be less alarmed than wild-caught animals by the novelty of the situation. Wild-caught animals are also older than lab-reared animals. Since we have no way of quantifying the exact age of the wild-caught animals, we did not analyze separately for the effect of age on behavior, and it was not possible to tease apart the

effect of age from the effect of rearing environment. These different rearing environments and ages may add variance to the results of our study.

The three additional factors were analyzed by dividing the data set into subsets of the appropriate category, and then checking for the effects of the treatments. For example, for rearing environment, all of the “resident lunge” behavior was divided into wild-caught residents and lab-reared residents. Then, each subset was analyzed for response to the opposite-sex and same-sex treatments.

## Results

### Aggressive Behavior

Female residents did not differ in number of lunges between same-sex and opposite-sex intruders (Figure 3-1A; Wilcoxon Signed Rank Test:  $p = 0.529$ , tied  $p = 0.523$ ,  $Z\text{-Value} = -0.630$ , Tied  $Z\text{-Value} = -0.639$ ,  $N = 13$ ). Male residents showed a significant treatment effect, with significantly more lunges towards same-sex intruders than towards opposite-sex intruders (Figure 3-1B; Wilcoxon Signed Rank Test:  $p = 0.002$ , tied  $p = 0.001$ ,  $Z\text{-Value} = -3.180$ , tied  $Z\text{-Value} = -3.196$ ,  $N = 14$ ). Number of resident lunges (averaged for each individual across both treatments) for each sex was not significantly different (Mann-Whitney U test:  $U = 111.5$ ,  $p = 0.320$ , tied  $p = 0.316$ ,  $N_1 = 13$ ,  $N_2 = 14$ ). When analysis was limited to same-sex encounters only, male residents exhibited significantly more lunges than female residents (Figure 3-2; Mann-Whitney U test:  $U = 140.0$ ,  $p = 0.017$ , tied  $p = 0.016$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Resident fights showed a similar pattern to resident lunges. Female residents did not differ in number of fights between same-sex and opposite-sex intruders (Figure 3-3A; Wilcoxon Signed Rank Test:  $p = 0.345$ , tied  $p = 0.336$ ,  $Z\text{-value} = -0.944$ , Tied- $Z\text{-Value} = -0.962$ ,  $N = 13$ ). Male residents did show a significant treatment effect, with significantly

more fights in the same-sex encounters than in opposite-sex encounters (Figure 3-3B; Wilcoxon Signed Rank Test:  $p = 0.002$ , tied  $p = 0.001$ ,  $Z$ -value =  $-3.180$ , Tied  $Z$ -Value =  $-3.266$ ,  $N = 14$ ). Number of resident fights (averaged for each individual across both treatments) for each sex was significantly different, with male residents exhibiting significantly more fights than female residents (Mann-Whitney U test:  $U = 140.5$ ,  $p = 0.051$ , tied  $p = 0.048$ ,  $N_1 = 14$ ,  $N_2 = 14$ ). When analysis was limited to same-sex encounters only, male residents also exhibited significantly more fights than female residents (Figure 3-4; Mann-Whitney U test:  $U = 136.0$ ,  $p = 0.029$ , tied  $p = 0.026$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Female intruders did not differ in number of lunges between same-sex and opposite-sex residents (Figure 3-5A; Wilcoxon Signed Rank Test:  $p = 0.176$ , tied  $p = 0.168$ ,  $Z$ -value =  $-1.352$ , Tied  $Z$ -value =  $-1.377$ ,  $N = 13$ ). Male intruders did show a significant treatment effect, with significantly more lunges towards same-sex residents than towards opposite-sex residents (Figure 3-5B; Wilcoxon Signed Rank Test:  $p = 0.019$ , tied  $p = 0.018$ ,  $Z$ -value =  $-2.344$ , Tied  $Z$ -value =  $-2.358$ ,  $N = 12$ ). Number of intruder lunges (averaged for each individual across both treatments) for each sex was not significantly different (Mann-Whitney U test:  $U = 132.000$ ,  $p = 0.406$ , tied  $p = 0.388$ ,  $N_1 = 16$ ,  $N_2 = 14$ ). When analysis was limited to same-sex encounters only, male intruders exhibited more lunges than female intruders, with the difference approaching significance (Figure 3-6; Mann-Whitney U test:  $U = 125.5$ ,  $p = 0.094$ , tied  $p = 0.075$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Intruder fights showed a similar pattern to intruder lunges. Female intruders did not differ in number of fights between same-sex and opposite-sex residents (Figure 3-7A;

Wilcoxon Signed Rank Test:  $p = 0.176$ , tied  $p = 0.160$ ,  $Z$ -Value =  $-1.352$ , Tied  $Z$ -Value =  $-1.403$ ,  $N = 13$ ). Male intruders did show a significant treatment effect, with significantly more fights in the same-sex encounters than in the opposite-sex encounters (Figure 3-7B; Wilcoxon Signed Rank Test:  $p = 0.008$ , tied  $p = 0.007$ ,  $Z$ -Value =  $-2.666$ , Tied  $Z$ -Value =  $-2.694$ ,  $N = 12$ ). Number of intruder fights (averaged for each individual across both treatments) for each sex was not significantly different (Mann-Whitney U test:  $U = 147.000$ ,  $p = 0.146$ , tied  $p = 0.140$ ,  $N_1 = 16$ ,  $N_2 = 14$ ). When analysis was limited to same-sex encounters only, male intruders exhibited significantly more fights than female intruders (Figure 3-8; Mann-Whitney U test:  $U = 134.5$ ,  $p = 0.035$ , tied  $p = 0.032$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Although resident mice exhibited more lunges than intruder mice (Figure 3-9), these differences were not significant. Within a given same-sex trial, resident females did not exhibit significantly more lunges than intruder females (Figure 3-9A; Wilcoxon Signed Rank Test:  $p = 0.529$ , tied- $p = 0.527$ ,  $Z$ -Value =  $-0.629$ , tied  $Z$ -value =  $-0.632$ ). Male residents did not exhibit significantly more lunges than intruder males (Figure 3-9B; Wilcoxon Signed Rank Test:  $p = 0.162$ , tied- $p = 0.160$ ,  $Z$ -value =  $-1.398$ , tied  $Z$ -value =  $-1.403$ ).

For the above behaviors, we analyzed the effects of current litter, fourth week of pregnancy, and rearing environment. We did not find any significant influence of these variables. Note that the majority of animals used in our trials were not pregnant (pregnant subject animals ranged from 11% to 33% of trials for a given treatment, with a mean of 22%) and did not have current pups (subject animals with pups ranged from 13% to 16% of trials for a given treatment, with a mean of 15%).

### **Out-of-Sight Behavior**

Female residents did not differ in OOS behavior over the three treatments (Figure 3-10A; Friedman test,  $p = 0.864$ , tied  $p = 0.853$ , Chi square = 0.292, Tied-Chi square = 0.318,  $N = 12$ ). Male residents also did not differ in OOS behavior over the three treatments (Figure 3-10B; Friedman test,  $p = 0.694$ , tied  $p = 0.679$ , Chi square = 0.731, Tied-Chi square = 0.776,  $N = 13$ ). Sex differences in OOS behavior (averaged for each individual across the three treatments) were not significant (Mann-Whitney U test:  $U = 121.000$ ,  $p = 0.485$ , tied  $p = 0.485$ ,  $N_1 = 15$ ,  $N_2 = 14$ ). There was also no significant difference between male and female resident OOS behavior when analysis was limited to same-sex encounters only (Mann-Whitney U test:  $U = 96.0$ ,  $p = 0.808$ , tied- $p = 0.807$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Male residents showed a rearing-experience-by-treatment interaction. Wild-caught male residents showed a difference approaching significance in OOS behavior to the three treatments (Figure 3-11A; Friedman Test:  $p = 0.074$ , Chi Square = 5.200,  $N = 5$ ), with pairwise comparisons showing significantly more OOS scans in same-sex treatments than in the no-intruder control (Conover multiple pairwise comparisons). Lab-reared male residents showed the opposite pattern, although it was not significant across the three treatments (Figure 3-11B; Friedman Test:  $p = 0.140$ , tied  $p = 0.114$ , Chi Square = 3.938, Tied Chi Square = 4.345,  $N = 8$ ), with pairwise comparisons showing significantly fewer OOS scans in same-sex treatments than in the no-intruder control (Conover multiple pairwise comparisons).

Female intruders showed a significant difference in OOS behavior over the three treatments (Figure 3-12A; Friedman test,  $p = 0.001$ , tied  $p = 0.001$ , Chi square = 13.423, tied chi square = 13.960,  $N = 13$ ), with significantly more OOS scans in the no-resident

control than in the same-sex and opposite-sex encounters (Conover multiple pairwise comparisons). Male intruders did not differ in OOS behavior over the three treatments (Figure 3-12B; Friedman test,  $p = 0.864$ , tied  $p = 0.859$ , Chi square = 0.292, tied chi square = 0.304,  $N = 12$ ). Sex differences in OOS behavior (averaged for each individual across the three treatments) were not significant (Mann-Whitney U test:  $U = 125.000$ ,  $p = 0.589$ , tied  $p = 0.588$ ,  $N_1 = 16$ ,  $N_2 = 14$ ). There was also no significant difference between male and female intruder OOS behavior when analysis was limited to same-sex encounters only (Mann-Whitney U test:  $U = 107.5$ ,  $p = 0.423$ , tied  $p = 0.411$ ,  $N_1 = 13$ ,  $N_2 = 14$ ).

Limiting the female intruder analysis to female intruders with no current pups showed a different and significant pattern across treatments (Figure 3-13; Friedman Test,  $p = 0.001$ , tied  $p < 0.001$ , Chi Square = 14.864, Tied Chi Square = 16.350,  $N = 11$ ). The fewest OOS scans were in the same-sex treatment, an intermediate level was exhibited in the opposite-sex treatment, and the highest level was exhibited in the no-resident control, with each treatment significantly different from the other (Conover multiple pairwise comparisons).

There were only two female intruders that had current pups across all three treatments. This was too small a sub-set to analyze. Although the two females exhibited high levels of OOS behavior, it is impossible to determine with such a small sample size whether the behavior was affected by presence of pups or whether the individuals happened to both exhibit a tendency to stay under a cage log.

There was also a rearing-experience-by-treatment effect among female intruders. Both wild-caught and lab-reared female intruders showed a significant treatment effect

(Figure 3-14; wild-caught: Friedman Test,  $p = 0.055$ , tied  $p = 0.050$ , Chi Square = 5.786, tied Chi Square = 6.000,  $N = 7$ ; lab-reared: Friedman Test:  $p = 0.018$ , tied  $p = 0.015$ , Chi Square = 8.083, Tied Chi Square = 8.435,  $N = 6$ ). The lab-reared female intruders showed the same pattern as the overall female intruder OOS behaviors, but the wild-caught showed a different pattern. Lab-reared females exhibited significantly lower OOS behavior in opposite-sex treatments than in no-resident controls, whereas the wild-caught females did not differ significantly between opposite-sex treatments and no-resident controls.

