MIAMI UNIVERSITY - THE GRADUATE SCHOOL

CERTIFICATE FOR APPROVING THE DISSERTATION

We hereby approve the Dissertation

of

Mark D. Spritzer

Candidate for the Degree:

Doctor of Philosophy

____

(Dr. Douglas B. Meikle), Co-Director

____

(Dr. Nancy G. Solomon), Co-Director

____

(Dr. Phillip J. Best), Reader

____

(Dr. Phyllis Callahan), Reader

____

(Dr. Thomas O. Crist), Reader

____

(Dr. Robert L. Schaefer), Graduate School Representative

ABSTRACT

SPATIAL ABILITY, DOMINANCE RANK, AND SEXUAL SELECTION AMONG MEADOW VOLES (*MICROTUS PENNSYLVANICUS*)

by Mark D. Spritzer

Sexual selection occurs through female choice, scramble competition and contest competition for mates. I investigated the relative importance of these mechanisms in determining reproductive success of male meadow voles (*Microtus pennsylvanicus*). Spatial ability and dominance rank were measured as traits believed to be selected by scramble and contest competition, respectively. Spatial ability and dominance rank of males were determined using water maze and neutral-arena trials, respectively. Males that varied in these traits were used for experiments conducted in outdoor enclosures. Home range size was determined using radio telemetry and trapping. Females were housed in nest boxes to determine the ability of males to locate females.

I tested the hypothesis that males with better spatial ability achieve greater reproductive success. Paternity was determined by amplifying polymorphic loci using nine microsatellite primers. Males with better spatial ability had larger home ranges and visited more females, but did not achieve greater reproductive success. This latter result did not seem to be due to a trade-off between mate-searching and mate-guarding abilities. Dominant males had better spatial-learning ability, and had quicker learning speed, but did not have better spatial memory than less aggressive subordinates. Spatial-learning ability was poorest and spatial-learning speed was slowest for males collected during a peak in population density, suggesting that a mate-searching phenotype may be density dependent.

I also tested the relative importance of spatial ability and dominance rank in determining female mating preferences and frequency of visitation to females' nests. Dominance rank was not correlated with nest visitation or home range size. Males better at simple spatial learning visited more females, while males better at a spatial-transfer task ranged widely and visited fewer females. Males with better spatial memory had smaller ranges and revisited the same females. In a laboratory experiment, females preferred males with good spatial ability and low dominance rank over males with poor spatial ability and high dominance rank. Females showed no preference between males with good spatial ability and high dominance rank and males with poor spatial ability and low dominance rank. Both female choice and scramble competition seem to favor males with better spatial ability.

SPATIAL ABILITY, DOMINANCE RANK, AND SEXUAL SELECTION AMONG MEADOW VOLES (*MICROTUS PENNSYLVANICUS*)

A DISSERTATION

Submitted to the Faculty of Miami University

In partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Department of Zoology

By

Mark D. Spritzer

Miami University

Oxford, Ohio

2003

Dissertation Co-directors: Drs. Douglas B. Meikle and Nancy G. Solomon

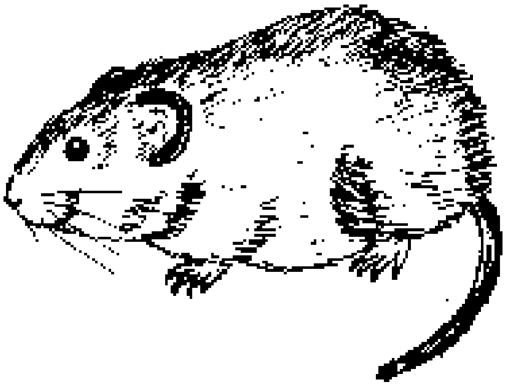
TABLE OF CONTENTS

Chapter 4: Female choice based on male spatial ability and dominance rank among meadow voles

Dedicated to Mom and Dad

for giving me an appreciation for the beauty of the natural world,

and to Natali for always being there for me.



ACKNOWLEDGEMENTS

First and foremost I thank my advisors Doug Meikle and Nancy Solomon for their help along every step of my long journey into the world of vole biology. I also thank my committee for their help and insightful suggestions: Phil Best, Phyllis Callahan, Tom Crist, and Robert Schaeffer. This project would not have been possible without the hard work and dedication of my research assistants: Amber Bennett, Lyndsey Burton, Lisa Dolney, Jared Fischer, Erin Halbert, Jake Hogan, Jenny Jenkins, Crystal Lee, Adam Marchak, Kelly Pogorzelski, Jane Sewell, Heidi Sprang, and Natali West. I also thank the members of the Solomon and Meikle labs for their help and friendship: Amanda Endsminger, Loren Hayes, Paula Hogan, Kirk Lin, Chris Maynard, David Mbora, Jason Mihalcin, Sarah Moore, Lindsey Rowland, Anne Lohrey, Christine Anderson, Megan Thobe, Natali West, and Shawn Wilder. Joe Jacquot gave me instruction in radio telemetry. Ann Rypstra generously allowed me the use of her video equipment. Brian Keane's advice was instrumental in completing the paternity analysis. I also thank Kathy Killian for introducing me to the exciting world of neurobiology. The hard work of the animal care personnel was essential in keeping my voles healthy. The field experiments would not have been possible without the help of Ryan Stander and the ERC workers. The Miami Instrumentation Lab helped with building and designing research equipment. Funding was provided by the American Society of Mammalogists, Animal Behavior Society, Miami University Graduate School, National Science Foundation (DDIG 0206437), and Sigma Xi. I would also like to thank my family and Natali for their love and support.

GENERAL INTRODUCTION

Sexual Selection

Darwin (1871) defined sexual selection as “the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction” (p. 256). Hence, sexual selection acts on heritable physiological, morphological, and behavioral traits that influence an individual’s ability to acquire mates (Andersson 1994; Murphy 1998). Among most species, males compete for females and females are the more choosy sex apparently because males have a lower parental investment than do females (Trivers 1972; Cunningham & Birkhead 1998). Darwin (1871) also noted that “in a multitude of cases the males which conquer other males, do not obtain possession of the females, independently of choice on the part of the latter” (p. 262). Thus, sexual selection occurs through multiple mechanisms that interact in complex ways (Bradbury & Davies 1987; Wiley & Poston 1996). My research focused on three mechanisms of sexual selection: (1) *Contest competition* involves direct intrasexual competition and selects for traits that increase an individual’s ability to deter rivals from gaining access to mates, such as large body size, weaponry, and threat signals; (2) *Scramble competition* involves indirect intrasexual competition and selects for traits that allow individuals to rapidly and accurately locate mates, such as perceptiveness, mobility, and spatial ability; (3) *Mate choice* involves one sex choosing mates based on conspicuous signals, such as coloration, ornaments, song, and olfactory cues. Although sexual selection is one of the most intensively studied areas in the field of behavioral ecology, surprisingly little is known about how different mechanisms of sexual selection contribute to the evolution of traits (Bradbury & Davies 1987; Andersson 1994).

The relationship between contest and scramble competition for mates is poorly understood. In general, scramble competition favors traits associated with mate searching and contest competition favors traits associated with mate guarding. Mate guarding refers to a male associating with a female for a period longer than the time needed to transfer sperm, and it usually involves males following, restraining, or otherwise preventing access to the mated female by other males (Mathews 2002). In contrast, mate searching involves the active pursuit of new females as mates (Schwegmeyer 1994). There are costs and benefits associated with both mate guarding and mate searching (Table 1). The primary benefit of mate guarding is increased probability of a successful mating, whereas the primary benefit of mate searching is increased probability of mating with multiple females. Mate guarding and mate searching are mutually exclusive behaviors, but the relative use of each of these behaviors, by individuals or among individuals within populations, is likely to be optimized by sexual selection (Schwegmeyer & Parker 1987; Yamamura & Tsuji 1989; Parker 2000). Scramble competition and contest competition may either select for similar or different male traits, and the direction of selection by scramble and contest competition may be positively correlated, negatively correlated, or uncorrelated. For example, a male that is good at mate guarding may not necessarily be good at mate searching (Schwagmeyer & Woonter 1986).

The relative importance of male-male competition and female choice acting upon a trait also remains unclear. In their review, Berglund et al. (1996) found that numerous traits serve the dual purpose of enhancing competition and attracting mates. This duality may be because weaponry and inter-male status signals that evolved through contest competition provide females with honest signals of male quality. Thus, male contest competition and female choice may act in a complementary manner upon male traits. In contrast, some studies have shown that male-male competition and female choice will often either select for entirely different suites of traits or cause balancing selection upon the same trait (Moore 1990; Droney 1992; Sorenson & Derrickson 1994; Howard et al. 1997; Cremer & Greenfield 1998; Able 1999; Moore & Moore 1999; Sih et al. 2002). Therefore, female choice may complement or oppose the effects of male-male competition upon a trait.

Meadow Voles

Sexual selection among meadow voles (*Microtus pennsylvanicus*) was the focus of my research. Meadow voles are rodents belonging to the family Muridae and the subfamily Arvicolinae (Anderson 1985). Rodents are the most diverse (2052 species) and geographically widespread group of mammals, and Muridae is the most diverse family of rodents (1336 species; Walker 1999). With 29 subspecies, meadow voles have the largest geographic range of any North American vole, with populations throughout Canada, Alaska, the Midwestern and New England states, and extending as far south as Georgia and New Mexico (Koeppl 1985).

The mating system of meadow voles is generally described as promiscuous since females mate with multiple males, and males mate with multiple females (Getz 1972; Madison 1980; Dewsbury 1981; Boonstra et al. 1993). There is some evidence, however, that late in the breeding season males and females live in pairs with males contributing to the care of offspring (Storey & Snow 1987; Parker et al. 2001; Parker & Lee 2002). Meadow voles exhibit either induced or spontaneous behavioral estrus that corresponds with an increase in estradiol levels (Meek & Lee 1993a, b; Fortier et al. 1996). Meek & Lee (1993b) found that the length of time females were exposed to males prior to entering behavioral estrus was highly variable, taking from 7 min to 4.5 days, and that females housed under long day lengths entered estrus quicker than females housed under short day lengths. This corresponds with field studies that have shown that some females will breed in the winter, but that breeding generally peaks from May to October and females within a population tend to breed asynchronously (Hamilton 1941; Beer & MacLeod 1961; Boonstra & Rodd 1983; Madison et al. 1984; Pugh et al. 1993). Captive studies have shown that females enter post-partum estrus about 50% of the time (Lee et al. 1970; Morrison et al. 1976; Dieterich & Preston 1977)

Ovulation is induced by copulation and occurs 12-18 h after copulation (Lee et al. 1970; Meek & Lee 1994). An increased number of ejaculatory series increase the probability of ovulation and the number of implanted embryos (Gray & Dewsbury 1975; Gray et al. 1977). The average length of gestation is 21 days with a range of 19 to 22 days (Lee & Horvath 1969). Females reduce their range sizes and activity levels at parturition (Madison 1978). Pre-implantation and post-implantation mortality are 0.3 and 0.1 ova per pregnancy, respectively (Tamarin, 1977). Exposure to a novel male results in pre-implantation and post-implantation pregnancy disruption (Storey & Snow 1990; Storey 1994). Mean litter sizes range from 4.0 to 6.2 (Beer & MacLeod 1961; Dieterich & Preston 1977; Tamarin 1977). Pups' eyes open at 8-9 days of age, and weaning occurs

12-14 days after birth (Lee & Horvath 1969). Males reach sexual maturity after 4.5-5.0 weeks, while females reach sexual maturity after 3.5-5 weeks (Sheridan & Tamarin 1987). Males are more likely to disperse than females (Boonstra & Rodd 1983; McShea 1990), and the average dispersal distance of males was about twice as far as that of females (Boonstra et al. 1987). The average reproductive lifespan for males and females under field conditions is about 4 weeks and 9 weeks respectively (Sheridan & Tamarin 1988). Sex ratios in field populations are near 1:1 (Tamarin 1977; Webster & Brooks 1981; Jacquot 1999).

Meadow voles have long been a model system for population ecology (e.g., Krebs et al. 1969) and they have become a model system for understanding the physiological basis of facultative changes in behavior (e.g., Parker & Lee 2001; Galea et al. 2002). I chose to work with meadow voles for multiple reasons: 1) scramble competition, contest competition, and female choice had all been previously suggested to occur among meadow voles, 2) their reproductive biology was well understood, 3) their short life-span and small size made both laboratory and field experiments feasible, and 4) microsatellite primers had been previously developed for related species which facilitated paternity analysis.

Overview of Chapters

Each chapter is written in the format of a manuscript for submission to the journal Animal Behaviour. Chapter 1 describes two field experiments that tested the hypothesis that male superiority at spatial tasks among meadow voles is the result of sexual selection. Specifically, I tested the predictions that: (1) males with better spatial ability have larger home ranges, (2) males with better spatial ability are better at locating females, (3) males with better spatial ability obtain greater reproductive success, and (4) receptive females mate with the first male that they contact. Chapter 2 describes the results of dominance and spatial ability testing conducted on five batches of males collected over a three years. The goal of Chapter 2 was to test the hypothesis that mate guarding and mate searching are alternative reproductive phenotypes of male meadow voles. I tested the predictions that: (1) a trade-off exists between spatial ability and dominance rank of males, and (2) spatial ability and aggression exhibit density-dependent changes. Chapter 3 describes another field experiment designed to determine: (1) the relative importance of spatial ability and dominance rank in determining frequency of visitation to females' nests, and (2) the relative importance of spatial ability and dominance rank in determining home range sizes of males. Finally, Chapter 4 describes a laboratory experiment designed to determine the relative influence of male spatial ability and dominance rank upon female preferences.

Table 1. Proposed reproductive tactics of male meadow voles with their respective benefits. The costs of each reproductive tactic are the converse of benefits for the other tactic.

Mate-guarding tactic	Mate-searching tactic
1. increased likelihood of successful mating (Salo & Dewsbury 1995; Parker et al. 2001)	**1.** increased number of matings (Schwegmeyer & Woontner 1986)
2. increased assurance of paternity (Storey et al. 1995)	**2.** increased phenotypic diversity of offspring (Plante et al. 1991; Penn & Potts 1999)
3. reduced risk of pregnancy disruption (Storey & Snow 1990; Storey 1994, 1996)	**3.** reduced risk of infertile mate
4. reduced risk of infanticide (Thomas 1988; Ebensperger 1998)	
5. reduced risk of predation (Ambrose 1972; Norrdahl & Korpimäki 1998)	
6. reduced risk of disease (Klein & Nelson 1998, 1999)	

Chapter 1

INFLUENCE OF SCRAMBLE COMPETITION FOR MATES UPON THE SPATIAL ABILITY OF MALE MEADOW VOLES

INTRODUCTION

Male competition for mates commonly occurs through direct aggressive interactions (Andersson 1994). In some species, however, indirect (scramble) competition may be as important or more important than direct competition in shaping the evolution of male behavior (Murphy 1998). For example, scramble competition was more important than male aggression in determining reproductive success among male thirteen-lined ground squirrels (Schwagmeyer & Woontner 1986). For most species, however, the importance of scramble competition in determining male reproductive success remains unknown.

Spatial ability is one of the main traits believed to be selected for by scramble competition (Gaulin & Hoffman 1988; Schwagmeyer 1994). Spatial ability is a complex trait that generally refers to the learning and memory of the position and relationship of the observer relative to environmental stimuli (Gaulin & Hoffman 1988; Allen 1999). Good spatial ability has been hypothesized to allow males to: (1) efficiently navigate between females, (2) relocate females as they become sexually receptive, and (3) avoid areas without receptive females (Schwagmeyer 1994). In this study, I tested the hypothesis that improved male spatial ability has been selected by scramble competition for mates among meadow voles (*Microtus pennsylvanicus*).

Meadow vole ranging patterns suggest the potential for scramble competition for mates. Males have larger home ranges than females, and females show intrasexual territoriality while males are non-territorial with home ranges that usually overlap multiple male and female ranges (Madison 1980). Two lines of evidence suggest that sex differences in home range size are the result of males' searching for mates. First, adult male meadow voles expand their home ranges during the breeding season, while females and sexually immature males do not (Webster & Brooks 1981; Boonstra & Rodd 1983; Gaulin & FitzGerald 1989; Jacquot 1999). Second, males exhibit larger home ranges than females in promiscuous vole species, while no sex differences in range size occur in monogamous vole species (Gaulin & FitzGerald 1986, 1988).