Rearing environment also affected male and female same-sex encounters. Lab-reared males exhibited significantly lower resident OOS behavior than lab-reared females during same-sex trials (Mann-Whitney U test:  $U = 39.0$ ,  $p = 0.053$ , tied  $p = 0.050$ , Z-value = -1.936, tied Z-value = -1.963,  $N_1 = 6$ ,  $N_2 = 8$ ). Wild-caught males exhibited slightly greater resident OOS behavior than wild-caught females, but this difference was not significant (Mann-Whitney U test:  $U = 30.5$ ,  $p = 0.175$ , tied  $p = 0.174$ , Z-value = -1.357, tied Z-value = -1.361,  $N_1 = 7$ ,  $N_2 = 6$ ).

Resident mice did not exhibit significantly different OOS behavior than intruder mice (Figure 3-15). Within a given same-sex trial, resident females did not exhibit significantly more lunges than intruder females (Figure 3-15A; Wilcoxon Signed Rank Test:  $p = 0.133$ , tied  $p = 0.132$ , Z-value = -1.503, tied Z-value = -1.504,  $N = 13$ ).

Resident males did not exhibit significantly more lunges than intruder males (Figures 3-15B; Wilcoxon Signed Rank Test:  $p = 0.208$ , tied  $p = 0.208$ , Z-value = -1.258, tied Z-value = -1.260,  $N = 14$ ).

Absence of current litter affected resident-intruder OOS comparisons. When the set was limited to those trials where neither participant had pups, female-female trials revealed significantly greater resident OOS behavior than intruder OOS behavior (Wilcoxon Signed Rank Test:  $p = 0.037$ , tied  $p = 0.036$ ,  $Z$ -value =  $-2.090$ , tied  $Z$ -value =  $-2.091$ ,  $N = 10$ ). Male-male trials where neither male had pups revealed greater resident OOS behavior than intruder OOS behavior, with the difference approaching significance (Wilcoxon Signed Rank Test:  $p = 0.080$ , tied  $p = 0.080$ ,  $Z$ -value =  $-1.750$ , tied  $Z$ -value =  $-1.752$ ,  $N = 9$ ).

Female controls were not significantly different from each other (Wilcoxon Singed Rank Test:  $p = 0.875$ , tied  $p = 0.874$ ,  $Z$ -Value =  $-0.157$ , tied  $Z$ -Value =  $-0.158$ ,  $N = 13$ ). Male controls were significantly different (Wilcoxon Signed Rank Test:  $p = 0.013$ , tied  $p = 0.013$ ,  $Z$ -Value =  $-2.490$ , tied  $Z$ -Value =  $-2.491$ ,  $N = 12$ ). Male no-intruder controls resulted in significantly greater OOS behavior than male no-resident controls.

### **Discussion**

Our original hypothesis was not supported by our results. Our aggressive behavior prediction (Prediction A) was not supported by our data. Female-female encounters were not significantly different from female-male encounters, and male-male encounters were significantly more aggressive than male-female encounters (Figures 3-1,3-3,3-5,3-7). This is the opposite of the pattern we had predicted based on our field data.

Our avoidance behavior prediction (Prediction B) was not supported by our data for females, but was consistent with our data for males. We have no support for elevated “out-of-sight” behaviors during same-sex trials (Figure 3-10). However, among resident wild-caught males we did find more out-of-sight behavior in same-sex trials than in the no-intruder control (Figure 3-11A).

Our site-specific dominance prediction (Prediction C) was also not supported by our data for females. Although residents were slightly more aggressive than intruders in same-sex trials, as had been predicted, this difference was not significant (Figure 3-9). Males, as predicted, did not show significantly different resident and intruder aggressive behavior. However, as with females, male residents showed a non-significant trend towards more aggression than intruder males.

### **Defense Behavior**

Since resident-intruder tests are thought to measure a form of territorial aggression (Bester-Meredith & Marler 2001), the elevated level of aggressive behaviors in male-male encounters could initially be thought to be consistent with male intrasexual territoriality. Since females displayed less aggression than males, and females showed no aggressive behavior difference between same-sex and opposite-sex treatments, our results do not seem consistent with female intrasexual territoriality. However, other resident-intruder experiments on arvicolines and peromyscines found aggressive behavior patterns similar to ours, but across a variety of different territorial and space-use patterns (Table 3-1). Examining resident-intruder results across these different social systems, it becomes apparent that the sex-specific patterns of aggression observed in our resident-intruder experiments seem to be a general pattern among different rodents, regardless of social systems. Most studies listed in Table 3-1 found some aggressive behavior directed towards intruders (defense behavior), and male resident aggression was consistently greater than female resident aggression. The one exception, where female residents were more aggressive than male residents, was for a species (*Clethrionomys glareolous*) in which the reproductive behavior of females is thought to be stimulated by aggressive behavior towards males (Kapusta et al. 1994). The results that were the most similar to

our study were experiments involving meadow voles (*Microtus pennsylvanicus*), which have been reported as exhibiting female intrasexual territoriality but not male intrasexual territoriality (Wolff 1985). Like the singing mice, meadow voles exhibited more male resident aggression than female resident aggression, male residents were more aggressive to same-sex than to opposite-sex intruders, and female residents did not differ in aggression levels between same-sex and opposite-sex intruders (all for reproductive animals with pups; Storey et al. 1994; Table 3-1). This is despite the fact that during the breeding season female meadow voles exhibit exclusive space use and are thought to actively defend territories against each other, and male meadow voles display overlapping home ranges (Wolff 1985).

Prairie voles (*Microtus ochrogaster*), which are mostly socially monogamous, showed equivalent levels of male aggression towards both same-sex and opposite-sex intruders (Table 3-1). In *M. ochrogaster*, male-female pairs defend territories against other pairs (Wolff 1985). Since singing mice exhibited a different aggression pattern, with males exhibiting significantly greater aggression towards same-sex than towards opposite-sex intruders, it is not likely that *S. xerampelinus* has a male-female pair territorial system.

Females in our study displayed more instances of “no-aggression” (zero instances of lunges and/or fights in either treatment) than did males (Figures 3-1,3-3,3-5,3-7). This would be consistent with a female preference for mutual avoidance in conspecifics encounters. However, females did exhibit aggressive behavior in 30-50% of the trials. Other resident-intruder studies that (unlike ours) have included nest-mate encounters have found that wintering communal groups and male-female pairs exhibited no or

extremely minimal same-sex and opposite-sex aggression between nest-mates (McShea 1990, Winslow et al. 1993). Our results show a level of aggression greater than would be expected towards nest-mates, for both sexes in both opposite-sex and same-sex encounters. This might be indicative of a typical “first encounter” behavior towards an unfamiliar conspecific of either sex. However, the most striking pattern in our aggressive behavior results is that male-male encounters showed significantly greater aggressive behavior than female-female and male-female trials.

We cannot rule out the possibility that the abundance of resources is influencing aggression in female *S. xerampelinus*. In the laboratory environment, where mice are exposed to a high abundance of resources, territorial behavior might decrease; in the wild, in populations where natural food sources may be more scarce and patchy, territoriality is common. A high abundance of resources generally does not favor female rodent territoriality (Ostfeld 1990). Females might then be expected to exhibit relaxed territorial behavior in the lab. Males would likely not be as affected, since male rodent territoriality is thought to be influenced more by distribution of females than by resources (Ostfeld 1990).

The reproductive state of the female should also be considered in interpreting our results. Most of the females in our resident-intruder trials were not lactating and did not have pups. Lactating females in other species, such as Peromyscines, are more aggressive than non-breeding females (Wolff 1989). Exclusive female home ranges in singing mice may be maintained by mutual avoidance when females are not breeding, and maintained by aggressive territorial behavior when females are lactating (but see Storey et al. 1994). During our 2004 mark-recapture study (Chapter 2), in which the five

resident females exhibited nearly completely exclusive home ranges, four of the five females were pregnant or lactating at some point during or immediately after the study.

### **Out-of-Sight Behavior**

Male wild-caught residents exhibited more out-of-sight (OOS)-alone behavior in response to a male intruder than in the no-intruder control (Figure 3-11A). This pattern was expressed in residents but not in intruders. Territorial males would be expected to be dominant in their territory, and intruders would be expected to exhibit significant avoidance, rather than residents. Our data are consistent with a non-territorial social system within male-male interactions.

Wild-caught resident males demonstrated more avoidance behavior than lab-reared resident males in the context of same-sex encounters. This rearing environment effect (Figure 3-11) was unexpected. Wild-caught resident males showed significantly more OOS in same-sex encounters than in no-intruder controls, but lab-reared resident males showed the opposite pattern. The primary differences between our wild-caught and lab-reared animals are rearing environment and age. For example, wild-caught animals will, over their pre-capture lifetimes, experience agonistic encounters with novel same-sex individuals in the wild, whereas lab-reared animals have only encountered their parents, siblings and opposite-sexed mate. This difference in experience appears to result in wild-caught males exhibiting avoidance behavior in response to extended same-sex agonistic interactions. Wild-caught animals were also older than lab-reared animals. Additionally, wild-caught animals are likely to find their caged environment more stressful than lab-reared animals. We would expect the wild-caught mice to gradually become less stressed as they adjust to their captive environment, but it is not known to what extent their stress responses decrease, and how long this would take. Our wild-caught subjects had at least

eight months of residency in our colony before the resident-intruder experiments. The fact that the subjects were still alive, producing litters, and apparently healthy after eight months indicates that they are at least not suffering from obvious pathological effects of chronic stress, such as reproductive failure or death (Sapolsky 1992, Chrousos et al. 1995).

A resident-intruder study on prairie voles (*Microtus ochrogaster*) similarly found agonistic behavioral differences between field-born and lab-reared animals (Harper & Batzli 1997). Lab-reared voles were significantly more aggressive than field-born voles. Harper and Batzli do not attribute the behavioral differences to age, since their related repeatability experiments showed that levels of adult aggression are relatively stable over time. They also do not attribute the behavioral differences to diet, since other experiments have shown that a high-quality diet (such as is typical in a laboratory environment) would result in less, rather than more, aggression exhibited by lab-reared animals (reviewed in Harper and Batzli 1997).

It is not yet clear what differences between lab-reared and wild-caught animals are responsible for the differences in agonistic behavior, nor is it clear which rearing experience results in a more natural behavior. The two different rearing experiences each have their advantages and disadvantages, in the context of natural development and stress. Staged encounters, both in the field and in the laboratory, are critical to behavioral studies, since they allow for detailed behavioral observations. We suggest that such staged encounters be performed on both wild-caught and lab-reared animals, to obtain behavioral data across the spectrum of these different rearing environments.

Female intruder OOS behavior showed slightly different responses to treatments depending on rearing environment and existence of current litter (Figures 3-12, 3-13, 3-14). However, in all cases, female intruder OOS levels were significantly higher for the no-resident control than for the same-sex encounters. Note that intruder females (Figure 3-12) show the opposite pattern of wild-caught resident males (Figure 3-11A); that is, females show less OOS behavior in same-sex encounters than in controls, and males show more OOS behavior in same-sex encounters than in controls. The reasons for this are not clear. Since female no-intruder controls and no-resident controls were not significantly different, females may simply prefer to spend more time under cover when alone, but not when another animal is present. This suggests strong nest site fidelity in females.

### **Site-Specific Dominance**

Although residents were slightly more aggressive than intruders, which would imply territoriality, this difference was not significant (Figure 3-9). Additionally, intruder males were significantly more aggressive towards resident males than towards resident females (Figures 3-5 & 3-7), which would not be expected for male intrasexual territoriality. This is because rodents have been shown in other studies to be dominant and more aggressive on their own territory, exhibiting more lunges; intruders have been shown to be submissive, and to exhibit more avoidance behavior, such as withdrawing and moving less than the resident (Eisenberg 1968, Wolff et al. 1983, Harper & Batzli 1997). Our data for male *S. xerampelinus* are consistent with a hypothesis of non-territorial male-male interactions. However, there are two alternative explanations that we should consider. The observed results may be due to the fact that we used breeding pairs for the experiments, or it may be due to the laboratory constraints of the experiment.

We used breeding pairs in this experiment, so in any given trial, the arena was a cage that was inhabited by both a male and a female. It could be that an intruder male was not reacting solely in response to the resident male. The intruder male would have been able to detect the (non-present) female resident in the cage since the bedding was not changed. This in turn may have led to more aggressive intruder behavior than would have been expected if the cage housed a single resident male. This possibility could be clarified if the experiment were repeated with singly housed males and females.

Another possibility is that the aggressive intruder behavior may be a laboratory artifact. Staged resident-intruder encounters are different than natural encounters in the field, since the lab encounters are forced, and avoidance is limited by the small cage size (Wolff et al. 1983, Ostfeld 1985b, Harper & Batzli 1997). Since the natural home range of *S. xerampelinus* is several hundred square-meters, an agonistic encounter might normally result in the intruder retreating immediately out of the resident's home range. Although we provided two logs as potential retreats, the small cage did not allow the intruder to terminate the encounter by leaving the arena. The length of the enforced 20-minute interaction may also have resulted in more intruder aggression than would have been seen in natural conditions. For example, observations during the trials indicated the male residents would typically initiate fights and would lunge during the initial encounter with the intruder. However, after a few minutes, the intruder would sometimes start to initiate chases and fights. This may have also affected the female-female trials, resulting in increased intruder aggression, and the lack of a significant difference between resident and intruder behavior. A resident-intruder study on prairie voles (*Microtus ochrogaster*), which are intrasexually territorial in both males and females, did not find support for

dominant male residents and subordinate male intruders (Harper & Batzli 1997). The authors noted that contestants seemed more interested in escaping from the arena than establishing dominance or exhibiting territory defense, and thus the use of staged encounters in these cases may greatly alter the context from natural encounters found in the wild. Future resident-intruder experiments on *S. xerampelinus* could minimize this problem by increasing the experimental arena size, even to the extent of an enclosed room, or a natural enclosure. This would allow for a more realistic encounter.

### **The *Scotinomys xerampelinus* Social System**

To briefly summarize our results in both field and laboratory, males were more aggressive than females and were more aggressive towards other males than towards females. Females did not differ in their levels of aggression in response to male and female conspecifics. Females also had more instances of “zero aggression” trials than males. There was no overall significant difference in out-of-sight behavior for either sex. The results show no support for site-specific dominance. In the field, females displayed exclusive space use, whereas males displayed intrasexual overlap. Males and females did not differ significantly in weight. With all of the above taken together, we can now describe the *S. xerampelinus* social system. We propose that females are dispersed, and that their non-overlapping intrasexual space use patterns are driven primarily by mutual avoidance and strong nest site fidelity, rather than territorial aggression. We propose that males exhibit overlapping intrasexual space use accompanied by substantial aggression and intolerance during intrasexual conspecific encounters, but that this aggression is unlikely to be accompanied by a resident advantage. Moreover, it seems likely that males also exhibit some mutual avoidance. There is also the possibility of small core territories defended by males.

Typically, space use studies interpret non-overlapping home ranges as evidence of territoriality, with the implication that home ranges are actively defended. However, as suggested by our laboratory data, it is possible that the exclusive space use that we observed among female *S. xerampelinus* in the field reflects a tendency towards mutual avoidance, rather than aggressive defense behavior. If mutual avoidance were the major mechanism driving exclusive space use, their system would not be appropriately described as purely territorial. This has implications for other rodents that are usually referred to as territorial. For example, other species show similar space-use and behavioral patterns to *S. xerampelinus*, such as *Microtus pennsylvanicus* (Table 3-1). *M. pennsylvanicus*, especially among females, also exhibits considerable mutual avoidance behavior relative to other microtines that are more aggressive in intraspecific encounters (Getz 1962, Colvin 1973, Madison 1980). Primarily due to their exclusive area use patterns, female *M. pennsylvanicus* has been described in the literature as territorial; however, as in *S. xerampelinus*, the social system may be more appropriately described as exclusive area use driven by mutual avoidance.

Males may exhibit more aggressive intrasexual social behavior (but may also show mutual avoidance), whereas females exhibit more mutual avoidance (but may also show some aggression). Male rodents in general are thought to be able to engage in more intense aggression than females. This is because males do not have to devote energy to gestation, and generally devote less energy to parental care, so they can apply more of their energy budgets to agonistic and defensive interactions (Ostfeld 1985a). The level at which costs of defense are greater than the benefits of defended resources would thus be higher for males. In the *S. xerampelinus* resident-intruder experiments, this would be

reflected by the observed male treatment effect, but the lack of a treatment effect among females.

Intense male intrasexual competition would be expected to result in sexual dimorphism (Heske & Ostfeld 1990). However, although our experiments showed extensive male-male aggression, singing mice are not sexually dimorphic in weight, gross morphology or coloration. This issue could be resolved if a frequent expression of male *S. xerampelinus* intrasexual social behavior in a natural context would be mutual avoidance. The effects of sexual selection on males, therefore, would be more apparent in spatial home range patterns and features related to mate attraction than in sexual dimorphism (Shier & Randall 2004).

Studies on both territorial and non-territorial males of other rodents have shown that mutual avoidance is sometimes observed in male-male interactions. Male kangaroo rats (*Dipodomys heermanni arenae*), which are not sexually dimorphic, have overlapping home ranges; although they will engage in fights, they are more likely to display mutual avoidance than aggression (Shier & Randall 2004). White-footed mice (*Peromyscus leucopus noveboracensis*) and cloudland deermice (*P. maniculatus nubiterrae*) exhibit mostly non-overlapping male home ranges (Wolff et al. 1983). Both species appear to exhibit the “dear enemy” phenomenon (Fisher 1954), with neighboring males showing no aggression towards each other, but trials between unfamiliar males resulting in aggressive behavior (Wolff et al. 1983).

If *S. xerampelinus* have the capacity for intense male-male aggression, but also exhibit some mutual avoidance in the field, this may explain the absence of sexual dimorphism, male spacing patterns in the wild, and male aggression in laboratory

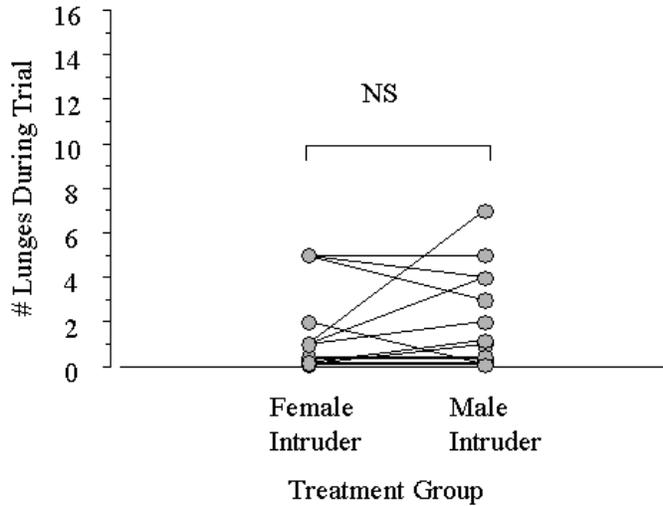
resident-intruder experiments. Note that although male and female spacing patterns differ, we are proposing a strong influence of mutual avoidance behavior in both male-male and female-female interactions. Male *S. xerampelinus* are probably not showing the same exclusive space use that females exhibit because males are attempting to maximize their access to females, which causes their home range areas to overlap despite the occasional yet intense male intrasexual aggression, whereas females are more influenced by resources and/or infanticide prevention (Emlen & Oring 1977, Ostfeld 1985a, Ostfeld 1990, Wolff & Peterson 1998).

Another possible aspect of the male social system consistent with our data is that males may have a small, defended region of their home range, but outside of this region they exhibit extensive overlap with other males, due to the distribution of females in the field. If this pattern were occurring, the small cores may have been too small to be detectable at our 85% home range contour analysis. Some peromyscines are hypothesized to display such a phenomenon, with small, defended core home range areas, but with large, overlapping peripheral areas that are defended minimally or not at all; in these cases, aggression seems to decrease as the animal moves away from the center of its range (Wolff et al. 1983). In order to detect such a pattern with *S. xerampelinus*, we would need more location fixes per animal than we were able to obtain in our fieldwork.

In conclusion, our resident-intruder laboratory experiments are consistent with non-territorial females, and non-territorial males that are nonetheless highly aggressive towards intrasexual conspecifics. Females appear to exhibit exclusive home range areas in the field, whereas male home ranges overlap both other males and other females. In chapter 4 we summarize our field and laboratory conclusions regarding *S. xerampelinus*

space use and mating system, we address the potential functions of the calling behavior, and we describe future research directions for this species.