Sex differences in range size correspond with sex differences in spatial ability among meadow voles. Reproductively active males outperform females in maze tests, whereas immature voles show no sex difference in spatial ability (Gaulin & FitzGerald 1986, 1989; Galea et al. 1994; Kavaliers et al. 1998). As one would predict if superior male spatial ability were the product of sexual selection, monogamous pine voles (*M. pinetorum*) do not show sex differences in maze performance (Gaulin & FitzGerald 1986). Furthermore, hippocampal volume is sexually dimorphic among meadow voles but not pine voles (Jacobs et al. 1990; Galea et al. 1999), and the hippocampus is the primary brain region responsible for the processing of spatial information (O'Keefe & Nadel 1978; Redish 1999). The prefrontal and parietal cortex have also been implicated in spatial cognition, and among reproductively active meadow voles, males show more dendritic arborization in these brain regions than do females (Kavaliers et al. 1998).

I tested four predictions based on the hypothesis that sex differences in spatial ability are the result of sexual selection: (1) males with better spatial ability have larger home ranges, (2) males with better spatial ability are better at locating females, (3) males with better spatial ability obtain greater reproductive success, and (4) receptive females mate with the first male that they contact. Minimal female choosiness is not critical for the occurrence of scramble competition, but this would give an advantage to males that are better able to locate females (Schwagmeyer 1988; Able 1999).

METHODS

Collection and Housing

I collected adult meadow voles at Miami University's Ecology Research Center (ERC) near Oxford, Ohio. Wild-caught males were used for experimentation to avoid the detrimental effects of lab rearing upon spatial ability (Würbel 2001; Schrijver et al. 2002). I established a breeding colony with other animals collected at the ERC as a source of virgin females for experiments. Pups were weaned at 21 days and housed with same-sex litter mates for an additional 20-30 days. Adult voles (other than breeding pairs) were housed singly in polycarbonate cages (18 × 28 × 12 cm) at Miami University's animal facility. Voles were maintained at 21°C on a cycle of 14 h light:10 h dark (lights on at 0800 hours). Rodent chow (Lab Diet #5013, PMI Nutrition International, Brentwood, MD) and water were provided ad libitum, and sunflower seeds and lettuce were provided as weekly supplements. Cotton Nestlets (Ancare, Bellmore, NY) and dried alfalfa were provided for bedding. Reproductive maturity was determined based on body mass (> 30 g) and conduction of the external genitalia: adult males had descended testes and adult females had perforate vaginas (Boonstra & Rodd 1983).

Water Maze Testing

The spatial ability of all males used in field experiments was tested using the Morris water maze (Stewart & Morris 1993). A circular pool (70 cm diameter and 45 cm height) was filled with water to a depth of 15 cm and divided into four equal quadrants with string raised above the pool. A 7 cm diameter clear plastic platform submerged 1.5 cm below the surface was used as the goal. The water temperature averaged 20.0 °C, and the water was made opaque using non-toxic white paint. I taped three white note cards with black shapes drawn on them at evenly spaced intervals around the edge of the water maze as salient visual cues. Various objects around the room were kept in consistent locations during testing as distal visual cues. The observer stood approximately 1 m away from the site where the vole was released. Because each vole was released at four different locations around the maze, the observer was not a consistent visual cue. All trials were video recorded from above.

I followed a four-phase protocol (preliminary, acquisition, transfer, and retention), and the daily testing sequence of voles was randomized. All inter-trial intervals on the same day were 45 s, during which each vole was dried off and placed in a holding cage. During the preliminary phase, each male was introduced into the maze on three consecutive trials, allowed to swim for 60 s, and then placed on the platform for 15 s. The preliminary phase was conducted during one day in a separate room from all other testing and the note cards were not in place, so that voles were not learning the task during this phase.

During the acquisition phase (conducted 24 h after the preliminary phase), I recorded the time it took each vole to reach the platform (escape latency). For each vole, the platform was assigned to one of the four randomly chosen quadrants. The platform remained in the same quadrant for all trials involving a particular vole. Four possible release sites were designated at equidistant points around the pool. One release site was set aside for use during the transfer phase. This site was counter-balanced such that half the voles had a release site that was closer to the platform than the other half (this was necessary because the platform was offset from the center of the pool). During the acquisition phase, I tested each vole on three consecutive trials per day for 5 blocks (days) of trials, such that each vole was introduced into the maze from the three different release sites in a random order each day. I terminated any trial that lasted 60 s by placing the vole on the platform for 15 s and then removing it from the maze. Similarly, whenever a vole reached the platform, it was allowed to remain there for 15 s before ending the trial.

During the transfer phase (conducted 24 h after the last acquisition trial), I introduced each vole into the maze from the release site not used during the acquisition phase. Three consecutive trials at the same release site were conducted for each vole during this phase. Finally, during the retention phase (conducted 24 h after the transfer phase), the platform was removed from the maze and voles were released into the maze for 60 s from one of the three release sites used during their acquisition trials. I recorded the time spent swimming in the quadrant where the platform had been. Path lengths from the release site to the platform were determined from the video recordings for block 5 of the acquisition trials and for the transfer trials. I traced each path onto acetate and then used a digital map-reader to determine path length.

My protocol resulted in three measures of spatial ability: (1) *acquisition path length* (average path length for block 5 of the acquisition trials), (2) *transfer path length* (average path length for the transfer trials), and (3) *retention time* (time spent in the target quadrant during the retention trials). Acquisition path length, and transfer path length provided different measures of spatial-learning ability, whereas retention time provided a measure of spatial memory. Path length has been commonly used in past studies to assess spatial-learning ability, and retention time is a common measure of spatial memory (D’Hooge & De Deyn 2001). I used both acquisition and transfer path lengths to measure spatial-learning ability because the transfer test required more complex navigational ability than did the acquisition test. Namely, performance during the acquisition trials required only learning a simple “praxic” response to locate the platform, whereas good performance during the transfer trials required more complex “route” or “locale” navigation (Redish 1999). To categorize voles based on spatial ability, I used a composite index: spatial ability score = (acquisition rank + transfer rank + retention rank) / 3.

I also measured the amount to time voles spent in the outer 50% of the water maze (within 10 cm of edge) to determine the percentage of time each male spent thigmotactic during blocks 1 and 5 of the acquisition trials. Past studies have suggested that high levels of thigmotaxis are indicative of high anxiety and/or low behavioral flexibility (Pleskacheva et al. 2000; Vyssotski et al. 2002).

Field Experiments

Experiment 1

This experiment tested the prediction that males with better spatial ability have larger home ranges. It was conducted at the ERC in four 40 × 40 m enclosures (Appendix 1) and lasted from August to October 2000. The size of the enclosures was chosen such that each enclosure was approximately as large as eight female home ranges (Ostfeld et al. 1988; Jacquot 1999). Each enclosure was bordered by a plastic drift fence (50 cm high) and a 10 m zone of mowed grass to prevent dispersal (Jacquot 1999). Prior to the experiment, I removed all small mammals from enclosures. Eight males were assigned systematically to each of four groups such that the variance in spatial ability scores was maximized within each group. Each group of males was released into an enclosure five days after releasing eight adult wild-caught females into each enclosure. Females were included to ensure natural ranging patterns by males. All animals were given numbered ear-tags (#1005, National Band and Tag Co., Newport, KY**)** for identification.

One week after releasing voles, I began trapping within each enclosure using a 7 × 7 grid of Sherman live traps spaced at 5 m intervals. Trapping was conducted for two consecutive nights per week to collect males for radio collaring (3.0 g, model SM-1, AVM Instruments). I weighed the voles prior to collaring to make certain that the collar was less than 10% of each male's body mass (Hamley & Falls 1975; Berteux et al. 1994). For each male, I used radio telemetry to collect 40 readings at 30 min intervals over five evenings (1700-2000 hours). I had intended to collect home range data for all 32 males, but each enclosure exhibited a rapid population decline, similar to that observed in other studies (e.g., Boonstra & Rodd 1983; Ims 1987). The total population had declined to 34% of the original density after two weeks and 14% of original after four weeks. Data were, therefore, collected for 10 males (2, 2, 1, and 5 from the four respective enclosures). The program Ranges V was used to calculate a 95% convex polygon (range area excluding outlying 5% of fixes) and maximum range length for each male (Kenward & Hodder 1996). I pooled the data from the four enclosures due to low sample size, but this seemed justified considering that there were no significant differences between the males from the enclosure where five males were tracked and the males from the other three enclosures in their 95% convex polygons (Mann-Whitney U test: U=20.0, N_1=N_2=5, P=0.12) or maximum range length (Mann-Whitney U test: U=13.0, N_1=N_2=5, P=0.92).

Experiment 2

This experiment tested whether males with good spatial ability locate more females and achieve greater reproductive success than males with poor spatial ability. This experiment also tested the prediction that females mate with the first male that they encounter. I used 80 wild-caught adult male meadow voles for this experiment and I housed and tested them for spatial ability as in Experiment 1. All animals used for the field experiment were toe-clipped (1-2 toes) for identification, and the toes were stored in SET buffer (1% SDS; 5 mM EDTA, pH 8.0; 10 mM Tris/HCl, pH 8.0) for subsequent DNA extraction.

The field experiment was conducted from July to October 2001 in four enclosures (described above). Prior to release, the males were ranked for their spatial ability using the composite index of spatial ability. The 24 highest ranking males (“good” spatial ability) and 24 lowest ranking males ("poor" spatial ability) were used for the experiment. I released six males with good spatial ability and six males with poor spatial ability into each enclosure. Following a four-day acclimation period and prior to introducing females into enclosures, I trapped for six days to obtain home range data. Trapping was continued within enclosures two nights per week throughout the experiment to update male home ranges and monitor male survivorship.

Eight lab-reared (F1 or F2), virgin females were used for each enclosure. These females were not closely related to each other or the males. Each female was housed in a nest box (40 × 40 × 10 cm), which controlled the distribution of females and allowed me to accurately determine male visitation to females' nests. Each wooden box had wire mesh walls and a one-way door that allowed males to enter and mate but prevented voles from leaving. Eight nest boxes with females were evenly distributed within each enclosure. Each box was supplied ad libitum with water and the same rodent chow that voles received in the lab as well as alfalfa for bedding. The sex ratio within each enclosure was initially male-biased (3 males: 2 females) to ensure that enough males would survive for data collection following any initial die-off.

To remove the potential confound caused by males entering boxes to obtain food rather than mates, the enclosures were planted with clover and seven feeding stations were evenly distributed between the nest boxes and replenished with rodent chow regularly. I also trained males to enter nest boxes in the laboratory prior to releasing them into enclosures, to minimize individual differences in the propensity to enter nest boxes. All males used in the field experiment had entered a nest box containing a female twice during one-hour training trials.

Each nest box was checked twice daily, approximately one hour after dawn and one hour before dusk, for the presence of males. Each male found in a nest box was identified and released at a random grid point within his home range (based on trapping data). Male visitation to nests was quantified using three measures: (1) total number of nest-box visits, (2) number of different nest boxes visited, and (3) number of visits to each male's most frequently visited nest box. The experiment ended eight weeks after the very first male entered a nest box.

The females were checked once per week by palpation for pregnancy, and pregnant females were brought back to the animal housing facility to rear pups. I replaced pregnant females 1-2 days prior to parturition with another lab-reared virgin female to avoid infanticide by males (Storey et al. 1994). In two cases, females gave birth before they were removed from their nest boxes. Fortunately, visiting males did not kill the pups, and both females gave birth to a second litter before the experiment ended. Except where indicated, all analyses of male reproductive success included all four litters from these two females.

Paternity Analysis

I determined the paternity of pups born during Experiment 2. Tail tips (0.5 cm) and toe-clippings were collected from all adults prior to release into field enclosures, and tail tips were collected from all pups at weaning. Tissue was placed in SET buffer (1% SDS; 5 mM EDTA, pH 8.0; 10 mM Tris/HCl, pH 8.0) and digested at room temperature with proteinase K (0.55 mg/ml final concentration). I extracted the samples twice with phenol followed by two extractions with a 24:1 chloroform/isoamyl alcohol solution (Sambrook et al. 1989).

I screened 35 microsatellite primers developed for other vole species (Ishibashi et al. 1997; Stewart et al. 1998; Ishibashi et al. 1999; Van de Zande et al. 2000). I optimized the PCR conditions for 28 of these primers that successfully amplified meadow vole DNA. Nine of these amplified only a fraction of the population suggesting the presence of null alleles (AV1, AV4, AV12, Moe1, Moe3, Moe5, Moe7, MSMM1, MSMM5), seven were monomorphic (AV3, AV7, AV9, AV10, AV11, MSCRB6, MSMM7), and nine were used for paternity analysis (Table 1).

Each 25 μl reaction mixture consisted of 50-100 ng of template DNA, 2.5 μl 10× buffer (Promega, Madison, WI), dNTP (0.20 mM each), 0.40 μM primers, and 0.50 U *Taq* DNA polymerase (Promega). The concentration of $MgCl_2$ used varied among primers (Table 1). PCR was conducted using the following profile: 94°C (5 min), 35 cycles [94°C (1 min), X°C (1 min), 72°C (1 min)], 72°C (5 min), where the annealing temperature (X) varied depending on the primer used (Table 1). PCR products with a molecular ladder (ϕX174 DNA/*Hin*f I marker; Promega) were electrophoresed on 8% acrylamide gels for 2.5-4.0 h at 80 volts using a Hoefer SE 250 mini-vertical gel electrophoresis unit (Amersham Biosciences, Piscataway, NJ). I stained the gels for 15 min in ethidium bromide and viewed them under UV light. The size of each band was determined to within 5 bp using an image analysis program (EagleSight ver. 3.2; Strategene, La Jolla, CA). The program CERVUS 2.0 was used to calculate observed heterozygosity, expected heterozygosity, null allele frequencies, and to test for Hardy-Weinberg equilibrium using the adult experimental voles (Brookfield 1996; Marshall et al. 1998). Not all adult females were tested with every primer, resulting in some variation in sample size (Table 1).

Meadow voles have a 21-day gestation length (Lee & Horvath 1969). However, to account for any variation in gestation length, I considered all males visiting a female's nest box 19-23 days prior to parturition as potential sires. Paternity for each pup was assigned by excluding all potential sires except one. If a potential sire did not possess a non-maternal allele possessed by a pup, then he was excluded as the sire (Appendix 2). Although I considered one primer sufficient to exclude a potential father, for 53.4% of all pups exclusion was based on two or more primers. As shown in Table 1, three alleles exhibited significant deviation from Hardy-Weinberg equilibrium and two of these also had relatively high null allele frequencies (AV14, Moe2). Therefore, the presence of null alleles was assumed when excluding potential sires with these two loci (Webster et al. 2001).

Statistical Analysis

For all analyses involving escape latencies and path lengths, the values from the three trials conducted with each vole were averaged. To determine if the voles exhibited learning during the acquisition phase, changes in escape latency (time to reach the platform) over the five blocks of acquisition trials and the transfer trials were analyzed with repeated measures ANOVA (Neter et al. 1996). For this analysis, experiment (1 or 2) was used as a between-subjects effect to determine if there were differences between the voles used in the two experiments. Similarly, I compared the percentage of time spent thigmotactic during blocks 1 and 5 of the acquisition trials with repeated measures

ANOVA. Post-hoc comparisons were made using *t* tests with Bonferroni adjusted *P* values. For these analyses the total number of males was 120 (40 from Experiment 1 and 80 from Experiment 2).

For Experiment 1, I compared spatial ability scores and percentage of time thigmotactic with the two measures of range size (95% convex polygon and maximum range length) using Spearman rank correlations. I used non-parametric tests for these analyses because the data did not meet the assumptions of parametric regression (Neter et al. 1996)

I considered only males that visited at least one nest box for analyses of the relationship between nest box visitation and male reproductive success because males not visiting any nest boxes could not sire litters. ANCOVA was initially used to analyze the relationship between nest visitation and number of pups or litters sired, but the enclosure effect was dropped from the model if it was not significant.

Mixed-model ANOVA's were initially used to analyze relationships between: (1) spatial ability and nest visitation, and (2) spatial ability and male reproductive success. The full model for these analyses included enclosure as a random effect, spatial ability as a fixed effect, and an interaction effect. The model was reduced to a *t* test when both the enclosure and interaction effects were not significant.

The relationship between number of different nest boxes visited and number of visits to each male's most frequently visited nest box was analyzed to determine if there was a trade-off between these two measures of nest visitation. I used both a linear and quadratic regression to analyze this relationship, but report only the latter because it provided a better fit.

Considering only males used in the field for Experiment 2, repeated measures ANOVA was used to compare thigmotaxis during blocks 1 and 5 (within-subjects effect) for good and poor spatial ability voles (between-subjects effect). For comparisons of thigmotaxis to nest visitation or reproductive success, enclosure was initially included as a random factor, but this factor was dropped from the analyses if it was not significant.