## 3-1A: Female Residents



## 3-1B: Male Residents

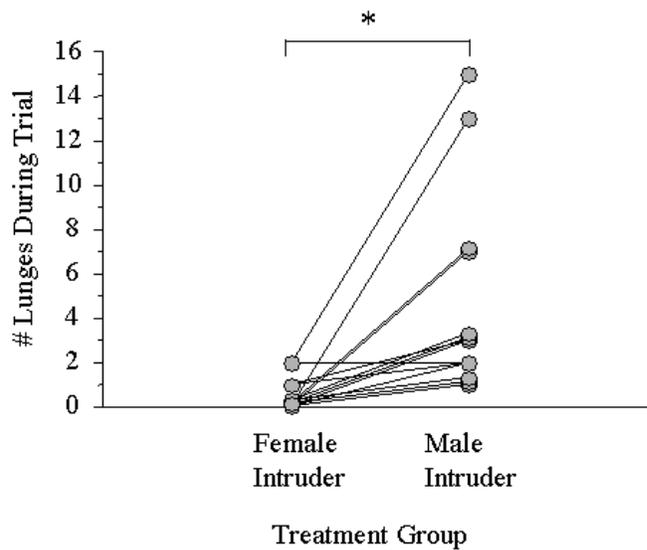


Figure 3-1. Resident lunges, same-sex versus opposite-sex encounters. A) Total lunges for each trial by female residents,  $N = 13$ , towards male and female intruders. B) Total lunges for each trial by male residents,  $N = 14$ , towards male and female intruders. NS: nonsignificant; \*  $P < 0.05$ . Lines represent individuals.

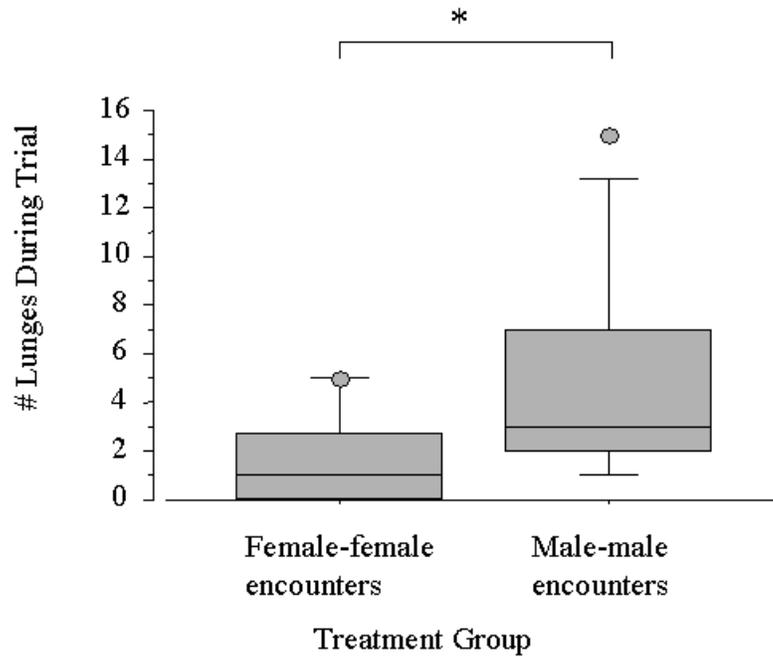


Figure 3-2. Resident lunges, same-sex encounters, male versus female. Resident lunges for each same-sex trial. Female-female encounters: N = 13. Male-male encounters: N = 14. NS: nonsignificant; \* P<0.05. Box plot representation of observations, from bottom up, is: <10th percentile, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, > 90th percentile.

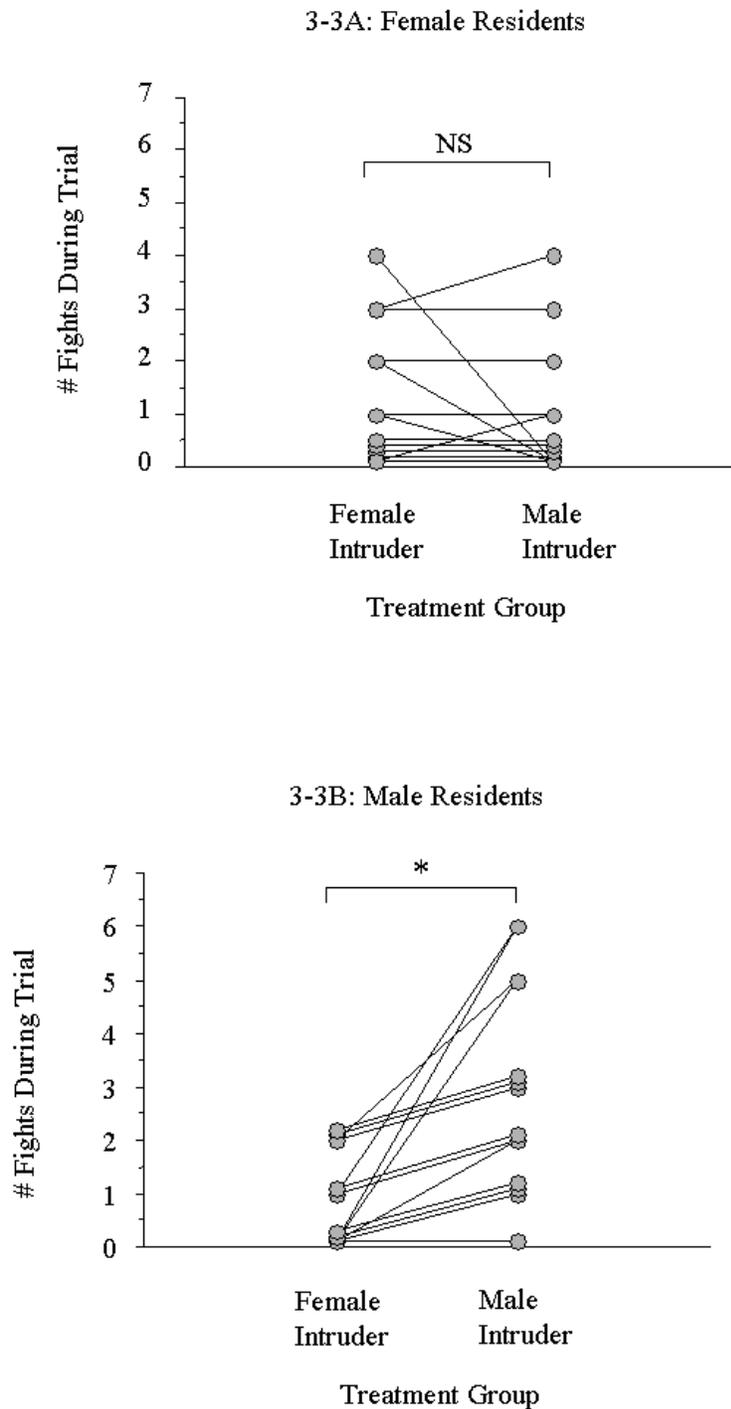


Figure 3-3. Resident fights, same-sex versus opposite-sex encounters. Total resident fights for each trial. A) Female residents, N = 13. B) Male residents, N = 14. NS: nonsignificant; \* P<0.05. Lines represent individuals.

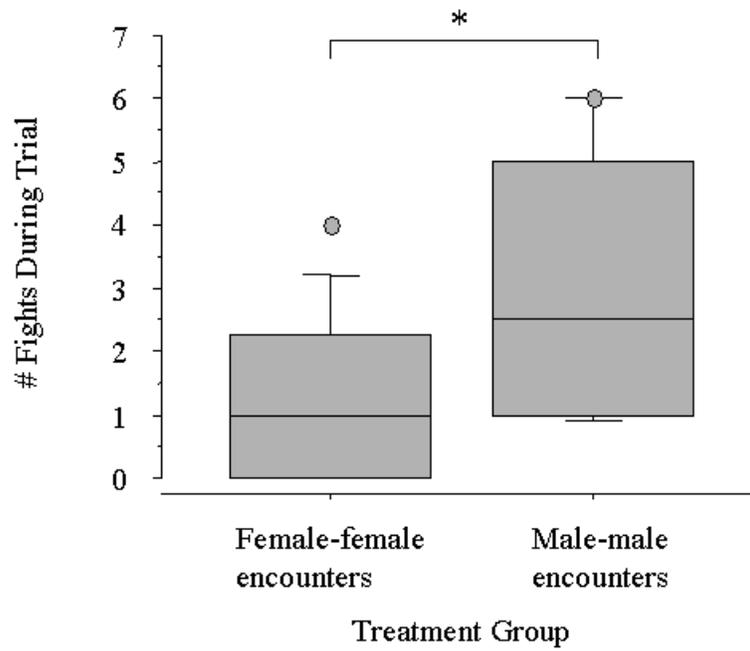


Figure 3-4. Resident fights, same-sex encounters, male versus female. Resident fights for each same-sex trial. Female-female encounters: N = 13. Male-male encounters: N = 14. NS: nonsignificant; \* P<0.05. Box plot representation of observations, from bottom up, is: <10th percentile, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, > 90th percentile.

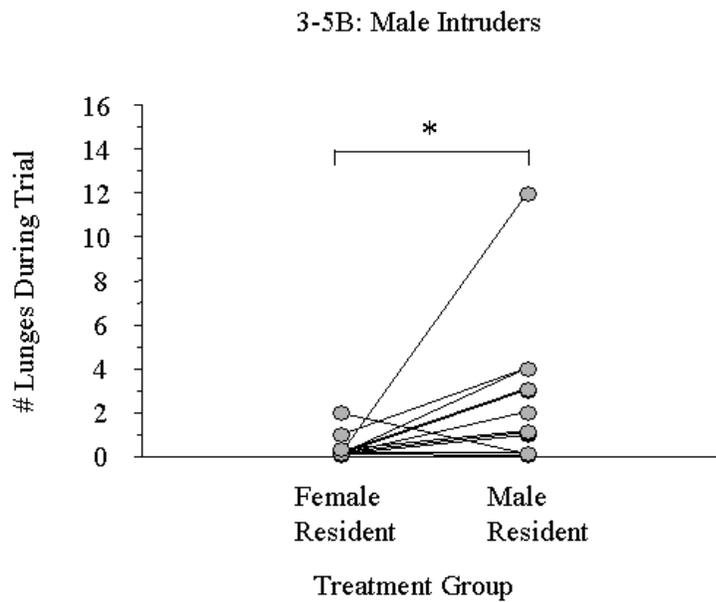
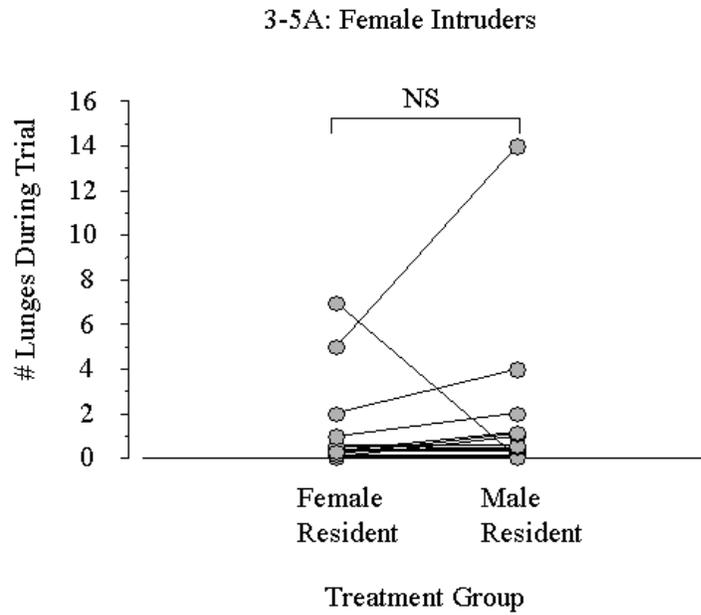


Figure 3-5. Intruder lunges, same-sex versus opposite-sex encounters. Total intruder lunges for each trial. A) Female intruders, N = 13. B) Male intruders, N = 12. NS: nonsignificant; \* P<0.05. Lines represent individuals.



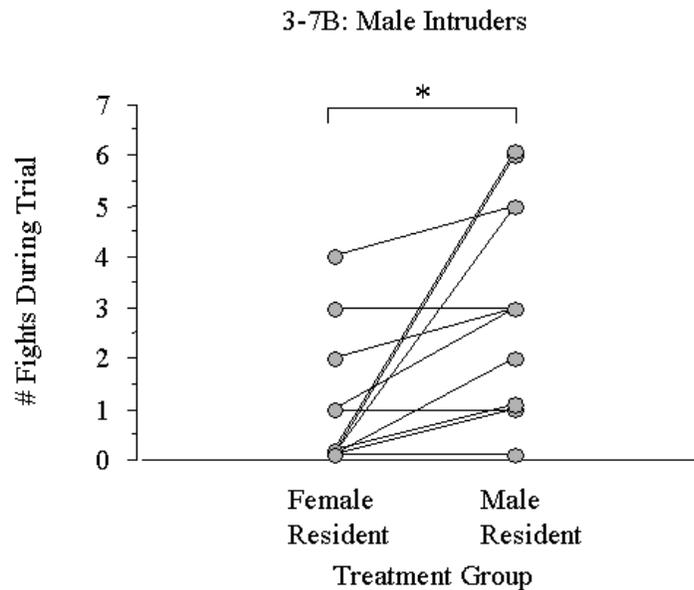
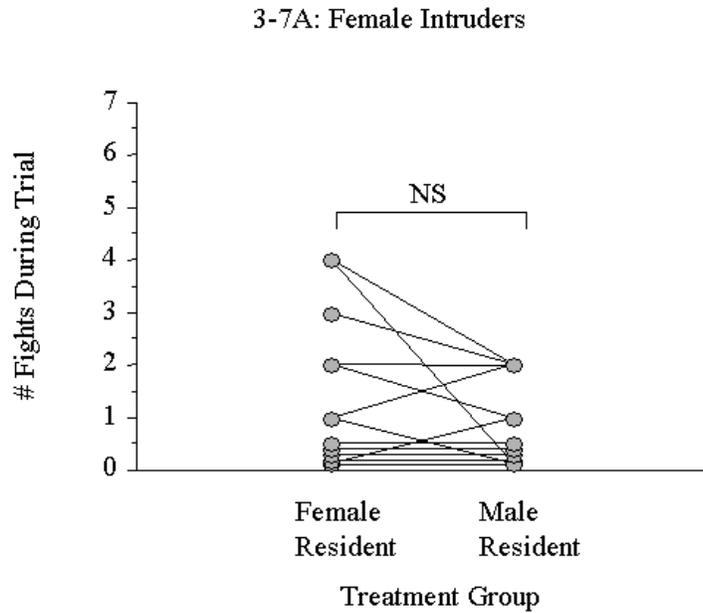


Figure 3-7. Intruder fights, same-sex versus opposite-sex encounters. Total intruder fights for each trial. A) Female intruders, N = 13. B) Male intruders, N = 12. NS: nonsignificant; \* P<0.05. Lines represent individuals.

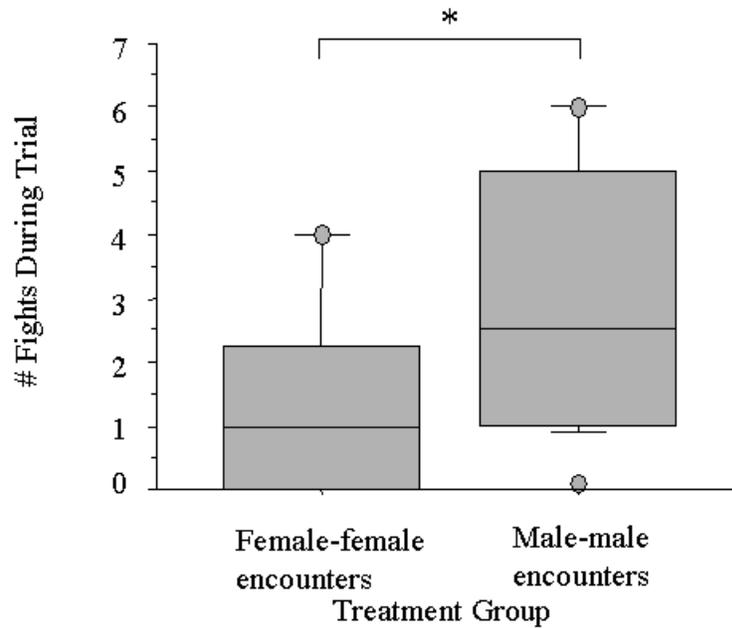


Figure 3-8. Intruder fights, same-sex encounters, male versus female. Intruder fights for each same-sex trial. Female-female encounters: N = 13. Male-male encounters: N = 14. NS: nonsignificant; \* P<0.05. Box plot representation of observations, from bottom up, is: <10th percentile, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, > 90th percentile.

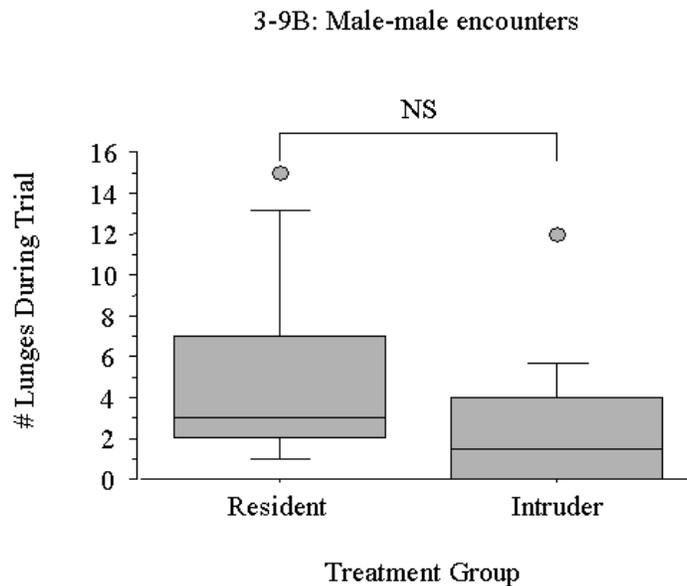
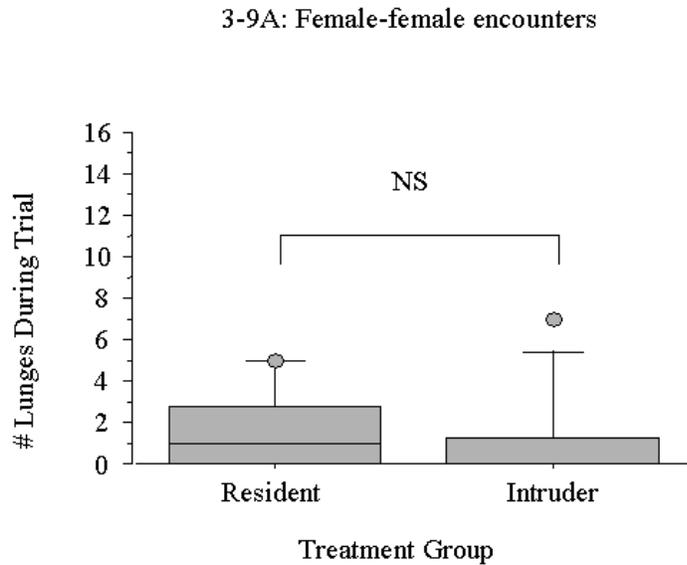


Figure 3-9. Lunges in same-sex encounters, residents versus intruders. A) Females, N = 13. B) Males, N = 14. NS: nonsignificant; \* P<0.05. Box plot representation of observations, from bottom up, is: <10th percentile, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, > 90th percentile.

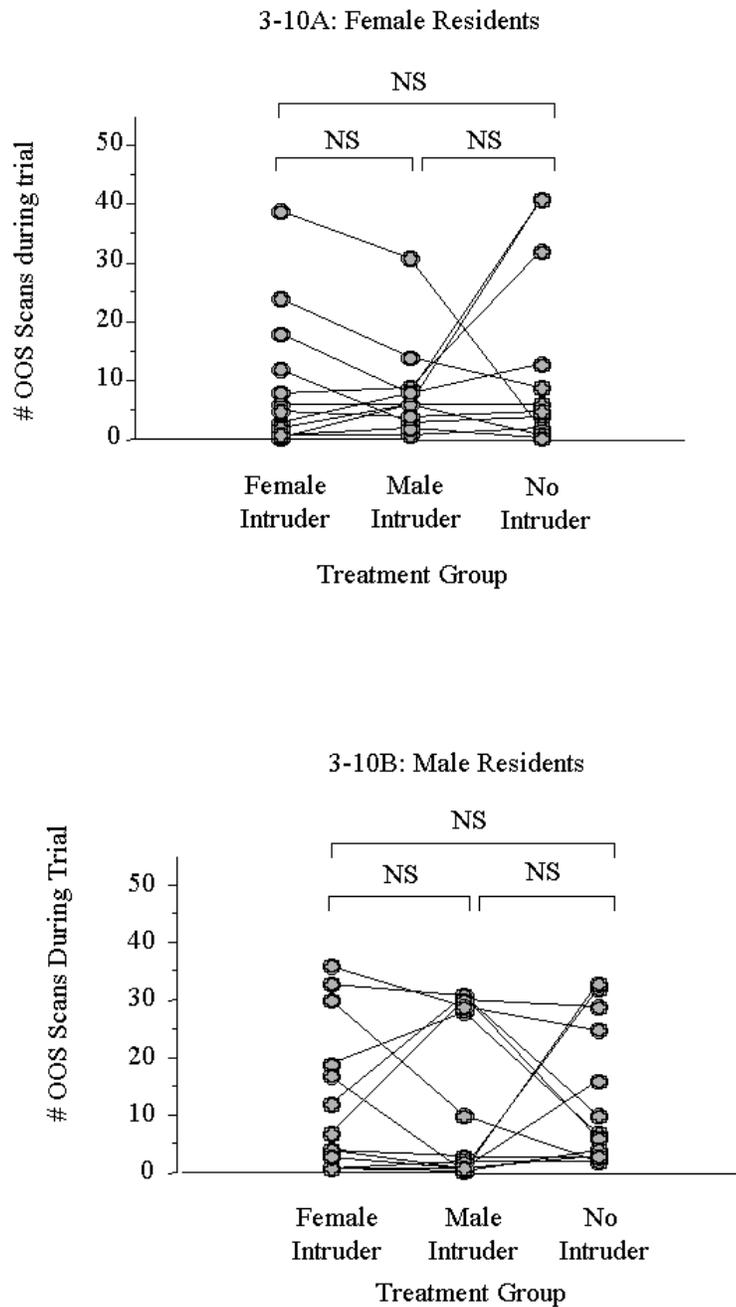
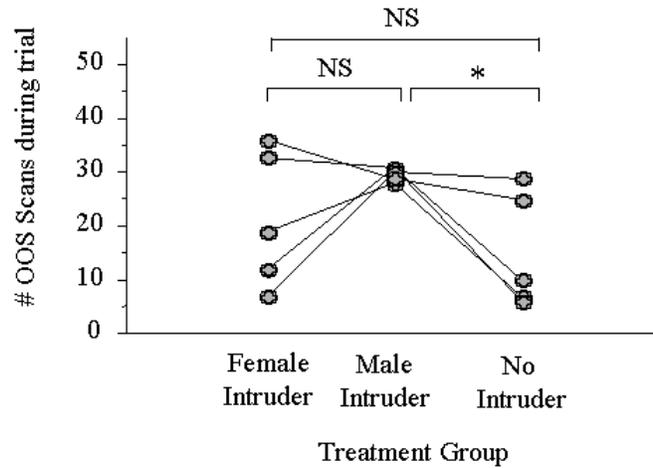