The visitation data for Experiment 2 were also analyzed to test female choosiness. Two adjustments to the dataset were made for these analyses: (1) only the first litter was used for the two females that gave birth to two litters, and (2) the male siring the majority of the litter was considered the sire for the two cases of multiple paternity. I assumed that the fertilization occurred on the date nearest to 21 days prior to parturition on which the sire visited the dam. I used a one-sample *t* test to determine if the number of different males visiting a female prior to fertilization was significantly greater than one, which is the expected value if each female was mating with the first male that visited her. For females that were visited by multiple males prior to fertilization ($N = 30$), I tested the hypothesis that the first male visiting a female was the most likely to be the sire. This was done by comparing the observed frequency of sires that visited dams in different order to the expected distribution based on the assumption that females mated at random with respect to order of male visitation. For example, females visited by two males prior to fertilization and not having an order preference were expected to mate 50% of the time with the first visitor and 50% of the time with the second visitor. Expected frequencies were calculated in a similar manner for females that were visited by 3-6 males (6 was the maximum number of males that visited a female prior to fertilization). For females that were visited by multiple males prior to fertilization, I also used a paired *t* test to test the hypothesis that the sire visited the dam more frequently than the average number of visits made by all other males visiting the dam prior to fertilization.

All statistical tests were conducted using SPSS 11.0, except repeated measures ANOVA's which were run in SAS (PROC MIXED). One-tailed *P* values were used to test *a priori* predictions that males with better spatial ability visited more nest boxes overall, visited more different nest boxes, and achieved higher reproductive success than males with poor spatial ability (Gaulin & FitzGerald 1986). A significance level of $\alpha=0.05$ was used for all tests, and all data are presented as $\overline{X}\pm$SE.

Ethical Note

Spatial ability was measured using the Morris water maze, which involved exposing voles to an aversive stimulus, cold water. I attempted to minimize the amount of stress that voles experienced by limiting trials to a maximum of 60 s and drying voles after each trial. The water maze has been previously used extensively with meadow voles (e.g., Galea et al. 1995; Kavaliers et al. 1998), and meadow voles are also excellent swimmers (Dagg & Windsor 1972).

For Experiment 2, two toes were clipped from each male and one or two toes were clipped from each female for identification. I used ear-tags to mark voles for Experiment 1 but found that voles often ripped out their tags in the field. Toe-clipping is commonly used for field studies involving voles (e.g., Jacquot 1999; Cochran & Solomon 2000; McGuire et al. 2002), and studies have shown that toe-clipping has no effect upon the survivorship and body weight of small mammals (Ambrose 1972; Korn 1987; Wood & Slade 1990; Braude & Ciszek 1998). In particular, clipping two toes, as in my study, was found to have no impact upon the survivorship of male meadow voles (Pavone & Boonstra 1985). In my study, survivorship was higher for voles used in Experiment 2 than for those used in Experiment 1, suggesting that toe-clipping did not have detrimental effects relative to ear-tagging. Meadow voles also seldom burrow, building their nests out of surface vegetation (Weilert & Shump 1977, personal observations).

RESULTS

Considering escape latencies during the acquisition and transfer trials, there was not a significant experiment × block interaction (Fig. 1a; $F_{5,585}$=1.92, P=0.090). Voles in both experiments exhibited differences in escape latency between blocks (block effect: $F_{5,585}$=103.83, P <0.0005), but escape latencies were not significantly different between Experiments 1 and 2 ($F_{1,117}$=0.089, P=0.77). Post hoc comparisons revealed that earlier blocks had significantly longer escape latencies than later blocks (all $P < 0.02$) except blocks 3 versus 4 (P=0.091) and block 5 versus the transfer trials (P >0.999). For percentage of time spent thigmotactic, the experiment × block interaction was not significant ($F_{1,117}$=1.93, P=0.17), and the overall percentage of time thigmotactic was not different between experiments ($F_{1,117}$=3.20, P=0.76). Males in both experiments exhibited a significant reduction in the percentage of time thigmotactic between blocks 1 and 5 of the acquisition trials (Fig. 1b; $F_{1,117}$=219.7, P<0.0005). Hence, the males used for the two experiments exhibited similar learning ability making the results of the two experiments comparable.

Experiment 1

Voles with better spatial ability had larger home ranges as measured by 95% convex polygons (Fig. 2; Spearman rank correlation: r_S=0.73, N=10, P=0.017). Maximum range length was not significantly correlated with spatial ability, although the relationship was positive (Spearman rank correlation: r_S=0.47, N=10, P=0.17). Percentage of time thigmotactic during the final block of the acquisition trials was not correlated with either 95% polygon size (Spearman rank correlation: r_S=-0.46, N=10, P=0.19) or maximum range length (Spearman rank correlation: r_S=-0.13, N=10, P=0.73).

Experiment 2

The first male entered a nest box 12 days after the females were introduced into the enclosures. During the 3584 box checks, 1497 instances of male visitation to nest boxes occurred. Of the males that entered nest boxes (N=33), the average latency to enter a nest box after the first male entered a nest box was 10.3±9.1 days. Therefore, 10 days was used as the minimum amount of time that males had to be present within the enclosures (captured in nest boxes or grid traps) to be considered for further data analyses. This resulted in the exclusion of 6 males. Fortunately, the experiment remained fairly balanced without these males (22 good spatial ability males, 20 poor spatial ability males). Four males (2 good spatial ability, 2 poor spatial ability) disappeared after the 10-day cutoff, and were therefore included in data analyses.

Spatial ability and nest visitation

A larger percentage of males with good spatial ability (95%) than males with poor spatial ability (59%) entered at least one nest box (χ^2_1=7.44, P<0.01). Males with good spatial ability were not, however, more likely than males with poor spatial ability to be the first male to visit a nest box: 53.1% of nest boxes were visited first by males with good spatial ability (Binomial test: P= 0.86). Males with good spatial ability visited more different nest boxes than males with poor spatial ability, suggesting that males with better spatial ability were better at locating multiple females (Fig. 3a; t_{40}=1.80, one-tailed P=0.039). Males with good spatial ability also had a greater total number of nest-box visits than males with poor spatial ability, although the relationship was only marginally significant (t_{40}=1.64, one-tailed P=0.054).

Males with good spatial ability had more visits to their most frequently visited nest boxes, suggesting that they were better able to relocate nests (Fig. 3b; Spatial ability: $F_{1,3}$=18.87, P=0.017; Enclosure: $F_{3,3}$=9.73, P=0.047; Spatial ability × Enclosure: $F_{3,34}$=0.11, P=0.95). However, males with good spatial ability were not more likely than males with poor spatial ability to be the most frequent visitor to a nest box: only 50.0% of nest boxes were visited most frequently by males with good spatial ability. Number of visits to the most frequently visited nest box and number of different nest boxes visited showed a curvilinear relationship (Fig. 4; Quadratic regression: r^2=0.41, $F_{2,39}$=13.30, P<0.00005). The left side of this curve includes males that made few nest box visits, the right side of this curve includes males that visited many different nest boxes but visited individual nest boxes relatively infrequently, and males at the peak of the curve maximized the number of visits per female.

Nest visitation and reproductive success

The 55 litters born during the experiment were fairly evenly distributed among the four enclosures (*N*s=10, 14, 15, 16). Average litter size was 4.9±0.20 pups. For 16 litters, the dam had escaped from her nest box during the fertilization period (19-23 days before parturition). These litters were excluded from analysis because females had increased opportunity to choose mates while outside of the nest boxes. One additional litter was not used for analyses because both of the potential sires were excluded using microsatellites, suggesting that either the female escaped from the nest box and returned before I noticed her absence or an unidentified male entered the nest box to mate and escaped prior to identification. For 12 litters, paternity was determined based on male visitation alone, and for 26 more litters paternity was assigned using microsatellites. These 38 litters (185 pups) were used for analyses of male reproductive success. Two (5.3%) of these litters exhibited multiple paternity, with two different males siring part of each litter.

Nest box visitation was a good predictor of male reproductive success. Considering only males that made at least one visit to a nest box, males that made more nest box visits sired more litters (Fig. 5a; r^2=0.36, $F_{1,30}$=16.95, P<0.0005) and more pups (r^2=0.35; $F_{1,30}$=16.06; P<0.0005). Males that visited more different nest boxes also sired more pups (ANCOVA, Different nest boxes visited: β=0.67; $F_{1,27}$=9.67, P=0.004; Enclosure: $F_{3.27}$=3.17, P=004) but not more litters (Fig. 5b; r^2=0.06, $F_{1,30}$=1.89, P=0.18).

Spatial ability and reproductive success

The overall percentages of good and poor spatial ability males that sired at least one litter (55.0% and 45.5%, respectively) were not significantly different (χ^2_1=0.091, NS). Although males with good spatial ability sired more litters than males with poor spatial ability (good: 1.00±0.29, poor: 0.82±0.26), the relationship was not statistically significant (t_{40}=0.47, one-tailed P=0.32). Similarly, males with good spatial ability sired more pups than males with poor spatial ability (good: 4.85±1.41, poor: 4.00±1.37), but the difference was not statistically significant (t_{40}=0.43, one-tailed P=0.34). Some males sired multiple litters in the same nest box, but there was no significant difference in the number of different nest boxes where males with good or poor spatial ability sired litters (t_{40}=0.68, one-tailed P=0.25). However, a male with good spatial ability was the only male to sire litters in four different nest boxes, the maximum for any male.

Thigmotaxis

Considering only the voles used for Experiment 2, males with good spatial ability were less thigmotactic than males with poor spatial ability ($F_{1,40}$=21.51, P <0.0001), and males were less thigmotactic during block 5 than block 1 of the acquisition trials (Repeated measures ANOVA: $F_{1,40}$=81.06, P<0.0001). There was also a nearly significant block × spatial ability interaction ($F_{1,40}$=3.89, P=0.056), which suggests that during the acquisition phase males with good spatial ability reduced their level of thigmotaxis to a greater degree than did males with poor spatial ability males. Post-hoc tests revealed that males with poor spatial ability showed more thigmotaxis than males with good spatial ability during both block 1 (t_{40}=2.96, adjusted P=0.042) and block 5 (t_{40}=4.99, adjusted P<0.0001).

Males that were less thigmotactic during the final block of acquisition trials made more visits to their most frequently visited nest boxes (Fig. 6; r^2=0.14, $F_{1,40}$=6.64, P=0.014). Males that were less thigmotactic also tended to have a greater total number of nest-box visits, but the relationship was only marginally significant (r^2=0.090, $F_{1,40}$=3.95, P=0.054). I found no relationship between percentage of time thigmotactic and number of different nest boxes visited (r^2=0.023, $F_{1,40}$=0.93, P=0.34). There was also no relationship between thigmotaxis and number of litters sired (r^2=0.029, $F_{2,39}$=1.19, P=0.28) or number of pups sired (r^2=0.020, $F_{1,37}$=0.83, P=0.37).

Female choosiness

Females were visited multiple times prior to fertilization (13.4±1.7 visits, N=36). Females were also visited by more than one male prior to fertilization (2.5±0.2 males; one-sample *t* test: t_{35}=7.19, P<0.0005). The first male to visit a female fertilized only 50% (N=18) of all litters. For females that were visited by multiple males prior to fertilization, the percentage of litters sired by males that visited in different order was not significantly different from a distribution based on random female choice (Fig. 7; χ^2_3=6.53, 0.05<P<0.1). For females visited by multiple males prior to fertilization, the sire visited the female significantly more often than other male visitors (sire: 7.6±1.7 visits; other males: 3.7±0.4; Paired *t* test: t_{29}=2.22, P=0.034).

DISCUSSION

My results provide some support for the hypothesis that male superiority at spatial tasks is the result of scramble competition for mates. I found that males with better spatial ability had larger home ranges (95% convex polygons). I also found that males with better spatial ability visited more different nest boxes and made more visits to their most frequently visited nest boxes. My paternity results did not support the prediction that males with better spatial ability would obtain greater reproductive success. My data also did not support the prediction that females would mate with the first male that they encountered. Females were more likely to mate with males that visited them more frequently.

Spatial Ability and Range Size

I found a positive correlation between spatial ability and home range size among male meadow voles, which supports the hypothesis that spatial ability is a sexually selected trait (Gaulin & FitzGerald 1986). In a previous study at my study site, Jacquot (1999) found that male meadow voles had larger home ranges than females during the breeding season and that each female's range was overlapped by multiple males. Madison (1980) showed that males are attracted to the home ranges of females when they enter post-partum estrus. Male meadow voles also have larger ranges than females, whereas monogamous pine voles (*M. pinetorum*) have no sex differences in range size (Gaulin & FitzGerald 1986). These observations suggest that better spatial ability allows males in promiscuous species to navigate better through large areas in search of mates (Gaulin & Fitzgerald 1986).

Spatial Ability and Nest Visitation

The primary benefit of better spatial ability among male meadow voles appears to be the ability to relocate females' nests. Males with better spatial ability visited their most frequently visited nest box more often than did males with poor spatial ability. Males that are better able to relocate a female may be better able to prevent other males from mating with her and better able to induce estrus (Storey et al. 1995; Meek & Lee 1993a, b). Males with better spatial ability also visited more different nest boxes suggesting that another benefit of good spatial ability may be that it helps males to locate more different females. If a male is able to sire litters with multiple females, he would not only gain an increase in the number of pups sired, but also any other benefits of multiple mating. One potential benefit would be producing offspring with more variable genotypes, which would potentially increase the probability of some offspring surviving in spatially and/or temporally variable environments (Petrie & Kempenaers 1998; Jennions & Petrie 2000; Stockley 2003).

There appears to have been an opportunity cost for males that visited multiple females because they did not visit any one female frequently. This trade-off could potentially lead to the evolution of alternative male reproductive tactics, specifically a mate-guarding tactic and a mate-searching tactic (Brockmann 2001; Sinervo 2001). Assuming that frequency of visitation to the most frequently visited nest box is indicative of mate guarding, males with poor spatial ability did not show a higher level of mate guarding than males with good spatial ability. Therefore, mate guarding behavior does not seem to be associated with poor spatial ability. I was somewhat surprised to find that some of the males with good spatial ability persistently visited the same nest box, suggesting that they were guarding their mates. Factors other than a male's spatial ability, such as female receptivity and the relative dominance rank of neighboring males, are likely to influence the amount of time that a male devotes to each female. Besides opportunity costs, other costs which could influence the number of nests a male visits include increased risk of predation (Ambrose 1972; Norrdahl & Korpimäki 1998), increased risk of conflicts with other males, and increased exposure to sexually transmitted diseases (Kokko et al. 2002).

A larger proportion of good than poor spatial ability males entered nest boxes. The results of Experiment 1 suggest that some males with poor spatial ability have relatively small home ranges. The smallest home range measured was 72 m^2, and each enclosure was 1600 m^2. Therefore, some males with poor spatial ability in Experiment 2 may have never encountered a nest box. Males with poor spatial ability may have also been slow to relocate nest boxes and were therefore more likely to encounter nest boxes already occupied by other males. Males with good spatial ability may have inhibited males with poor spatial ability from interacting with females. This idea is supported by the fact that relatively few observations of male visitation involved multiple males in the same nest box (only 9.8% of observations). Thus, males with poor spatial ability may have avoided costly agonistic encounters by not entering nest boxes (Turner & Iverson 1973; Rose 1979). Previous evidence suggests that male meadow voles establish stable dominance hierarchies and that subordinates actively avoid interacting with dominant individuals (Caplis 1978; Boonstra & Rodd 1983). Males may have also used scent marks on the runways near nest boxes to inhibit other males from entering (Johnston et al. 1997a, b; Luque-Larena et al. 2001).

Spatial Ability and Reproductive Success

Males with a greater total number of nest box visits achieved greater reproductive success as measured by the number of litters and pups sired. However, males that visited more different nest boxes did not sire more litters. These results suggest that males gained reproductive benefits by visiting particular females multiple times. There may be an optimal level of visitation per nest that allows males to maximize their reproductive success. Multiple visits to the same female may facilitate mate guarding, induction of estrus, and maintenance of pregnancy (Mallory & Clulow 1977; Taylor et al. 1992; Meek & Lee 1993; Storey 1994, 1996). In a laboratory experiment, males engaging in post-copulatory mate guarding achieved greater reproductive success than males that did not guard their mates (Storey et al. 1995).

It was surprising to find that males with better spatial ability did not sire more offspring because males that visited more nest boxes sired more offspring and males with better spatial ability visited more nest boxes. Males with poor spatial ability were clearly at a reproductive disadvantage in that a relatively large proportion of them did not visit any nest boxes. However, some males with poor spatial ability sired multiple litters. In particular, two males with poor spatial ability sired four litters each, the maximum number of litters sired by any male and 44.4% of all litters sired by males with poor spatial ability.