Figure 3-10. Resident out-of-sight (OOS). Total resident scans for OOS-alone behavior. “OOS-Alone” indicates that the animal was alone under the log. OOS-together (both animals under one log) was excluded from the above analysis. A) Female residents, N = 12. B) Male residents, N = 13. NS: nonsignificant; \* P<0.05. Lines represent individuals.

## 3-11A: Wild-Caught Male Residents



## 3-11B: Lab-Reared Male Residents

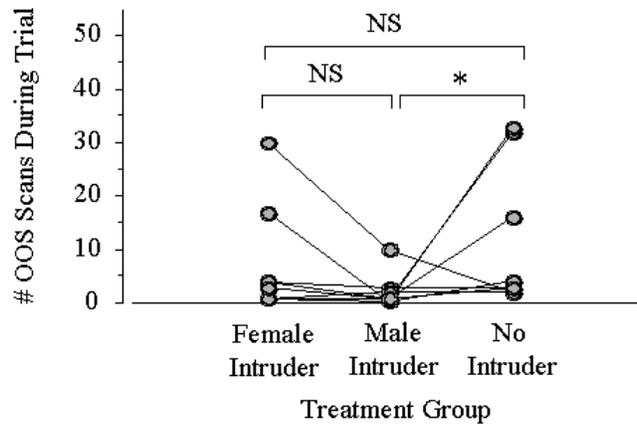


Figure 3-11. Male resident Out-of-sight (OOS) – rearing effect. Total resident scans for OOS-alone behavior. “OOS-alone” indicates that the animal was alone under the log. OOS-together (both animals under one log) was excluded from the above analysis. A) Male wild-caught residents, N = 5. B) Male lab-reared residents, N = 8. NS: nonsignificant; \* P<0.05. Lines represent individuals.

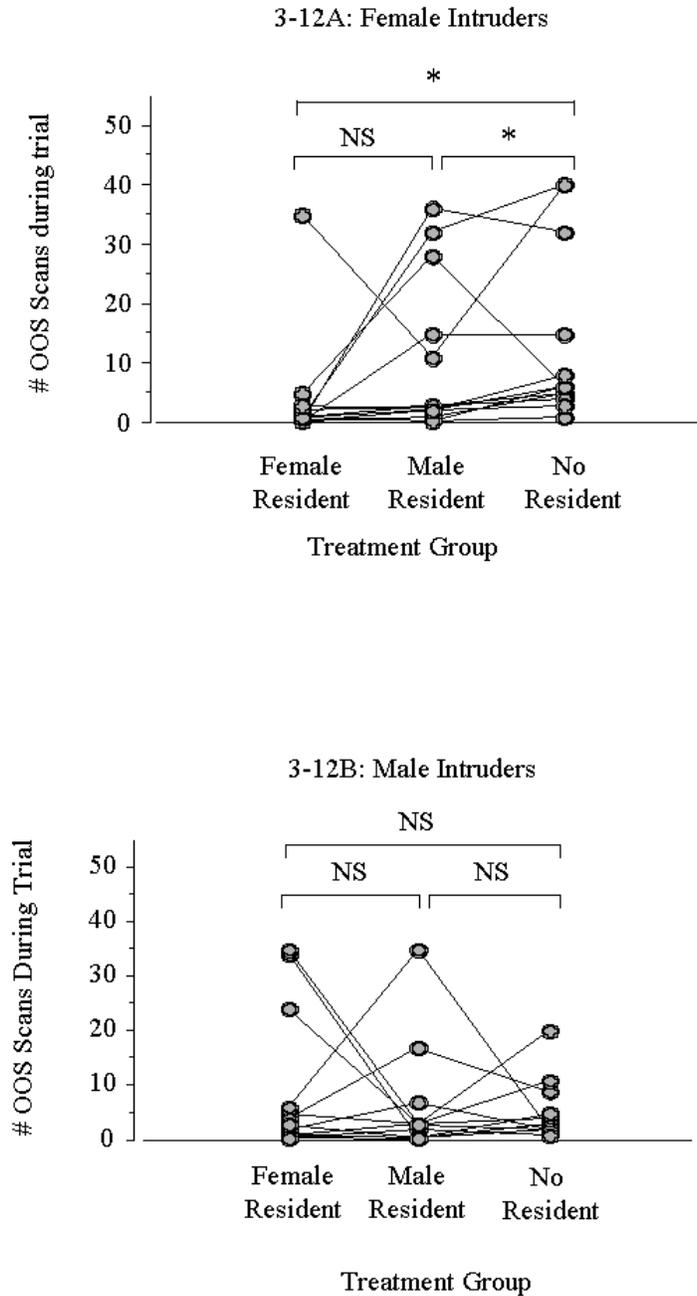


Figure 3-12. Intruder out-of-sight (OOS). Total intruder scans for OOS-alone behavior. “OOS-alone” indicates that the animal was alone under the log. OOS-together (both animals under one log) was excluded from the above analysis. A) Female intruders, N = 13. B) Male intruders, N = 12. NS: nonsignificant; \* P<0.05. Lines represent individuals.

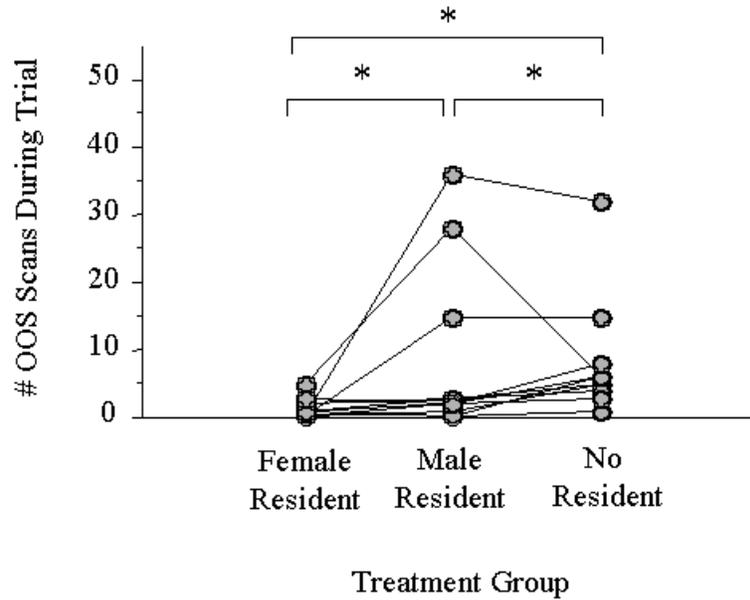


Figure 3-13. Female intruder out-of-sight (OOS), no pups. Total intruder scans for OOS-Alone behavior. “OOS-alone” indicates that the animal was alone under the log. OOS-together (both animals under one log) was excluded from the above analysis. Only females that did not have current litters for any of the three trials were included in the above analysis. N = 11. NS: nonsignificant; \* P<0.05. Lines represent individuals.

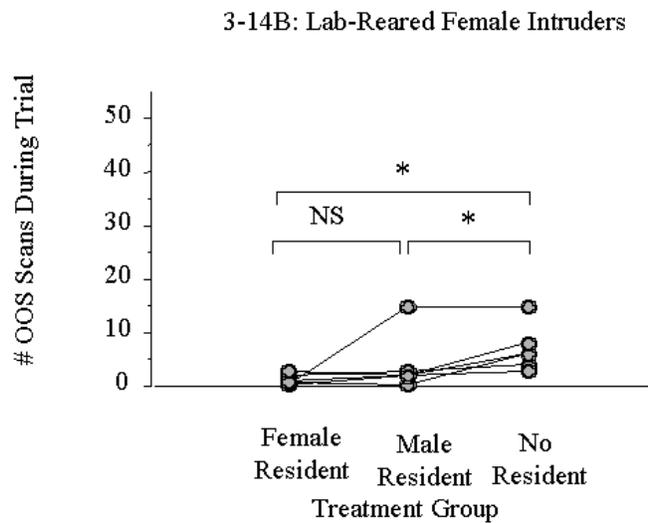
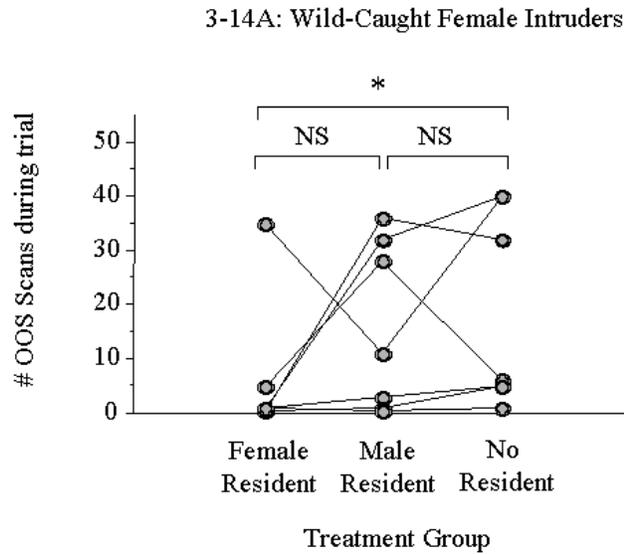


Figure 3-14. Female intruder out-of-sight (OOS) – rearing effect. Total intruder scans for OOS-alone behavior. “OOS-alone” indicates that the animal was alone under the log. OOS-together (both animals under one log) was excluded from the above analysis. A) Wild-caught female intruders, N = 7. B) Lab-reared female intruders, N = 6. NS: nonsignificant; \* P<0.05. Lines represent individuals.

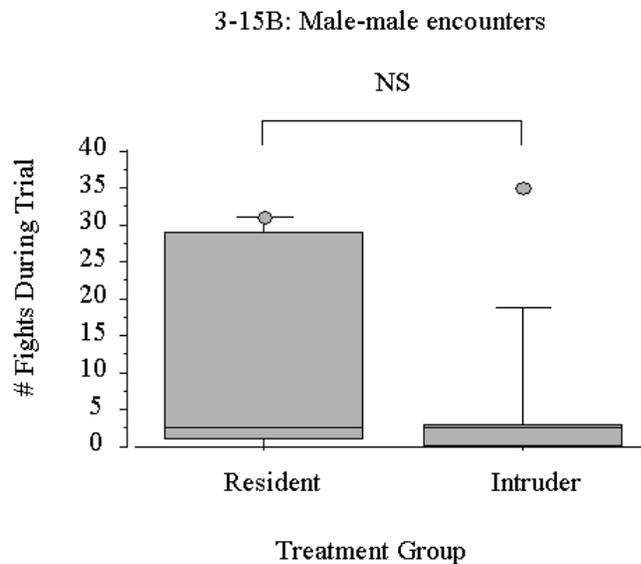
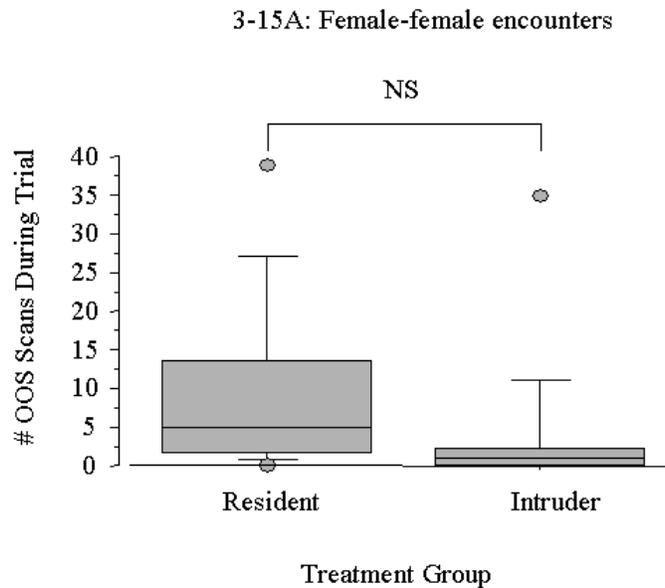


Figure 3-15. Out-of-sight (OOS) in same-sex encounters, residents versus intruders. A) Female-female encounters, N = 13. B) Male-male encounters, N = 14. NS: Nonsignificant; \*  $P < 0.05$ . Box plot representation of observations, from bottom up, is: <10th percentile, 10th percentile, 25th percentile, median, 75th percentile, 90th percentile, > 90th percentile.

Table 3-1. Resident-intruder experiments on arvicoline and peromyscine rodents

Species	Territorial?	Exclusive HR?	Defense behavior?	Site-specific dominance?	Results	Citation
<i>Microtus pennsylvanicus</i>	♀♀	♀♀	YES	n/a	Resident aggression: SS > OS	McShea 1990
			YES	n/a	♂ resident aggression: SS > OS ♀ resident aggression: SS = OS Resident aggression: ♂ > ♀	Storey et al. 1994
<i>M. montanus</i>	♀♀, ♂♂	♀♀, ♂♂	YES	n/a	Resident aggression: ♂ > ♀	Pierce et al. 1991, Pellis et al. 1992
<i>M. ochrogaster</i>	♂♀ pair	♂♀ pair	YES	n/a	Resident aggression: ♂ > ♀	Pierce et al. 1991, Pellis et al. 1992
			YES	n/a	♂ resident aggression: SS = OS Resident aggression: intruder > mate	Winslow et al. 1993
			YES	♀: YES ♂: NO	Resident aggression: ♂ > ♀	Harper & Batzli 1997
<i>Clethrionomys glareolus</i>	♀♀	♀♀	YES (♀ only)	n/a	Resident aggression: ♀ > ♂	Kapusta et al. 1994
<i>C. rufocanus</i>	♀♀	♀♀	NO	YES	Avoidance: resident ♀ < intruder ♀	Andreassen & Ims 1990
<i>Peromyscus leucopus noveboracensis</i>	Varies	Varies	YES	YES	Aggression: resident ♂ > intruder ♂ Aggression: resident ♀ > intruder ♀	Wolff et al. 1983
<i>P. maniculatus nubiterrae</i>	Varies	Varies	YES	YES	Aggression: resident ♂ > intruder ♂ Aggression: resident ♀ > intruder ♀	Wolff et al. 1983

Resident-intruder experiments. Territorial and exclusive range column citations as follows: *Microtus* spp. – Wolff 1985, *Clethrionomys* spp. – Ostfeld 1985a, *Peromyscus* spp. – Ribble 2003. Territorial column: ♀♀ = female intrasexual territoriality, ♂♂ = male intrasexual territoriality, ♂♀ pair = male-female pairs defend against both sexes. Exclusive HR column: HR = Home Range; ♀♀ = no female-female HR overlap, ♂♂ = no male-male overlap, ♂♀ pair = male-female pairs occupy home ranges that are exclusive from other individuals. Defensive behavior, site-specific dominance and notes columns are from resident-intruder experiments as indicated in citation column. Defense behavior = aggressive behavior towards an intruder. Notes column: SS = same sex; OS = opposite sex. Resident-intruder experiments reviewed in Harper 1996.

## CHAPTER 4 SUMMARY

### **Space Use**

Our *Scotinomys xerampelinus* fieldwork (Chapter 2) revealed minimal female home range area overlap. This suggests female intrasexual exclusive space use, which was one of our criteria for territoriality, although such space use could also be driven by mutual avoidance. Males displayed considerable intrasexual home range area overlap. The population also exhibited extensive intersexual overlap.

The *S. xerampelinus* resident-intruder experiments (Chapter 3) did not show support for site-specific dominance. Females did not differ in their levels of aggression in response to male and female conspecifics. Females also had more instances of “zero aggression” trials. Males were more aggressive than females, and were more aggressive to other males than to females. These aggression patterns seem to be a general rodent trend (Table 3-1). Intruder males were more aggressive to resident males than to resident females. In a territorial system, intruders would be expected to exhibit avoidance behavior, not aggressive behavior.

Our data suggest a relatively dispersed female population, in which exclusive space use is driven largely by mutual avoidance. Males seem to exhibit substantial aggression during intrasexual conspecific encounters, yet still maintain home ranges that overlap both males and females. The lack of sexual size dimorphism suggests that males exhibit a degree of mutual avoidance as well as aggression. At the scale of our observations and the density of our study population, neither sex in this species appears to exhibit clear

territorial behavior. However, our data for males would also be consistent with small territorial cores, surrounded by overlapping undefended peripheral areas.

### **Mating System**

*S. xerampelinus* social structure seems more closely correlated with promiscuity than with polygyny or social monogamy (Chapter 2). Male and female home ranges overlapped on average with several opposite-sexed individuals, females did not have overlapping home ranges, females were relatively dispersed, there was no sexual dimorphism, and in the laboratory paternal care was observed. These are all correlates of rodent promiscuous mating systems (Chapter 2). Further field observations, a larger sample size of animals, and paternity analysis of litters are needed to evaluate this hypothesis about the *S. xerampelinus* mating system.

### **Social Flexibility**

In the laboratory environment, singing mice easily adapt to a “forced monogamy” of breeding pairs. Females with litters tolerate males, and males exhibit paternal care. Our initial breeding pairs produced 29 pups, of which 27 survived to weaning-age with the father present in the cage. Males were frequently observed huddling over pups in the nest. In the second field season, a male-female pair was detected nesting together in the field for several weeks. Although the population as a whole and over the two field seasons seems to be promiscuous and the neither sex appears to exhibit territoriality, there appears to be the potential for some intraspecific variation of the *S. xerampelinus* social and mating systems. We would not be surprised if at certain densities and environmental conditions singing mice exhibit facultative social monogamy.

Intraspecific variability between populations and environments is known to occur in small mammals (Borowski 2003, Luque-Larena et al. 2004, Endries & Adler 2005).

This intraspecific variation in the expression of different types of social systems has been termed “social flexibility” (Lott 1984, Schradin & Pillay 2005), and is a form of phenotypic plasticity (Ostfeld 1990). Social flexibility is influenced by ecological constraints, such as resource abundance and distribution, predation pressure, and population density (Emlen & Oring 1977, Harris & Leitner 2004, Luque-Larena et al. 2004). Rodent social flexibility has been reported mostly in captive animals, and observations in natural populations have historically been relatively rare (Schradin & Pillay 2005). But recently there have been an increasing number of reports on such phenotypic plasticity in the field. The African striped mouse (*Rhabdomys pumilio*) exhibits polygynous multi-adult territorial groups in succulent karoo habitat, but is promiscuous and solitary in moist grasslands (Schradin & Pillay 2005). Prairie voles (*Microtus ochrogaster*) have been reported to occur in multi-adult groups, solitary females, solitary males, and pairs, with such diversity occurring both within and between populations (McGuire & Getz 1998, Roberts et al. 1998, Schradin & Pillay 2005). Field studies on the Central American spiny rat (*Proechimys semispinosus*) report variation from social monogamy to promiscuity that is correlated with population density (Endries & Adler 2005).

It seems that despite such variation, small mammals tend to exhibit modal social systems (Ostfeld 1990). For example, although social flexibility exists in microtines, most vole species are predisposed to exhibit a particular mating system (Wolff 1985, Dewsbury 1991, Luque-Larena et al. 2004). The extent of variation around these modes is not currently known, but can be a critical factor to research approaches, for example in the use of the comparative method, which relies on the categorization of species and

populations (Ostfeld 1990). Future studies on *S. xerampelinus* in the field under differing environmental conditions will reveal the extent of its social flexibility.