Female meadow voles often require induction of behavioral estrus through prolonged exposure to a male (Meek & Lee 1993a, b). Even after a female has entered estrus, some females require repeated bouts of copulation to induce ovulation and insure successful implantation (Lee et al. 1970; Gary et al. 1977; Meek & Lee 1993a). Although I attempted to minimize the influence of female choice in my study by housing females in nest boxes, females may have still successfully avoided mating with undesirable males. Meek & Lee (1993b) demonstrated that the addition of a small container into cages was sufficient to increase mating latency. I commonly observed females hiding behind food dishes and water bottles, which may have been attempts to avoid unwanted matings. Females may also obtain benefits by mating with multiple males. Berteaux et al. (1999) demonstrated that female meadow voles preferentially mate with multiple males rather than one, and Boonstra et al. (1993) documented multiple paternity under field conditions. Many hypotheses have been proposed for why females mate with multiple males (Ebensperger 1998; Petrie & Kempenaers 1998; Jennions & Petrie 2000; Stockley 2003). Regardless of the function, multiple mating by females could reduce the benefits of good spatial ability among males.

Although females seemed to mate at random with respect to the order of male visitation, males that visited particular females more frequently gained a reproductive advantage. This may have occurred because frequent visits to a female increased the probability of encountering a female after estrus had been induced. Females may have also preferred to mate with males that they were more familiar with, as demonstrated by captive studies (Salo & Dewsbury 1995; Parker et al. 2001). Males with good spatial ability were not more likely than males with poor spatial ability to be the most frequent visitor to a particular nest box. Therefore, female preference for familiar males may have also reduced the benefits of good spatial ability among males.

Removing males from nest boxes twice per day could also explain why males with poor spatial ability achieved some matings. Meek & Lee (1993b) found that females housed under long day length, as in my study, required an average of 13.4 hr of exposure to males before mating occurred. Because I removed males from nest boxes every 12 hours, at least two visits to the same nest box were probably necessary to induce estrus for some females. Males with good spatial ability visited more different nest boxes than did males with poor spatial ability, and therefore they may have been more likely to visit a different nest box after inducing estrus in a particular female. Some males with poor spatial ability may have opportunistically mated with females that had been induced into behavioral estrus by males with good spatial ability. Furthermore, housing males in nest boxes for as much as 12 hr could have prevented males with good spatial ability from visiting as many females as they might have if they had not been restrained. Hence, restraining males in nest boxes may have created a disadvantage for males with good spatial ability by preventing them from optimizing the amount of time spent with each female.

In spite of the possible problems with using the nest boxes, they allowed me to collect extensive data on nest visitation that would have been difficult to obtain by any other means. Another method used to determine rates of nest visitation among voles involves setting traps around natural female nests (Solomon & Jacquot 2002). The main disadvantages of this method are that males can avoid the traps to get in and out of female nests, and males captured in traps may have just been passing by a female's nest rather than visiting it. My nest boxes also mimicked more natural field conditions in which females establish evenly distributed territories and male home ranges overlap the ranges of multiple females (Madison 1980; Ostfeld et al. 1988; Jacquot 1999). Female nest boxes were visited by an average of 2.5 males prior to fertilization, which is similar to the number of males that overlap female home ranges under more natural conditions (Madison 1980; Jacquot 1999).

In addition to sexual selection, numerous alternative hypotheses have been proposed to explain sex differences in spatial ability (Sherry & Hampson 1997). Two are relevant to meadow voles: (1) the "dispersal hypothesis", and (2) the "fertility and parental care hypothesis". The dispersal hypothesis suggests that in species with sex-biased dispersal, selection will favor better spatial ability in the sex that disperses further. In support of this hypothesis, some studies have documented male-biased dispersal among meadow voles (Boonstra & Rodd 1983; McShea 1990). The fertility and parental care hypothesis suggests that female reproductive success is enhanced by reduced mobility and spatial ability during the breeding season. This hypothesis is supported by studies showing that spatial ability of female meadow voles deceases during the breeding season due to increased estradiol levels (Galea et al. 1995, 1999; Galea & McEwen 1999; Ormerod & Galea 2001). Also in support of this hypothesis, female reproductive success and home range size are negatively correlated (Ostfeld et al. 1988; Sheridan & Tamarin 1988). Females do not show a decrease in range size during the breeding season (Webster & Brooks 1981; Gualin & FitzGerald 1989), but they do exhibit a more subtle decrease in activity near parturition (Madison 1978). However, neither of these alternative hypotheses explains the increase in males' home ranges during the breeding season (Webster & Brooks 1981; Gaulin & FitzGerald 1989; Jacquot 1999). It is likely that a combination of selective pressures, including sexual selection, have shaped sex differences in spatial ability among meadow voles. The relative importance of these selective pressures remains to be tested.

In summary, my experiments provided some support for the hypothesis that scramble competition for mates selects for males with better spatial ability. As predicted, males with good spatial ability had larger home ranges and visited more nest boxes than males with poor spatial ability. Males that successfully sired offspring visited their mate more often than did other males. In contrast, males that visited more different females did not achieve greater reproductive success. Therefore, the primary reproductive advantage of good spatial ability appears to be the ability to relocate a particular female rather than locating multiple females. However, males with better spatial ability did not achieve greater reproductive success. This result may be due, in part, to experimental artifacts created by the nest boxes. Female preferences for mating with multiple males may have also reduced the reproductive success of males with good spatial ability.

REFERENCES

Able, D. J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioural Ecology and Socioibiology*, **46,** 423-428.

Allen, G. L. 1999. Spatial abilities, cognitive maps, and wayfinding. In: *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes* (Ed. by R. G. Golledge), pp. 46-80. Baltimore, Maryland: The Johns Hopkins University Press.

Ambrose, H. W., III. 1972. Effect of habitat familiarity and toe-clipping on owl predation on *Microtus pennsylvanicus*. *Journal of Mammalogy*, **53,** 909-912.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Berteaux, D., Duhamel, R. & Bergeron, J.-M. 1994. Can radio collars affect dominance relationships in Microtus? *Canadian Journal of Zoology*, **72,** 785-789.

Berteaux, D., Dety, J. & Rengifo, J. B. 1999. Multiple paternity in meadow voles (*Microtus pennsylvanicus*): investigating the role of the female. *Behavioral Ecology and Sociobiology*, **45,** 283-291.

Boonstra, R. & Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology*, **52,** 757-780.

Boonstra, R., Xia, X. & Pavone, L. 1993. Mating system of the meadow vole, *Microtus pennsylvanicus*. *Behavioral Eco*logy, **4,** 83-89.

Braude, S. & Ciszek, D. 1998. Survival of naked mole-rats marked by implantable transponders and toe-clipping. *Journal of Mammalogy*, **79,** 360-363.

Brockmann, H. J. 2001. The evolution of alternative strategies and tactics. *Advances in the Study of Behavior*, **30,** 1-51.

Brookfield, J. F. Y. 1996. A simple new method for estimating null allele frequency from heterozygote deficiency. *Molecular Ecology*, **5,** 453-455.

Caplis, P. Neighbor recognition by the meadow vole (*Microtus pennsylvanicus*) and the role of olfactory cues. Master's thesis, McGill University.

Champagne, D., Dupuy, J.-B., Rochford, J. & Poirier, J. 2002. Apolipoprotein E knockout mice display procedural deficits in the Morris water maze: Analysis of learning strategies in three versions of the task. *Neuroscience*, **114,** 641-654.

Cochran, G. R. & Solomon, N. G. 2000. Effects of food supplementation on the social organization of prairie voles (*Microtus ochrogaster*). *Journal of Mammalogy,* **81,** 746-757.

Conrad, C. D., Galea, L. A., Kuroda, Y. & McEwen, B. S. 1996. Chronic stress impairs rat spatial memory on the Y maze, and the effect is blocked by tianeptine pretreatment. *Behavioral Neuroscience*, **110,** 1321-1334.

Dagg, A. I. & Windsor, D. E. 1972. Swimming in northern terrestrial mammals. *Canadian Journal of Zoology*, **50,** 117-130.

D'Hooge, R. & De Deyn, P. P. 2001. Applications of the Morris water maze in the study of learning and memory. *Brain Research Reviews*, **36,** 60-90.

Ebensperger, L. A. 1998. Do female rodents use promiscuity to prevent male infanticide? *Ethology Ecology and Evolution*, **10,** 129-141.

Galea, L. A. M. & McEwen, B. S. 1999. Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience*, **89,** 955-964.

Galea, L. A. M., Ossenkopp, K.-P. & Kavaliers, M. 1994. Developmental changes in spatial learning in the Morris water-maze in young meadow voles, *Microtus pennsylvanicus*. *Behavioral Brain Research*, **60,** 43-50.

Galea, L. A. M., Kavaliers, M., Ossenkopp, K.-P. & Hampson, E. 1995. Gonadal hormone levels and spatial learning performance in the Morris water maze in male and female meadow voles, *Microtus pennsylvanicus*. *Hormones and Behavior*, **29,** 106-125.

Galea, L. A. M., Perrot-Sinal, T. S., Kavaliers, M. & Ossenkopp, K.-P. 1999. Relations of hippocampal volume and dentate gyrus width to gonadal hormone levels in male and female meadow voles. *Brain Research*, **821,** 383-391.

Gaulin, S. J. C. & FitzGerald, R. W. 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist*, **127,** 74-88.

Gaulin, S. J. C. & FitzGerald, R. W. 1988. Home-range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy*, **69,** 311-319.

Gaulin, S. J. C. & FitzGerald, R. W. 1989. Sexual selection for spatial-learning ability. *Animal Behaviour*, **37,** 322-331.

Gaulin, S. J. C. & Hoffman, H. A. 1988. Evolution and development of sex differences in spatial ability. In: *Human Reproductive Behaviour: A Darwinian Perspective* (Ed. by L. Betzig, M. B. Mulder, & P. Turke), pp. 7-152. New York: Cambridge University Press.

Gray, G. D., Kenney, A. M. & D. A. Dewsbury. 1977. Adaptive significance of the copulatory behavior pattern of male meadow voles (*Microtus pennsylvanicus*) in relation to induction of ovulation and implantation in females. *Journal of Comparative Physiological Psychology*, **91,** 1308-1319.

Hamley, J. M. & Falls, J. B. 1975. Reduced activity in transmitter-carrying voles. *Canadian Journal of Zoology*, **53,** 1476-1478.

Ims, R. A. 1987. Determinants of competitive success in *Clethrionomys rufocanus*. *Ecology*, **68,** 1812-1818.

Ishibashi, Y., Yoshinaga, Y., Saitoh, T., Abe, S., Iida, H. & Yoshida, M. C. 1999. Polymorphic microsatellite DNA markers in the field vole *Microtus montebelli*. *Molecular Ecology*, **8,** 163-164.

Ishibashi, Y., Saitoh, T., Abe, S. & Yoshid, M. C. 1997. Cross-species amplification of microsatellite DNA in Old World microtine rodents with PCR primers for the gray-sided vole, *Clethrionomys rufocanus*. *Mammal Study,* **22**, 5-10.

Jacobs, L. F., Gaulin, S. J., Sherry, D. F. & Hoffman, G. E. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Science, USA*, **87,** 6349-6352.

Jacquot, J. J. 1999. Use of space and movement of two vole species in response to habitat quality. Ph.D. thesis, Miami University.

Jarrard, L. E. 1993. On the role of the hippocampus in learning and memory in the rat. *Behavioral and Neural Biology,* **60,** 9-26.

Jennions, M. D. & Petrie, M. 2000. Why do females mate multiply? A review of the genetic benefits. *Biological Reviews,* **75,** 21-64.

Johnston, R. E., Sorokin, E. S. & Ferkin, M. H. 1997a. Female voles discriminate males' over-marks and prefer top-scent marls. *Animal Behaviour*, **54,** 679-690.

Johnston, R. E., Sorokin, E. S. & Ferkin, M. H. 1997b. Scent counter-marking by male meadow voles: females prefer the top-scent male. *Ethology,* **103,** 443-453.

Korn, H. 1987. Effects of live-trapping and toe-clipping on body weight of European and African rodent species. *Oecologia*, **71,** 597-600.

Kavaliers, M., Ossenkopp, K.-P., Galea, L. A. M. & Kolb, B. 1998. Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Research,* **810,** 41-47.

Kenward, R. E., & Hodder, K. H. 1996. *Ranges V: An Analysis System for Biological Location Data*. Dorset, United Kingdom: Institute of Terrestrial Ecology.

Kokko, H., Ranta, E., Ruxton, G. & Lundberg, P. 2002. Sexually transmitted disease and the evolution of mating systems. *Evolution*, **56,** 1091-1100.

Lee, C. & Horvath, D. J. 1969. Management of the meadow vole (*Microtus pennsylvanicus*). *Laboratory Animal Care,* **19,** 88-91.

Lee, C., Horvath, D. J., Metcalfe, R. W. & Inskeep, E. K. 1970. Ovulation in *Microtus pennsylvanicus* in a laboratory environment. *Laboratory Animal Care,* **20,** 1098-1102.

Lipp, H.-P. & Wolfer, D. P. 1998. Genetically modified mice and cognition. *Current Opinions in Neurobiology,* **8,** 272-280.

Luque-Larena, J. J., López, P., Gosálbez, J. 2001. Scent matching modulates space use and agonistic behaviour between male snow voles, *Chionomys nivalis*. *Animal Behaviour*, **62,** 1089-1095.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology and Sociobiology*, **7,** 65-71.

Madison, D. M. 1978. Movement indicators of reproductive events among female meadow voles as revealed by radiotelemetry. *Journal of Mammalogy*, **59,** 835-843.

Mallory, F. F. & Clulow, F. V. 1977. Evidence of pregnancy failure in the wild meadow vole, *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **55,** 1-17.

Marshall, T. C., Slate, J., Kruuk, L. E. B. & Pemberton, J. M. 1998. Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology*, **7,** 639-655.

McGuire, B., Getz, L. L. & Oli, M. K. 2002. Fitness consequences of sociality in prairie voles, Microtus ochrogaster: influence of group size and composition. *Animal Behaviour*, **64,** 645-654.

McShea, W. J. 1990. Social tolerance and proximate mechanisms of dispersal among winter groups of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, **39,** 346-351.

Meek, L. R. & Lee, T. M. 1993a. Female meadow voles have a preferred mating pattern predicted by photoperiod, which influences fertility. *Physiology and Behavior*, **54,** 1201-1210.

Meek. L. R. & Lee, T. M. 1993b. Prediction of fertility by mating latency and photoperiod in nulliparous and primiparous meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility*, **97,** 353-357.

Morris, R. 1984. Development of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods*, **11,** 47-60.

Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution*, **52,** 8-18.

Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996. *Applied Linear Statistical Models*. 4th edn. Boston: WCB/McGraw-Hill.

Norrdahl, K. & Korpimaki E. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, **79,** 226-232.

O'Keefe, J. & Nadel, L. 1978. *The Hippocampus as a Cognitive Map.* Oxford: Oxford University Press.

Ormerod, B. K. & Galea, L. A. M. 2001. Reproductive status influences cell proliferation and cell survival in the dentate gyrus of adult female meadow voles: possible regulatory role for estradiol. *Neuroscience*, **102,** 369-379.

Ostfeld, R. S. & Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76,** 521-532.

Ostfeld, R. S., Pugh, S. R., Seamon, J. O. & Tamarin, R. H. 1988. Space use and reproductive success in a population of meadow voles. *Journal of Animal Ecology*, **57**, 385-394.

Pavone, L. V. & Boonstra, R. 1985. The effects of toe clipping on the survival of the meadow vole (*Microtus pennsylvanicus*). *Canadian Journal of Zoology*, **63,** 499-501.

Parker, K. J., Phillips, K. M & Lee, T. M. 2001. Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour,* **61,** 1217-1226.

Petrie, M. & Kempenaers, B. 1998. Extra-pair paternity in birds: explaining variation between species and populations. *Trends in Ecology and Evolution*, **13,** 52-58.

Pleskacheva, M. G., Wolfer, D. P, Kupriyanova, I. F., Nikolenko, D. L., Scheffrahn, H., Dell'Omo, G., Lipp, H.-P. 2000. Hippocampal mossy fibers and swimming navigation learning in two vole species occupying different habitats. *Hippocampus*, **10,** 17-30.

Redish, A. D. 1999. *Beyond the Cognitive Map: From Place Cells to Episodic Memory.* Massachusetts: The MIT Press.

Rose R. K. 1979. Levels of wounding in the meadow vole *Microtus pennsylvanicus. Journal of Mammalogy*, **60,**37-45.

Salo, A. L. & Dewsbury, D. A. 1995. Three experiments on mate choice in meadow voles (*Microtus pennsylvanicus*). *Journal of Comparative Psychology*, **109,** 42-46.

Sambrook, J., Fritsch, E. F. & Maniatis, T. 1989. *Molecular Cloning: A Laboratory Manual*, 2nd edn. New York: Cold Spring Harbor Laboratory Press.