### **Functions of the Singing Mouse Calling Behavior**

This research was undertaken partially to provide a foundation for investigations into the function of singing mouse calling behavior. The mice produce trill-like calls that range from human-audible frequencies into the ultrasonic (Hooper & Carleton 1976). The call starts at a relatively high pitch, and then gradually lowers in pitch and both the notes and inter-note intervals gradually increase in length. The call is essentially one syllable, or note, that is repeated and modulated over the course of the call. In *Scotinomys teguina* the call lasts 7-10 seconds, and in *S. xerampelinus* the call is somewhat shorter, sounding like the truncated beginning of a *S. teguina* call. *Scotinomys* calls have been observed in various contexts, with males calling more frequently than females, spontaneous calls in both sexes without noticeable external stimulus, calls exhibited by males recently paired with females, and by females that have just given birth (Hooper & Carleton 1976, Blondel pers.obs). In interspecific staged encounter experiments, the dominant male (which was not always of the same species) exhibited more calling behavior than the subordinate male (Hooper & Carleton 1976).

Our *Scotinomys xerampelinus* research suggests exclusive female space use, but not accompanied by site-specific dominance, and also suggests that male-male contact in close quarters can result in elevated aggression levels. Therefore the song could potentially play a role in agonistic interactions. The mice show patterns of space use that seem consistent with promiscuity; if this proves to be generally true, the call may prove significantly important for mate attraction as well. Vocal communication in mammals also frequently functions as alarm calls (Poole 1985). Thus, possible functions of vocal

communication in the singing mouse include alarm, agonistic, and mate attraction functions.

The *S. xerampelinus* call is unlikely to be an alarm call, due to the context of when the call is made, and due to its acoustic properties. An alarm call would likely be higher in pitch and frequency (Poole 1985), and would not extend into relatively lower frequencies that are exhibited by the *Scotinomys* call. Alarm calls also would not occur in situations such as birth of a new litter and pairing with a new mate, as exhibited by *Scotinomys* (Hooper & Carleton 1976).

Both an agonistic and a mate attraction function would benefit from a long-distance transmission of a call. The relatively low-frequency characteristics of the final portion of the *Scotinomys* call suggest that it is intended for an audience that is not in the immediate vicinity of the sender. The spacing patterns observed in the field would allow for the mice to send and receive vocal signals without requiring physical contact. This would fit well with our suggestion of female intrasexual exclusive space use and agonistic male-male interactions. This type of social spacing organization would result in selection for sex-specific advertisement calls, so that animals could differentiate between a prospective mate and a potentially agonistic same-sex encounter.

The *S. xerampelinus* call could also serve in mate attraction as a costly signal that would serve as an indicator of good genes. The length and frequency of the calls could be correlated with singer quality. If there are detectable individual differences in the song, it could also serve in individual identification.

### **Future Research Directions**

The function of the *S. xerampelinus* call can now be investigated further. Because the call may have a mate attraction component, laboratory playback experiments

examining phonotaxis should be performed. Energetics of calling behavior should be measured, to quantify some of the costs involved, and their potential indication of a high quality mate.

Additional information about the acoustical properties of the *S. xerampelinus* call itself needs to be collected in order to clarify its function. The *S. xerampelinus* vocalization should be subjected to extensive acoustical analyses in a similar manner to the recent analysis of male *Mus musculus* ultrasonic songs (Holy & Guo 2005). This will provide insight to the variability, complexity and potential function of the call. Call differences should be analyzed for differences at the population, sex and individual level. If any differences are found, lab experiments should verify whether these differences are detectable by the mice. Calls have been observed in various contexts, and calls should be recorded in all of these different contexts and analyzed for differences.

Further field information also needs to be collected on calling behavior, in order to clarify the potential audience and intended recipient of the signal. The degradation of the call should be measured in the natural habitat, to establish how close a conspecific must be in order to hear it. Calling frequency of individuals in the field should also be measured.

Our previous *S. xerampelinus* radio-tracking work involved a simple radio transmitter that emitted a pulse on a given frequency. We have preliminary circuit designs for a radio transmitter that would be integrated with a microphone, which would convey both location and calling information. In this way we would be able to identify spacing patterns for individuals, and also identify when and where they emitted calls. Further development of this method would require collaboration with an electrical or

biomedical engineer. However, once implemented, the data collected would be invaluable in describing the natural *S. xerampelinus* calling behavior, and assessing its function.

The relationship between calling characteristics and condition should be explored. Do more frequent calls and/or longer calls correlate with condition? Do frequent callers achieve more mating success? Do their offspring have increased survivorship and fitness?

Further investigations should be undertaken into the social system of this species. *Scotinomys* has a midventral sebaceous gland that is used for scent marking (Hooper & Carleton 1976). Scent marking is a criterion that is sometimes used in definitions of mammalian territoriality (Maher & Lott 1995). *Scotinomys* scent marking behavior should be observed in order to clarify and confirm our field and lab territoriality results.

Several aspects concerning the mating system still need to be clarified. Although we now know that the male-female spatial living patterns suggest promiscuity, we do not know the exact reproductive strategies. Paternity analyses using highly polymorphic microsatellite loci, as have been successfully used in other mammalian systems (Bryja & Stopka 2005), would clarify the reproductive relationships among individuals.

Additionally, experiments should investigate the influences determining female singing mouse spacing behavior. Possibilities proposed for other rodents include resource distribution, predator pressure, and infanticide-prevention (Emlen & Oring 1977, Ostfeld 1990, Wolff & Peterson 1998). Paternal care has been observed in the lab, but it should be determined if this behavior occurs in the field as well. Observations of additional *S. xerampelinus* populations in the field, focusing on a diversity of

environmental conditions, in addition to manipulative semi-natural enclosure experiments, would help define the extent of any intraspecific variability in the social and mating system of this species.

APPENDIX  
ETHOGRAM FOR *Scotinomys xerampelinus*

Note: this is not a full ethogram for the species. This is an ethogram specifically designed for use in the series of resident-intruder experiments used in the accompanying research report. Parts of this ethogram have been adapted from the Adult *Peromyscus* ethogram by John Eisenberg (Eisenberg 1968).

**Affiliative interactions**

- Allo-grooming – Repetitive manipulation of the fur of another animal, including licking, touching and patting with paw, everywhere except in the vicinity of the ano-genital region and stomach. The head is bobbed up and down. The animal receiving the allo-grooming usually remains motionless.
- Nasal-nasal contact – Animal presses its nose to the other animal's nose.
- Ano-genital-nose contact – nose of mouse is in ano-genital area of con-specific.
- Nasal-stomach contact – nose of mouse is on stomach of other animal, which is lying on its back.
- Lie-on-back-contact – animal lies on its back, while other animal makes nasal-stomach and nasal-ano-genital contact.
- Mounting – one individual grips with the forelimbs anterior to the other animal's pelvis, sometimes with thrusting (pelvic movements).
- Huddling – physical contact between two individuals, usually side-to-side, without any of the other defined affiliative behaviors occurring. Animals have eyes open and are not asleep.

**Agonistic interactions**

- Fight – two animals in contact (usually ventral-ventral), rolling around together, with mouths open. Movement is more rapid than during allo-grooming, both animals are moving, and biting is attempted.
- Lunge – one animal moves suddenly towards other animal with open mouth.

- Paw-slap – both animals stand on hind legs facing each other, and extend arms, making swiping movements at each other with paws. Usually some degree of contact between paws occurs.

### **Ambiguous and/or solo (non-interactive) behaviors**

- Eating – kitten chow, seeds, or any other item; frequently held in paws by animal; animal's mouth makes contact with item, and item decreases in size or visibly disappears into animal's mouth.
- Following – one animal follows the other animal closely. This behavior is usually immediately followed by another behavior (i.e. fight, ano-genital-nose contact, out-of-sight, etc).
- Followed – animal is being followed by the other animal, at a distance of 10 cm or less. This behavior is usually quickly followed by another behavior (i.e. fight, ano-genital-nose contact, out-of-sight, etc).
- Jumping – entire body moves up into the air, such that all four legs are in air and maintaining no physical contact with ground.
- Scratching – fast, repetitive movement of paws (either forepaw or hindpaw) on own body; does not involve licking.
- Self-grooming – repetitive manipulation of the fur, including licking and touching with paw.
- Sleeping alone – animal is in horizontal posture with eyes closed, and apparent muscle relaxation; occasionally in curled position.
- Sleeping group – same as “Sleeping alone,” with the addition of physical contact with another animal.
- Solo locomotion – locomotion around cage without following or being followed by another animal.
- Calling – head is tilted back, and animal emits a stereotyped staccato vocalization that lasts for 7-10 seconds, starts at a high pitch, and ends at a lower pitch. This behavior occurs on all four legs, and also on rear legs only, with animal sitting back on its haunches.
- Squeak – sudden, sharp vocalization.
- Chitter – short, soft vocalization.
- Digging – removing substrate with fore legs; animal stays on top of substrate.

- Burrow – burrows beneath litter, with substrate covering up animal.
- Stationary-all-four – animal is on all four legs, is not moving, and is not exhibiting any of the above behaviors.
- Stationary-hind – animal is on two hind legs, is not moving, and is not exhibiting any of the above behaviors.
- Out of sight – hidden under log - specify which log.

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## BIOGRAPHICAL SKETCH

Dimitri Vincent Blondel was born 17 August 1974 to Linda Ruth Wilder and Pierre Claude Robert Blondel in Montreuil, France. He was raised in Charlottesville, Virginia, and graduated from Charlottesville High School in 1992. His undergraduate education was at Duke University, Durham, North Carolina.

While at Duke, Mr. Blondel took a primate field biology course at the Duke Primate Center where he studied the social behavior of free-ranging red-fronted lemurs (*Eulemur fulvus rufus*). It was during this experience that he developed a keen interest in field biology and animal behavior. This interest was further crystallized by a research project on aggressive behavior among herded ostrich (*Struthio camelus*) during a School for Field Studies undergraduate study abroad program at the Center for Wildlife Management Studies, Kenya. Mr. Blondel graduated with distinction with the Bachelor of Arts degree in biology and French in 1996.

After graduation, Mr. Blondel gained further experience in both laboratory and field research while working as a research assistant to Dr. Richard B. Forward, Jr., at the Duke Marine Laboratory in Beaufort, North Carolina. The research involved the physiological ecology of the blue crab (*Callinectes sapidus*). Mr. Blondel subsequently spent four years working on network management software for Lucent Technologies (formerly Ascend Communications) in Bohemia, New York. He was able to continue pursuing his interest in field research during this time by participating in a study on the

ecology and breeding biology of the laughing gull (*Larus atricilla*), under the supervision of Dr. Kevin Brown, in the Jamaica Bay Wildlife Refuge, New York.

Mr. Blondel is a member of the Animal Behavior Society, the International Society for Behavioral Ecology, and the American Society of Mammalogists. He is particularly interested in intraspecific variations in social systems. He plans to continue his behavioral ecology research while pursuing a doctoral degree at the University of Florida.