Schwagmeyer, P. L. 1988. Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *American Naturalist*, **131,** 885-892.

Schwagmeyer, P. L. 1994. Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology*, **98,** 265-276.

Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioral Ecology Sociobiology*, **19,** 359-364.

Schrijver, N. C. A., Baher, N. I., Weiss, I. C. & H. Würbel. 2002. Dissociable effects of isolation rearing and environmental enrichment on exploration, spatial learning and HPA activity in adult rats. *Pharmacology, Biochemistry and Behavior,* **73,** 209-224.

Sheridan, M. & Tamarin, R. H. 1988. Space use, longevity, and reproductive success in meadow voles. *Behavioral Ecology and Sociobiology,* **22,** 85-90.

Sherry, D. F. & E. Hampson. 1997. Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends in Cognitive Science*, **1,** 50-56.

Sinervo, B. 2001. Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica,* **112-113,** 417-434.

Solomon, N. G. & Jacquot, J. J. 2002. Characteristics of resident and wandering prairie voles, Microtus ochrogaster. *Canadian Journal of Zoology*, **80,** 951-955.

Stewart, C. A. & Morris, R. G. M. 1993. The watermaze. In: *Behavioral Neuroscience: A Practical Approach.* (Ed. by Sahgal, A.), pp. 107-122. New York: Oxford University Press.

Stewart, W. A., Piertney, S. B. & Dallas, J. F. 1998. Isolation and characterization of highly polymorphic microsatellites in the water vole, *Arvicola terrestris*. *Molecular Ecology*, **7,** 1258-1259.

Stockley, P. 2003. Female multiple mating behaviour, early reproduction failure and litter size variation in mammals. *Proceedings of the Royal Society of London Series B*, **270,** 271-278.

Storey, A. E. 1994. Pre-implantation pregnancy disruption in female meadow voles *Microtus pennsylvanicus* (Rodentia: Muridae): male competition or female mate choice? *Ethology*, **98,** 89-100.

Storey, A. E. 1996. Behavioral interactions increase pregnancy blocking by unfamiliar male meadow voles. *Physiology & Behavior*, **60,** 1093-1098.

Storey, A. E., Bradbury, C. G. & Joyce, T. L. 1994. Nest attendance in male meadow voles: the role of the female in regulating male interactions with pups. *Animal Behaviour*, **47,** 1037-1046.

Storey, A. E., French, R. J. & Payne, R. 1995. Sperm competition and mate guarding in meadow voles (*Microtus pennsylvanicus*). *Ethology*, **101,** 265-279.

Taylor, S. A., Salo, A. L. & Dewsbury, D. A. 1992. Estrus induction in four species of voles (Microtus*). Journal of Comparative Psychology,* **106,** 366-373.

Turner, B. N. & Iverson, S. L. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. *Ecology,* **54,** 967-981.

Van de Zande, L., Van Apeldoorn, R. C., Blijdenstein, A. F., De Jong, D., Van Delden, W. & Bijlsma, R. 2000. Microsatellite analysis of population structure and genetic differentiation within and between populations of the root vole, *Microtus oeconomus* in the Netherlands. *Molecular Ecology,* **9,** 1652-1656.

Vyssotski, A. L, Dell'Omo, G., Poletaeva, I. I., Vyssotski, D. L, Minichiello, L., Klein, R., Wolfer, D. P. & Lipp, H.-P. 2002. Long-term monitoring of hippocampus-dependent behavior in naturalistic settings: mutant mice lacking neuortrophin receptor TrkB in the forebrain show spatial learning but impaired behavioral flexibility. *Hippocampus,* **12,** 27-38.

Webster, A. B. & Brooks, R. J. 1981b. Daily movements and short activity periods of free-ranging meadow voles *Microtus pennsylvanicus*. *Oikos*, **37,** 80-87.

Webster, M. S., Chuang-Dobbs, H. C. & Holmes, R. T. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. *Behavioral Ecology,* **12,** 439-446.

Weilert, N. G. & Shump, K. A. 1977. Physical parameters of *Microtus* nest construction. *Transactions of the Kansas Academy of Science*, **79,** 161-164.

Wood, M. D. & Slade, N. A. 1990. Comparison of ear-tagging and toe-clipping in prairie voles, *Microtus ochrogaster*. *Journal of Mammalogy*, **71,** 252-255.

Würbel, H. 2001. Ideal homes? Housing effects on rodent brain and behaviour. *Trends in Neuroscience,* **24,** 207-211.

Table 1. Characteristics of microsatellite primers used for paternity analysis including observed heterozygosity (H_O), expected heterozygosity (H_E) and null allele frequency (*r*).

Locus	No. alleles	*N*	Allele range (bp)	T_a (℃)	$MgCl_2$ (mM)	H_O	H_E	*P**	*r*	Reference
AV13	8	72	153-201	53	2.0	0.61	0.78	NS	0.12	Stewart et al. 1998
AV14	11	72	165-218	55	2.0	0.65	0.87	< 0.01	0.14	Stewart et al. 1998
AV15	10	65	182-253	55	2.0	0.82	0.88	NS	0.04	Stewart et al. 1998
Moe2	7	72	158-195	62	1.5	0.58	0.82	< 0.001	0.17	Van de Zande et al. 2000
Moe4	2	74	123-142	59	1.5	0.28	0.33	NS	0.08	Van de Zande et al. 2000
MSCRB5	5	69	129-163	58	1.5	0.65	0.75	NS	0.06	Ishibashi et al. 1997
MSMM2	11	70	170-254	57	1.5	0.79	0.87	< 0.01	0.05	Ishibashi et al. 1999
MSMM3	7	73	102-146	55	1.5	0.69	0.85	NS	0.10	Ishibashi et al. 1999
MSMM6	2	73	156-183	65	2.0	0.32	0.35	NS	0.05	Ishibashi et al. 1999

* Significance of deviation from Hardy-Weinberg equilibrium based on Chi-square goodness-of-fit test

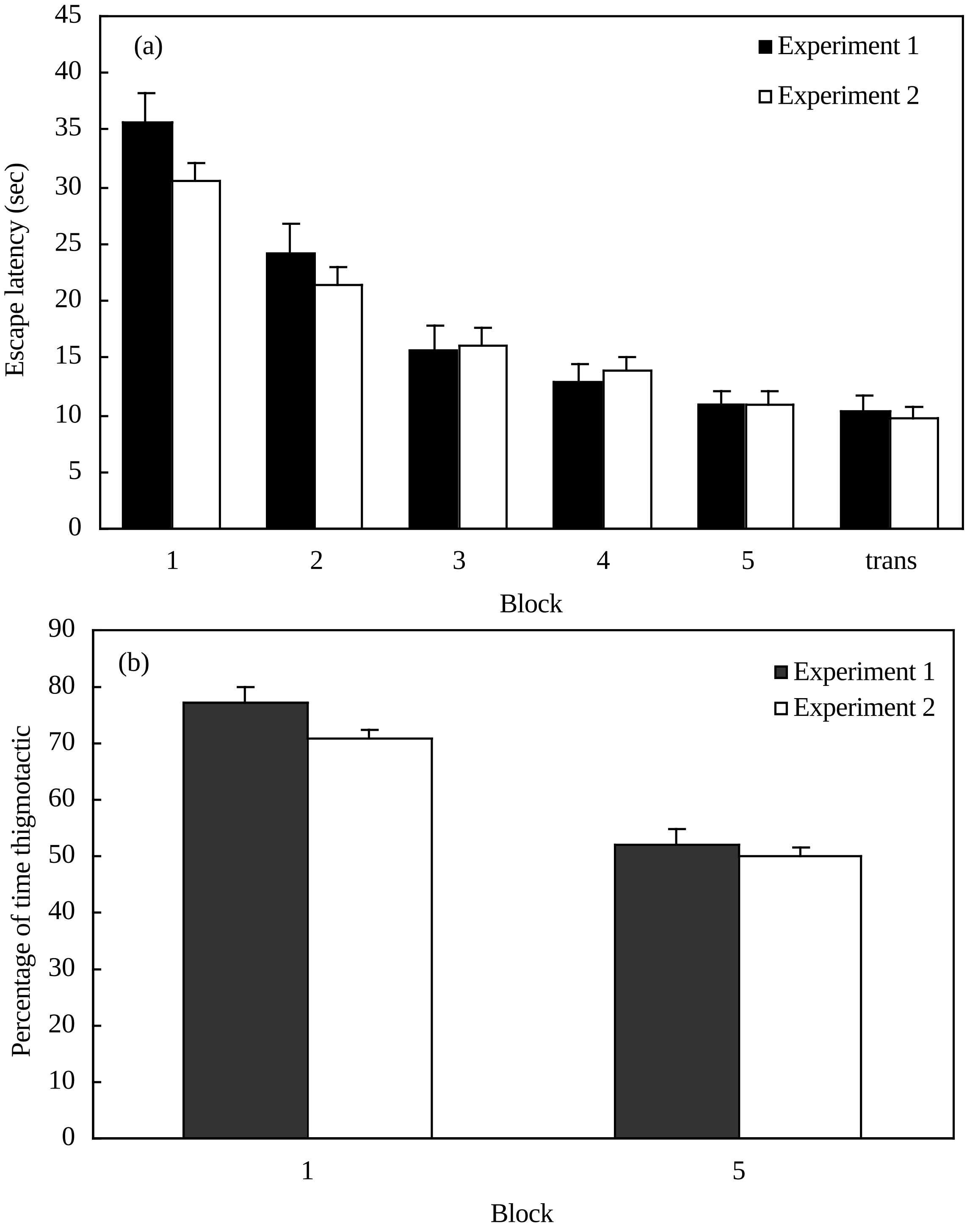


Figure 1. (a) Escape latencies to reach the platform over five blocks of water maze acquisition trials and the transfer trials for males used during Experiments 1 and 2. (b) Percentage of time spent in thigmotaxis (swimming in outer 50% of water maze) during blocks 1 and 5 of the acquisition trials during Experiments 1 and 2. All values are shown as $\overline{X}$ ±SE.

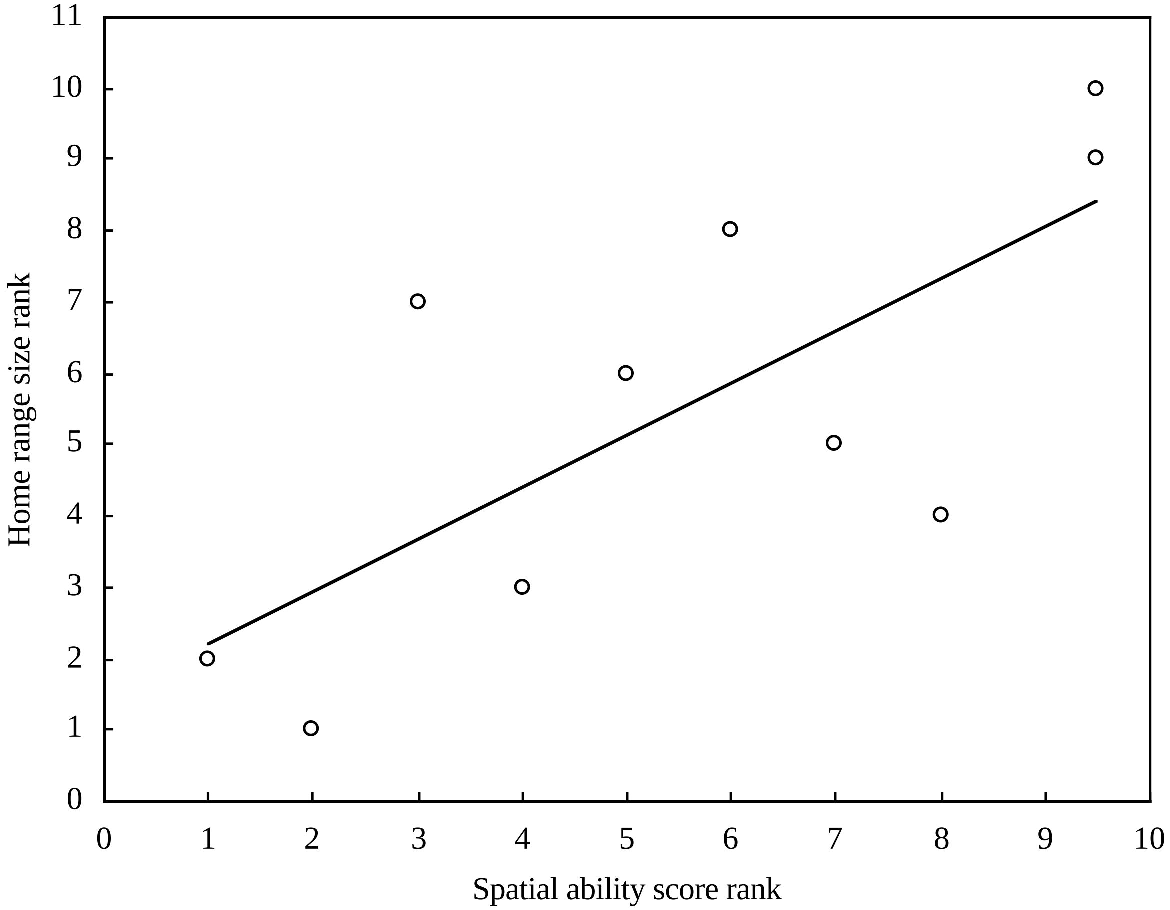


Figure 2. Relationship between home range sizes (95% convex polygons) and spatial ability scores of males. Values were ranked for Spearman correlation (see text).

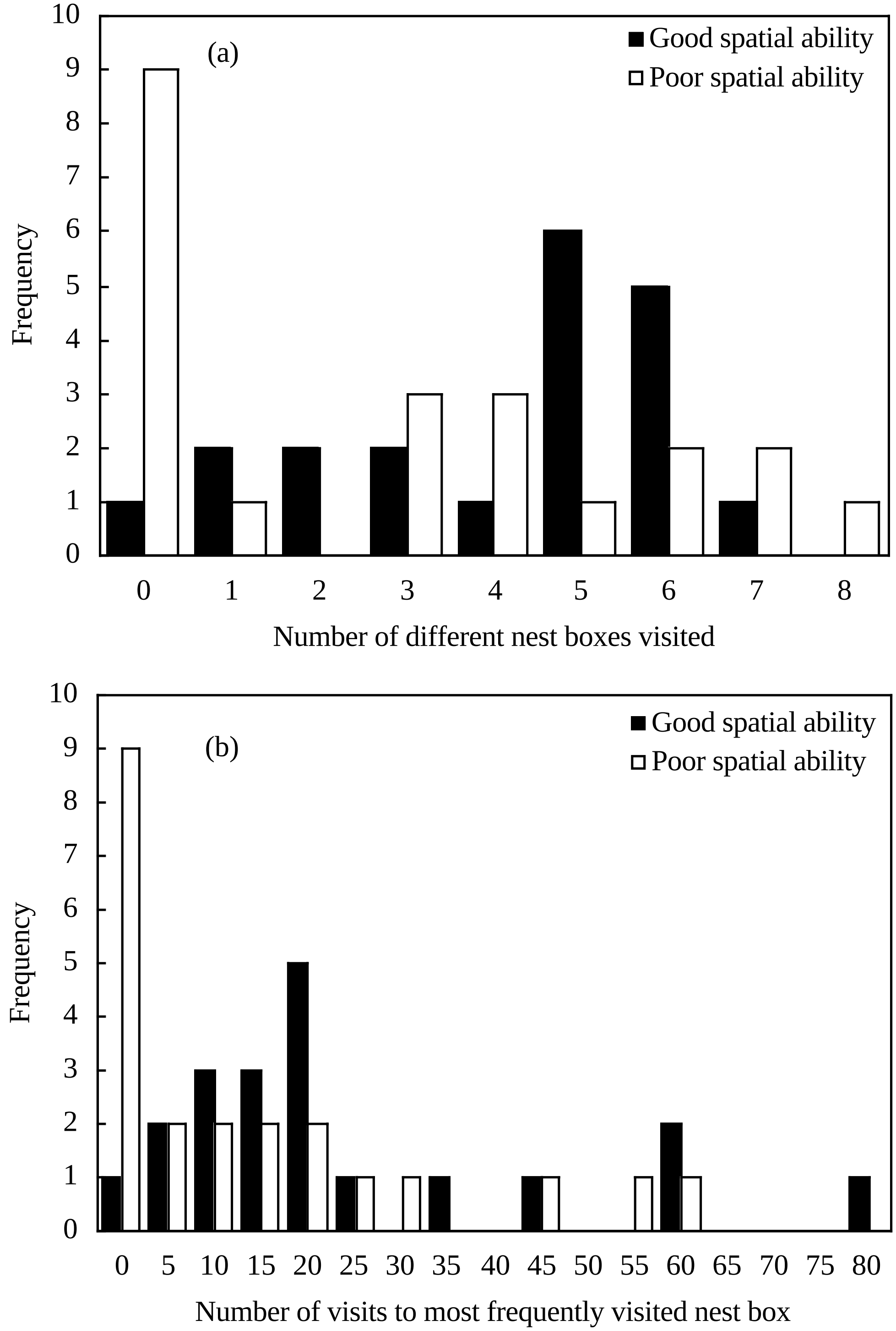


Figure 3. Frequency histograms for (a) number of different nest boxes visited and (b) number of visits to the most frequently visited nest box by males with good and poor spatial ability.

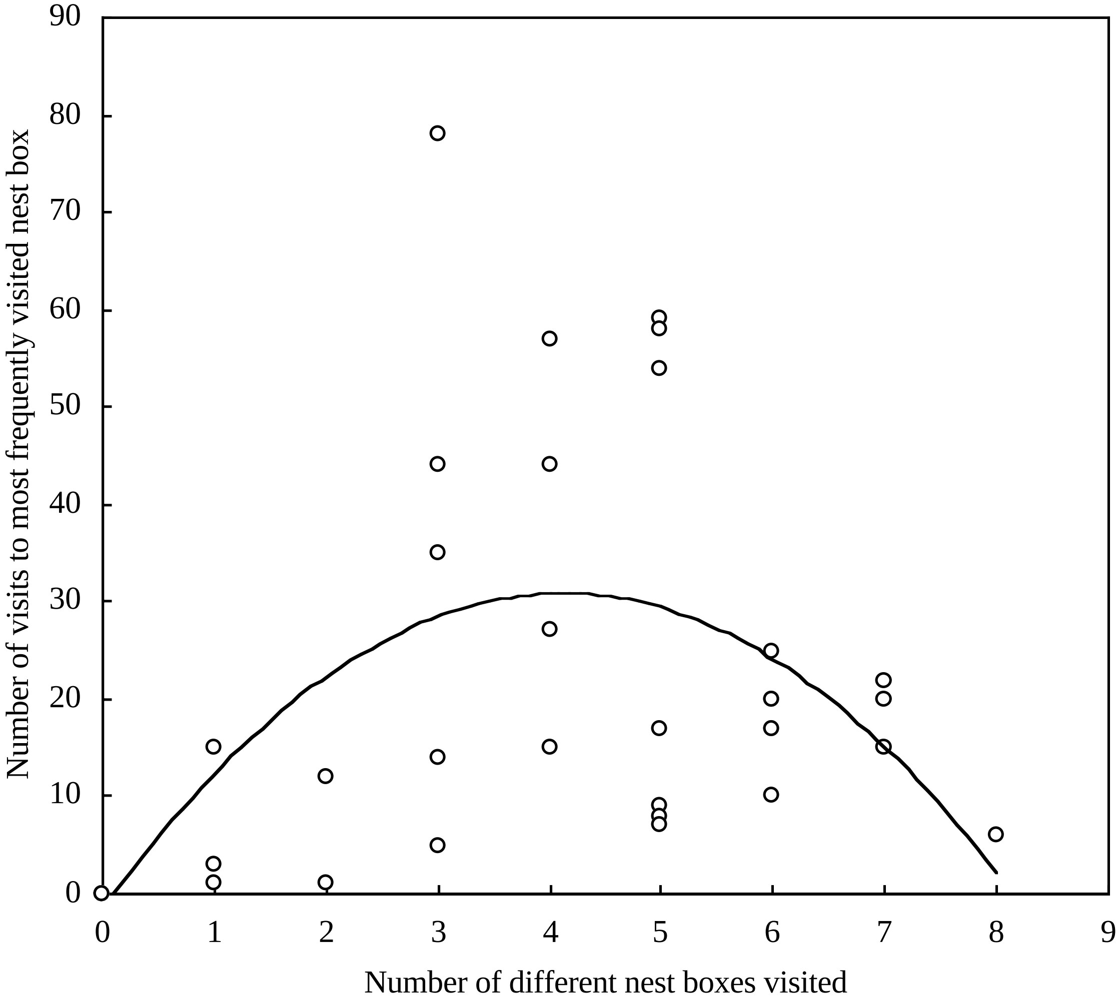


Figure 4. Quadratic regression of the maximum number of visits to a nest box on the number of different nest boxes visited by males.

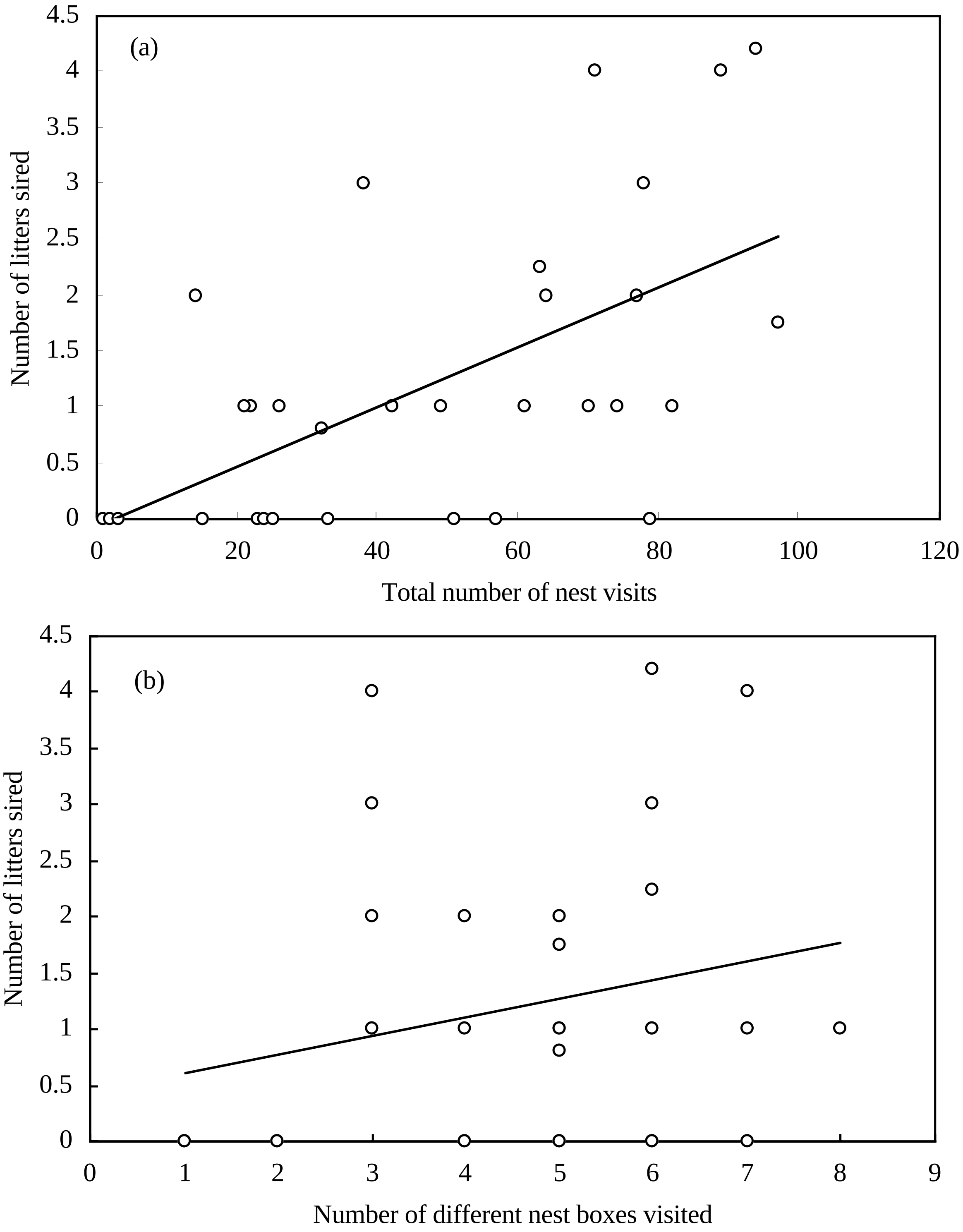


Figure 5. Linear regressions of the number of litters sired against (a) total number of nest visits and (b) number of different nests visited by males that visited at least one nest box.

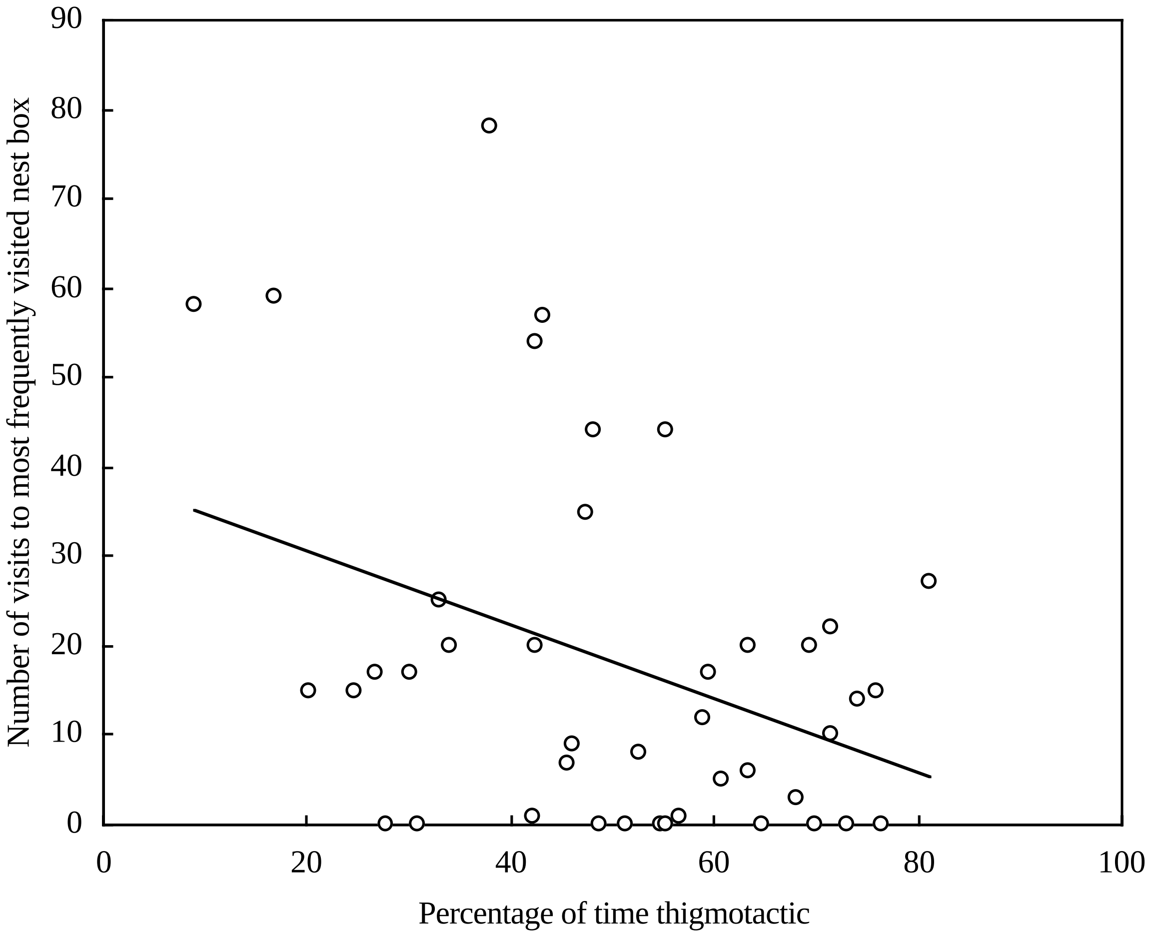


Figure 6. Linear regression of number of visits to each male's most frequently visited nest box against percentage of time spent thigmotactic (swimming in outer 50% of water maze) during the final block of acquisition trials.

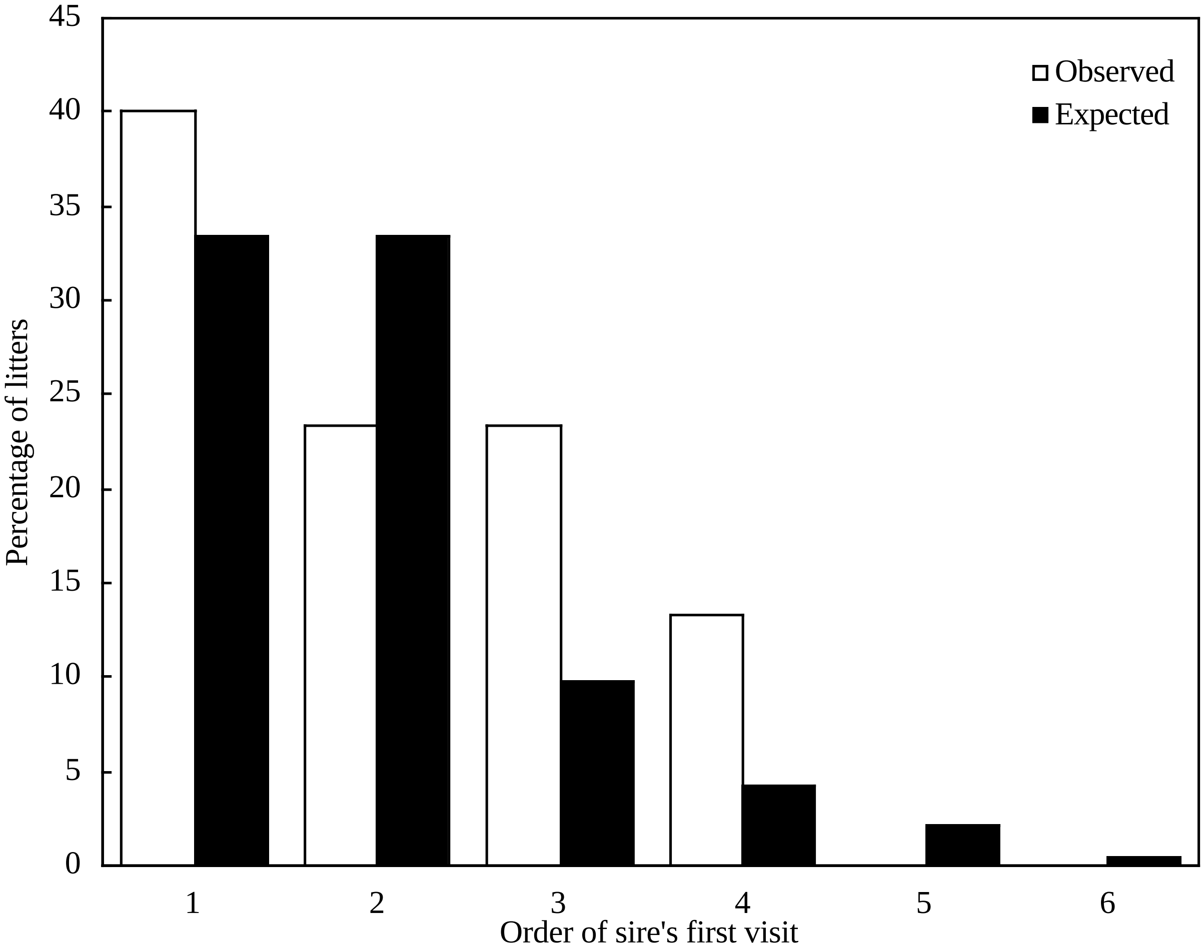


Figure 7. Observed and expected percentages of litters sired by males that visited female in different order prior to fertilization. Expected values are based on the assumption that females mated at random with respect to the order of male visitation to nest boxes.

Chapter 2

THE RELATIONSHIP BETWEEN DOMINANCE RANK AND SPATIAL ABILITY AMONG MALE MEADOW VOLES: EVIDENCE FOR ALTERNATIVE REPRODUCTIVE PHENOTYPES?

INTRODUCTION

Alternative male reproductive phenotypes (strategies or tactics) are a common feature in a wide range of animal taxa (Arak 1984; Dominey 1984; Gross 1996; Brockmann 2001; Sinervo 2001a). Negative frequency-dependent selection is believed to be the primary mechanism maintaining alternative strategies in populations (Brockmann 2001; Sinervo 2001a). Within a population, the strategies that individuals exhibit might be obligatory for their entire adult lifetime, and such strategies could be maintained in a population if they have equal reproductive payoffs under equilibrium conditions (Arak 1984; Brockmann 2001). In contrast, alternative reproductive tactics may have unequal reproductive payoffs (Arak 1984; Brockmann 2001), with individuals switching from one tactic to the other depending upon their internal condition (i.e., age or health). In this case, selection will result in an evolutionarily stable switch point that dictates the conditions under which an individual should switch tactics (Gross 1996; Brockmann 2001).

I previously found that male meadow voles with good spatial ability did not have higher reproductive success than males with poor spatial ability even though they were visiting more different females' nests (Chapter 1). This suggested that males with good spatial ability engaged in a mate-searching strategy while other males may have engaged in a mate-guarding strategy and that the reproductive success of males engaged in these two strategies was similar. Mate guarding refers to a male associating with a female for a period longer than the time needed to transfer sperm, and it usually involves males following, restraining, or otherwise preventing access to the mated female by other males (Mathews 2002). In contrast, mate searching involves the active pursuit of new females as mates (Schwegmeyer 1994). In numerous rodent species, males employ a combination of mate-guarding and mate-searching tactics (Barash 1981; Van Oortmerssen & Busser 1989; Randall 1991; Jackson 1999; Randall et al. 2002; Solomon & Jacquot 2002). Mate-guarding and mate-searching abilities are likely to be favored by contest and scramble competition, respectively (Andersson 1994). Scramble competition and contest competition may select for either complementary or opposing male traits. For example, a highly aggressive male may not necessarily be good at locating widely distributed females. On the other hand, a male with above average spatial ability may be poor at mate guarding. Among thirteen-lined ground squirrels, for example, mate searching is more important than mate guarding in determining male reproductive success (Schwagmeyer & Woonter 1986; Schwagmeyer & Parker 1987; Schwagmeyer 1988).

In my study, dominance rank and spatial ability were used as measures of mate-guarding and mate-searching ability, respectively. An individual is defined as dominant over another if it consistently wins agonistic interactions between the two individuals (Drews 1993). Among mammals, mate-guarding ability has been inferred primarily by examining dominance relationships among males (e.g., Cox & Le Boeuf 1977; Lisk et al. 1989; Berard et al. 1994). Spatial ability is a complex trait that generally refers to the learning and memory of the position and relationship of the observer relative to environmental stimuli (Gaulin & Hoffman 1988; Allen 1999). Spatial ability is an important trait for males engaged in competitive mate searching because it allows males to efficiently navigate between females and relocate females as they become sexually receptive (Gaulin & Hoffman 1988; Schwagmeyer 1994).

Evidence suggests that male meadow voles (*Microtus pennsylvanicus*) engage in both mate-guarding and mate-searching tactics. Male ranges overlap those of multiple other males and multiple females, while females form intrasexual territories during the breeding season (Madison 1980). Inter-male aggression peaks during the breeding season and males seem to form stable dominance hierarchies (Turner & Iverson 1973; Rose 1979; Boonstra & Rodd 1983). Dominant males also guard females to improve their own reproductive success at this time (Webster & Brooks 1981a; Storey et al. 1995). During the breeding season, adult males expand their home ranges, presumably to search for mates (Dueser et al. 1981; Webster & Brooks 1981b; Gaulin & FitzGerald 1989). Males with larger home ranges also have better spatial ability (Chapter 1). Reproductively active males out-perform females in maze tests and have larger hippocampuses than do females, suggesting that spatial ability is a sexually selected trait among meadow voles (Gaulin & FitzGerald 1986, 1989; Jacobs et al. 1990; Kavaliers et al. 1993). Finally, males with better spatial ability are able to locate more females' nests (Chapter 1).

The goal of this experiment was to test the hypothesis that mate guarding and mate searching are alternative reproductive phenotypes among male meadow voles. I tested two predictions based on this hypothesis. First, I predicted that there would be a negative relationship between dominance rank and spatial ability. Such a trade-off is expected if mate guarding and mate searching are being maintained as discrete strategies by negative frequency-dependent selection (Brockmann 2001; Sinervo 2001a). This trade-off is also expected if selection has resulted in a conditional switch point between mate guarding and mate searching tactics because individuals would be expected to get better at one tactic relative to the other as their internal condition changed (Gross 1996). Second, I predicted seasonal changes in male spatial ability and aggression. This prediction is based on the assumption that the relative success of mate guarding and mate searching among meadow voles is density dependent (Greenfield & Shelly 1985; Lucas & Howard 1995; Sinervo 2001b). Alternative phenotypes are likely to be density dependent among meadow voles because vole populations exhibit regular seasonal and multi-year cycles in population densities (Krebs et al. 1969; Krebs 1970; Boonstra et al. 1994; Ostfeld & Canham 1995).

METHODS

Collection and Housing

Wild meadow voles were collected in two adjacent fields at Miami University's Ecology Research Center (ERC) near Oxford, Ohio. Grids of Sherman live traps (5m spacing) baited with cracked corn were set at dusk and checked at dawn. Upon capture, each vole was weighed (± 0.1 g) and sexed. Adults weighed more than 30 g and had descended testes (Boonstra & Rodd 1983). Five batches of adult males were collected for behavioral testing: April-May 2000 (*N*=40), March-May 2001 (*N*=79), October-November 2001 (*N*=39), April-May 2002 (*N*=39), and September-October 2002 (*N*=40). For each collection batch, I made a relative estimate of population density based on the number of males captured per trap night. Female voles were not included in the density calculation because they were released unmarked at the site of capture. Using number of males captured per trap night as an estimate of population density assumes that: (1) sex ratios remained constant among collection batches, and (2) trapability remained constant among collection batches.

Voles were housed singly in clear polycarbonate cages (18 × 28 × 12 cm) at Miami University's animal facility. Voles were maintained at 21°C on a cycle of 14 h light:10 h dark (lights on at 0800 hours). Rodent chow (Lab Diet #5013, PMI Nutrition International, Brentwood, MD) and water were provided ad libitum, and sunflower seeds and lettuce were provided as weekly supplements. Cotton Nestlets (Ancare, Bellmore, NY) and dried alfalfa were provided for bedding. All males experienced a summer light cycle for approximately one month prior to behavioral testing, and they had descended testes during behavioral testing. The voles were weighed after each set of behavioral tests to monitor their health.

Water Maze Testing

The spatial ability of all 237 males was tested using the Morris water maze (Stewart & Morris 1993). A circular pool (90 cm diameter and 45 cm height) was filled with water to a depth of 15 cm and divided into four equal quadrants with string raised above the pool. A 7 cm diameter clear plastic platform submerged 1.5 cm below the surface was used as the goal. The water temperature averaged 20.0 °C, and the water was made opaque using non-toxic white paint. I taped three white note cards with black shapes drawn on them at evenly spaced intervals around the edge of the water maze as visual cues. Various objects around the room were kept in consistent locations during testing as distal visual cues. The observer stood approximately 1 m away from the site where the vole was released. Because each vole was released at four different locations around the maze, the observer was not a consistent visual cue. All trials were video recorded.

I followed a four-phase protocol (preliminary, acquisition, transfer, and retention), and the daily testing sequence of voles was randomized. All inter-trial intervals on the same day were 45 s, during which each vole was first dried off with a towel and then placed in a holding cage. During the preliminary phase, each male was introduced into the maze, allowed to swim for 60 s, and then placed on the platform for 15 s. Each vole was given three consecutive preliminary trials on the same day. The preliminary phase was conducted during one day in a separate room from all other testing and the note cards were not in place, so the voles were not acquiring the task during this phase.

During the acquisition phase (conducted 24 h after the preliminary phase), I recorded the time it took each vole to reach the platform (escape latency). For each vole, the platform was assigned to one of the four randomly chosen quadrants. The platform remained in the same quadrant for all trials involving a particular vole. Four possible release sites were designated at equidistant points around the pool. One release site was set aside for each vole to use during the transfer phase (see below). This site was chosen using a semi-random method counter-balanced such that half the voles had a release site that was closer to the platform than the other half (this was necessary because the platform was offset from the center of the pool). During the acquisition phase, I tested each vole on three consecutive trials per day for 5 blocks (days) of trials, such that each vole was introduced into the maze from the three different release sites in a random order each day. Any trial that lasted more than 60 s was terminated by placing the vole on the platform for 15 s and then removing it from the maze. Similarly, whenever a vole reached the platform, it was allowed to remain there for 15 s before ending the trial.

During the transfer phase (conducted 24 h after the last acquisition trial), I introduced each vole into the maze from the release site not used during the acquisition phase. This phase measured the voles' ability to transfer what they had learned during the acquisition phase to a novel context. Three consecutive trials at the same release site were conducted for each vole during this phase. Finally, during the retention phase (conducted 24 h after the transfer phase), the platform was removed from the maze and voles were released into the maze for 60 s from one of the three release sites used during their acquisition trials. From video recordings, I determined path lengths for block 5 of the acquisition trials and the transfer trials and time spent swimming in the quadrant where the platform had previously been during the retention trials.

My protocol resulted in five measures of spatial ability: (1) *escape latency* (time to reach the platform during acquisition and transfer trials), (2) *acquisition path length* (average path length of block 5 of the acquisition trials), (3) *number of acquisition trials* (the number of trials, from 1 to 15, needed by voles before they reached the platform within the 60 s time limit), (4) *transfer path length* (average path length of the transfer trials), and (5) *retention time* (time spent in the target quadrant during the retention trials). Number of acquisition trials provided an index of learning speed. Escape latencies, acquisition path length, and transfer path length provided different indices of learning ability. Retention time provided an index of spatial memory. I used both acquisition and transfer path lengths to measure learning ability because the transfer test required more complex navigational ability than did the acquisition test. Namely, performance during the acquisition trials required only learning a simple motor (praxic) response to locate the platform, whereas good performance during the transfer trials required more complex "route" or "locale" navigation (Redish 1999). These measures of spatial ability have been commonly used in past studies with the Morris water maze (D'Hooge & De Deyn 2001).

Dominance Testing

I collected dominance data for three groups of 32 males from three different collection batches (Spring 2000, Fall 2001, and Spring 2002). Following water-maze testing, males were divided into groups of 8 such that variance in spatial ability within each of the groups was maximized. I conducted pairwise dominance trials among all males within a group of eight but not between groups. Thus, dominance data were collected for four groups of eight males from each of three batches of voles (96 males total).

I tested male dominance following methods similar to those described in past studies (Huck & Banks 1982; Shapiro & Dewsbury 1986; Harper & Batzli 1997). All tests were conducted indoors during the light part of the cycle in a circular Plexiglas arena (50 cm high, 60 cm diameter). A removable opaque partition was placed across the center of the arena at the start of each trial, and the voles were placed on either side of the partition for a 5 min habituation period. The tip of each male's tail was marked with fluorescent powder for identification during trials (color was alternated for consecutive trials). I collected data from behind an opaque plastic sheet with a small opening for observation. I recorded the timing and frequency of aggressive interactions during 15 min trials using all-occurrence sampling. The behaviors recorded were similar to those used in past studies (Colvin 1973; Turner & Iverson 1973): threat, lunge, chase, box, and wrestle. The “chase” category included cases in which one vole rapidly pursued the other as well as displacement behavior in which the aggressor moved toward a stationary vole causing him to retreat while the aggressor acquired the position of the retreating vole. I recorded threat behavior (rearing on hind-legs) only if the recipient responded by retreating or showing a submissive posture. This was done to avoid recording behaviors not clearly associated with the establishment of dominance. Because severe wounding never occurred, none of the trials had to be interrupted. A male was considered dominant if he exhibited more aggression towards his opponent than vice versa. Each pair was tested on repeated trials until the same individual was dominant in two out of three trials. After testing, each vole was given an ordinal dominance rank (0-7) based on the number of other individuals he dominated.

Statistical Analysis

The relationship between the spatial-ability variables and the arena-trial variables were analyzed using two methods. First, I divided the voles into high-ranking (4-7) and low-ranking (0-3) groups and treated dominance rank as a fixed factor. Second, simple linear regressions were used to compare dominance rank and average number of attacks per trial. For all these analyses, I initially included the three collection batches as a fixed factor. However, effects of collection batch were not significant, and the results of the analyses did not noticeably change when the batch effects were removed. Therefore, I did not report batch effects for any of the analyses comparing the spatial-ability variables and arena-trial variables. Changes in escape latency over the five blocks of acquisition trials were determined using repeated-measures ANOVA, with block as the within-subjects effect and dominance group (ranks 0-3 or ranks 4-7) as the between-subjects effect. Bonferroni-adjusted *t* tests were used for post-hoc comparisons between consecutive blocks and between dominance groups within each block. Dominance group was also used as a between-subjects effect for repeated-measures ANOVA's comparing differences in thigmotaxis between blocks 1 and 5 of the acquisition trials and comparing differences in path length between block 5 and the transfer trials.

The average of each male's mass at capture and after behavioral testing was used for analyses involving body mass. To test for conditional changes in male spatial ability, the relationship between body mass and each of the spatial ability variables was determined using Pearson correlation coefficients. The relationships among each of the spatial ability variables were also determined using Pearson correlation coefficients.

I found a peak in vole density in Spring 2002. Therefore, I analyzed the spatial ability variables and body mass for density-dependent effects by comparing the data from Spring 2002 to the four other batches compiled using *t* tests. Average number of attacks per arena trial was analyzed similarly by comparing the Spring 2002 data to the two other collection batches for which these data were collected (Spring 2000 and Fall 2001).

All path length and escape latency data were log transformed to meet analysis assumptions (Neter et al. 1996). A significance level of $\alpha=0.05$ was used for all tests, and all means are presented as $\bar{X}\pm$SE. Note that for all post-hoc *t* tests, I report

Bonferonni adjusted *P* values, meaning that the *P* value was multiplied by the number of planned post-hoc comparisons used for a particular test. All statistical tests were conducted using SPSS 11.0, except repeated measures ANOVA's which were run in SAS (PROC MIXED).

Ethical Note

Water maze testing involved exposing voles to an aversive stimulus (water). I attempted to minimize the amount of stress that voles experienced by limiting trials to a maximum of 60 s and drying voles after each trial. The water maze has been previously used extensively with meadow voles (e.g., Kavaliers et al. 1993; Galea et al. 1995), and meadow voles are also excellent swimmers (Dagg & Windsor 1972). The dominance trials also exposed males to potential injury, but no cases of noticeable wounding occurred. Similar methods have been used successfully in previous studies involving meadow voles (e.g., Colvin 1973; Turner & Iverson 1973).

RESULTS

Correlations between the different measures of spatial ability revealed that spatial-learning speed (acquisition trials), spatial-learning ability (acquisition and transfer path lengths), and spatial memory (retention time) tended to be positively correlated (Table 1). Note that longer acquisition and transfer paths are indicative of poorer spatial-learning ability. Males that were more thigmotactic during the final block of acquisition trials took more trials to locate the platform, had longer acquisition and transfer paths, and poorer retention times (Table 1). Body mass was not correlated with any of the spatial ability variables or thigmotaxis (Table 1), suggesting that spatial ability is not dependent upon male condition.

Spatial Ability vs. Dominance Rank

For the final block of acquisition trials, path length and escape latency were significantly positively correlated (Pearson correlation: $r=0.95$, $N=237$, $P<0.0005$). This indicated that voles were all swimming at about the same speed, and that escape latency during the other blocks of acquisition trials was indicative of spatial-learning ability rather than swimming ability. The males exhibited a reduction in escape latencies over the 5 days of training, but males with high dominance ranks had better spatial-learning ability than those with low dominance rank (Fig. 1a). Male escape latencies differed between blocks ($F_{5,470}=132.22$, $P<0.0001$) and males with high dominance ranks had shorter escape latencies than males with low dominance ranks ($F_{1,94}=8.76$, $P=0.004$). There was also a significant interaction between block and dominance group such that later blocks showed an increased difference between the dominance groups ($F_{5,470}=2.62$, $P=0.024$). Post-hoc t tests revealed that males with high dominance ranks had better spatial-learning ability (shorter escape latencies) than those with low dominance ranks for the final block of the acquisition trials ($t_{470}=3.15$, adjusted $P=0.019$) and the transfer trials ($t_{470}=3.15$, adjusted $P=0.0022$). Males also showed a significant difference in the percentage of time spent thigmotactic between blocks 1 and 5 of the acquisition trials (Fig. 1b; $\mathrm{F}_{1,94}=164.93$, $\mathrm{P}<0.0001$), but there was no difference in thigmotaxis between males with high and low dominance ranks ($\mathrm{F}_{1,94}=0.73$, $P=0.39$) and no interaction between block and dominance group ($\mathrm{F}_{1,94}=0.89$, $P=0.35$). Thus, males with higher dominance rank exhibited better spatial-learning ability, and this was not due to differences in a propensity for thigmotaxis.

Repeated measures ANOVA revealed that males with high dominance rank had shorter path lengths than males with low dominance rank (Fig. 2; $F_{1,94}=14.95$, $P<0.0005$), transfer paths were shorter than acquisition paths ($F_{1,94}=10.74$, $P<0.001$), and the interaction between phase (acquisition or transfer) and dominance group was not significant ($F_{1,94}=0.084$, $P=0.77$). Post-hoc tests revealed that males with high dominance ranks had shorter acquisition paths ($t_{94}=3.60$, $P=0.0010$) and transfer paths ($t_{94}=3.35$, $P=0.0024$) than males with low dominance ranks. Retention times were not significantly different for males with high and low dominance ranks ($t_{94}=0.35$, $P=0.73$). Both high and low dominance voles had significantly longer retention times than expected for a random swim path (high dominance rank: $t_{50}=9.12$, $P<0.0005$; low dominance rank: $t_{44}=8.40$, $P<0.0005$). Although males with low dominance rank took more acquisition trials to reach the platform than males with high dominance rank, the difference was not statistically significant (high dominance: $\overline{X}=2.57\pm0.34$ trials; low dominance: $\overline{X}=3.44\pm0.56$ trials; $t_{94}=1.38$, $P=0.17$). Swimming speed was not significantly different for males with high and low dominance during the final block of acquisition trials ($t_{94}=0.76$, $P=0.45$) but males with high dominance rank showed a non-significant tendency to swim faster than males with low dominance rank during the transfer trials (high dominance: $\overline{X}=25.97\pm0.90$ cm/s; low dominance: $\overline{X}=23.50\pm0.97$ cm/s; $t_{94}=1.84$, $P=0.067$). Overall, therefore, males with high dominance rank had better spatial-learning ability, tended to have quicker spatial-learning speed, but showed no difference in spatial memory compared to males with low dominance rank.

Dominance rank and average number of attacks per trial were positively correlated (Pearson correlation: *r*=0.55, *N*=96, *P*<0.0001), indicating that dominant males also tended to be more aggressive. Body mass was also not correlated with dominance rank (Pearson correlation: *r*=0.033, *N=96*, *P*=0.75) or average number of attacks (Pearson correlation: *r*=0.089, *N*=96, *P*=0.39). Males that engaged in more attacks per trial had shorter acquisition paths (Pearson correlation: *r*=0.26, *N*=96, *P*=0.009), and tended to have shorter transfer paths (Pearson correlation: *r*=0.17, *N*=96, *P*=0.07). Retention time was not correlated with average number of attacks (Pearson correlation: *r*<0.0001, *N*-96, *P*=0.88). Males with a higher number of attacks per trial tended to require fewer acquisition trials to locate the platform, but the relationship was not significant (Pearson correlation: *r*=0.18, *N*=96, *P*=0.075). Percentage of time spent thigmotactic during the final block of acquisition trials was not correlated with average number of attacks per trial (*r*=0.06, *N*=96, *P*=0.56). Overall, the results obtained using correlations corroborate those obtained using ANOVA: more aggressive voles showed better spatial-learning ability, tended to show quicker learning speed, but did not have better spatial memory than less aggressive subordinates.

Density Dependence

Vole density was similar during four of the five collection batches (range: 0.016-0.030 males/trap night) but showed a distinct peak in the Spring 2002 (0.11 males/trap night; Fig. 3a). Male spatial-learning speed (acquisition trials to reach the platform) was poorer during Spring 2002 compared to the other collection batches (Fig. 3b; t_{235}=2.27, *P*=0.024). Acquisition path lengths were longer during Spring 2002 compared to the other collection batches (t_{235}=2.22, P=0.027). There were no significant differences between Spring 2002 and the other collection batches for retention time (t_{235}=0.71, P=0.48), transfer path length (t_{235}=0.045, P=0.96), and percentage of time thigmotactic (t_{235}=0.44, P=0.66). Average number of attacks per trial also showed no significant difference between Spring 2002 and the other two collection batches for which these data were collected(t_{94}=0.94, P=0.35). Therefore, I found some seasonal variation in spatial-learning speed and spatial-learning ability, but not aggression or spatial memory. Finally, male body mass was greater during Spring 2002 compared to the other collection batches (t_{235}=4.44, P<0.0005).

DISCUSSION

Spatial Ability vs. Dominance Rank

My results did not support the prediction that there is a trade-off between dominance rank and spatial ability. Instead, I found that males with higher dominance rank had better spatial ability. However, not all aspects of spatial ability were related to dominance rank in the same way. Specifically, males with higher dominance rank had better performance (speed and accuracy) during the acquisition and transfer tasks but not during the retention task. Thus, males with higher dominance rank had better spatial-learning ability, tended to learn spatial tasks quicker, but did not have better spatial memory than males with low dominance rank. I found no evidence that there are discrete mate-guarding and mate-searching phenotypes among meadow voles. These results suggest that mate-guarding and mate-searching are unlikely to be maintained by negative frequency-dependent selection as alternative mating strategies within meadow vole populations. Furthermore, my results suggest that the relative use of mate-guarding and mate-searching tactics is unlikely to depend upon male condition because: (1) there was not a trade-off between spatial ability and dominance rank, and (2) male body mass was not related to spatial ability or dominance rank.

My results indicate that selection for improved spatial ability may also favor selection for traits associated with high dominance rank and vice versa. Studies with a number of other rodent species also suggest that males that are better at locating females tend to also have higher dominance rank (Koprowski 1993a, b; Waterman 1998; Barnard & Lou 2002). Furthermore, past studies have shown that both the propensity to be dominant and spatial ability are heritable traits among rodents (Upchurch & Wehner 1988, 1989; Dewsbury 1990; Drickamer 1992; Sluyter et al. 1996; Horne & Ylönen 1998). Presumably, better spatial ability allows males to locate mates more efficiently, and high dominance rank allows males to more effectively guard their mates after locating them. Thus, contest competition and scramble competition seem to favor a correlated suite of traits among meadow voles, and perhaps other rodent species.

Numerous past studies suggest that spatial ability and dominance rank are both likely to be favored by sexual selection among meadow voles. Males outperform females in maze tests (Gaulin & FitzGerald 1986, 1989 Kavaliers et al. 1993). In contrast, monogamous pine voles (*M. pinetorum*) and prairie voles (*M. ochrogaster*) do not show a sex difference in maze tests (Gaulin & FitzGerald 1986). Male meadow voles also have larger home ranges than females but monogamous voles do not show a sex difference in range size (Gaulin & FitzGerald 1986, 1988). Furthermore, the hippocampus is larger among male than female meadow voles, but pine voles show no sexual dimorphism in hippocampal size (Jacobs et al. 1990). Overall, these results suggest that superior male spatial ability among meadow voles has been favored by sexual selection. Traits associated with high dominance rank are also likely to be favored by sexual selection among meadow voles. In the field, wounding rates are about 11 times higher among males than among females during the breeding season (Boonstra & Boag 1992). In laboratory experiments in which females were allowed to interact with pairs of males, the dominant male mated with the female more often and sired more offspring than the subordinate (Storey et al. 1995). Dominant males seem to engage in mate guarding: shortly before and after mating, they follow females closely and aggression toward the subordinate increases after mating begins (Storey et al. 1995).

Males with poor spatial ability and low dominance rank might be “making the best of a bad job” (Arak 1984; Koprowski 1993a), meaning that they engage in a reproductive strategy with lower pay-offs than males with good spatial ability and high dominance rank. It remains unclear, however, what type of mating strategy these males would employ. I previously found that males with poor spatial ability had relatively small home ranges (Chapter 1), which indicates that they are not likely to engage in a mate-searching strategy. Alternatively, males with poor spatial ability and low dominance rank might engage in a satellite tactic similar to that used by subordinate tree squirrels (Koprowski 1993a, b). A satellite tactic generally involves waiting unobtrusively near a dominant male or in his territory in order to gain opportunistic access to females that are controlled by the dominant individual (Waltz 1982; Lucas & Howard 1995). I previously found that a large percentage of males with poor spatial ability did not visit any female nests (Chapter 1), indicating that they might be engaging in a satellite tactic in which they wait near female nests to potentially mate with unguarded females as they come and go from their nests.

My results indicate that meadow vole populations include some individuals with both good spatial ability and high dominance rank. Whether these males are more likely to engage in mate guarding or mate searching also remains unclear. Mate guarding and mate searching are mutually exclusive behaviors, and I previously found that males who spent more time with a particular female visited fewer different females (Chapter 1). Selection has probably led to an optimal strategy among males with good spatial ability and high dominance rank, which dictates the amount of time spent with each female. The relative prevalence of mate-searching and mate-guarding tactics should be dictated by the relative benefits of each. Estrus and ovulation are induced among meadow voles, and therefore a male would be expected to spend at least enough time with a female to induce estrus (Meek & Lee 1993). Previous studies suggest that mate guarding is more likely to occur in species with a higher occurrence of multiple paternity (Schwegmeyer & Parker 1987; Sherman 1989; Yamamura & Tsuji 1989). Storey et al. (1995) reported that sequential mating by two male meadow voles resulted in the second male to mate siring about 60% of pups, suggesting that mate guarding would be somewhat beneficial. Guarding after ovulation would probably only be beneficial as a way to reduce the likelihood of post-implantation pregnancy disruption by novel males (Mallory & Clulow 1977; Storey & Snow 1990).

I previously found that males with better spatial ability did not achieve greater reproductive success and hypothesized that this was due to males with good spatial ability having poor mate-guarding ability (Chapter 1). My current results suggest that this is not the case because males with better spatial-learning ability also had higher dominance rank. Therefore alternative explanations are needed for why males with good spatial ability were not achieving more successful matings (Chapter 1). Female preferences for male traits uncorrelated with spatial ability or dominance rank is a plausible explanation. In particular, females' preferences for familiar males (Salo & Dewsbury 1995; Parker et al. 2001) and their propensity to mate with multiple males (Storey et al. 1995; Berteux et al. 1999) might reduce the benefits of high dominance rank and good spatial ability for males.

In contrast to my results, some evidence suggests that discrete alternative mating strategies exist among house mice. Specifically, some mice are highly aggressive while others almost never attack during resident-intruder trials (Benus et al. 1991). Wild house mice live in demes, with each male establishing a territory (Van Oortmerssen & Busser 1989). The aggressive male phenotype may have a reproductive advantage within the deme, whereas the passive phenotype may be favored during periods of migration and territory establishment (Van Oortmerssen & Busser 1989; Benus et al. 1991). Meadow voles are less aggressive than house mice and other vole species (Colvin 1973; Dewsbury 1983; personal observations). The difference in aggressiveness between meadow voles and house mice may ultimately be due to differences in the spatial distribution of females. Compared to the clumped demic social structure of house mice, female meadow voles are widely distributed (Madison 1980). Therefore, there may be stronger disruptive selection for alternative mating strategies among male mice than among male meadow voles due to interspecific differences in the ability to monopolize multiple females.

Testosterone may be the causal link between my observed positive relationship between dominance rank and spatial ability among meadow voles. Testosterone seems to have positive organizational and activational effects upon spatial ability among male meadow voles. Voles from litters with a male-biased sex ratio, and presumably higher *in utero* testosterone exposure, have better spatial-learning ability but not better spatial memory than voles from female-biased litters (Galea et al. 1994a). Similarly, increased prenatal testosterone has been shown to improve spatial ability among rats (Williams et al. 1990; Roof & Havens 1992; Isgor & Sengelaub 1998). Juvenile meadow voles do not show a sex difference in spatial ability, which suggests that adult differences in spatial ability may, at least in part, be due to activational effects of testosterone (Galea et al. 1994b). Surprisingly, Galea et al. (1995) found that plasma testosterone level in male meadow voles was not related to their spatial ability. However, males with higher testosterone levels do have larger overall hippocampal volumes (Galea & McEwen 1999; Galea et al. 1999) and testosterone promotes the survival of new cells in the dentate gyrus (Ormerod & Galea 2003). Thus, elevated testosterone levels are likely to promote neuron survival in the male hippocampus during the breeding season when males are ranging more widely in search of mates.

Studies with a variety of rodent species have shown that testosterone also has organizational and activational effects upon dominance behavior, with males exposed to higher prenatal testosterone levels and higher circulating testosterone levels as adults being more aggressive and achieving higher dominance rank than males exposed to lower testosterone levels (Drickamer et al. 1973; Edwards & Rowe 1975; Wagner et al. 1979; Gipps 1982; Huck et al. 1986; Vom Saal 1987; Zielinski & Vandenbergh 1993; Sluyter et al. 1996). Among meadow voles, Turner et al. (1980) demonstrated that under field conditions, castration leads to decreased intermale aggression. Levels of aggression peak among males during the breeding season (Christian 1971; Turner & Iverson 1973; Rose 1979) and male testosterone levels also increase during the breeding season (Galea & McEwen 1999). Furthermore, males with scrotal testes have higher levels of wounding than males with abdominal testes (Rose 1979). Immature males also have fewer wounds than adults (Christian 1971; Rose 1979). Thus, testosterone has a positive organizational effect and possibly a positive activational effect upon male spatial ability and has a positive activational effect and possibly a positive organizational effect upon male aggressiveness among meadow voles. Although other hormones are likely to be involved (Boonstra & Boag 1992; Galea & McEwen 1999), testosterone should be investigated further for its role in the positive relationship between male spatial ability and dominance rank.

I did not find a relationship between dominance rank or aggression and spatial memory as measured by retention time. This may indicate that dominance behavior and spatial memory are controlled by separate physiological pathways (Redish 1999). Unlike spatial-learning ability, testosterone does not seem to influence spatial memory among meadow voles (Galea et al. 1994a). I observed relatively weak relationships between retention time and the other measures of spatial learning ability, which also suggests that spatial memory and spatial learning are controlled by different physiological pathways.

Density Dependence

I found some evidence for density-dependent changes in spatial ability, which suggests that the relative abundance of males with a mate-searching phenotype may also be density dependent. Spatial memory and aggression did not show changes with differences in population density, but males with the poorest spatial-learning speed and spatial-learning ability were collected when density peaked. This suggests that males that learn spatial tasks more quickly and accurately are less common during periods of high density. In support of this idea, Ostfeld & Canham (1995) found that meadow voles move shorter distances under higher density conditions, and I previously demonstrated a positive correlation between range size and spatial ability (Chapter 1). Males might locate mates more easily during periods of high population density, but there may be strong selective pressure for better spatial ability to facilitate mate searching when population density is low and females are more difficult to locate. A previous study at my study site found that meadow voles had an average life span of only 4-8 weeks (Hall et al. 1991), indicating that populations might be able to respond rapidly to changes in selective pressures created by density fluctuations. Thus, mate-searching may be a density-dependent reproductive phenotype among male meadow voles similar to density-dependent strategies documented for other species (e.g., Greenfield & Shelly 1985; Lucas & Howard 1995; Sinervo 2001b).

Cyclic changes in population density are a common phenomenon among rodent populations (e.g., Krebs 1970; Lidicker 1973; Chitty 1987). Among meadow voles, population density generally peaks in the late fall and is at its lowest in the summer, but occasional peaks in early spring, similar to my observation for spring 2002, have been seen in previous studies (Krebs et al. 1969; Dueser et al. 1981; Boonstra et al. 1994). Chitty (1960, 1967) was among the first to hypothesize that variation in selective pressures during different phases in rodent population cycles could select for variation in behavioral phenotypes. In support of this hypothesis, some studies have demonstrated that level of aggression within meadow vole populations is density dependent (Krebs 1970; Boonstra & Boag 1992). In contrast, Turner & Iverson (1973) did not find a relationship between aggression and population density. I also did not find differences in aggression between males collected during periods of high and low population density, which was somewhat surprising considering that I observed a positive relationship between male aggression and spatial-learning ability. Desnsity dependence of spatial-learning ability but not aggression may have occurred because the relationship between these two variables, although statistically significant, was fairly weak (r=0.26). However, I found no evidence for a trade-off between spatial ability and aggression which suggests that density-dependent selection has not caused disruptive selection for mate-guarding and mate-searching phenotypes among male voles.

I observed a peak in male body mass that corresponded with the peak in density, as has been observed in some previous studies (e.g., Krebs et al. 1969; Chitty 1987). However, I did not find significant correlations between body mass and dominance rank or aggression. Similarly, Krebs (1970) found no relationship between a variety of measures of aggression and body mass. This indicates that seasonal changes in body mass should not be assumed to be indicative of changes in levels of aggression.

It should be noted, however, that my estimate of population density (number of males captured per trap night) had some limitations. First, it was assumed that the sex ratio remained constant with changes in density. This assumption is supported by past studies that have demonstrated only minor changes in sex ratio during changes in population density (Krebs et al. 1969; Myers & Krebs 1971). Second, it was assumed that trapability did not change across the collection batches. Differences in trapability are most likely to occur during different seasons due to changes in ambient temperature and food availability (Krebs et al. 1969). Vole density peaked during one of the three spring collection batches, and the other two spring collection batches had population densities similar to the two fall collection batches. This suggests that there were not changes in trapabilty that corresponded with the seasons, and therefore trapabilty may have been similar across the five collection batches.

In summary, my results suggest that mate searching and mate guarding are not discrete alternative reproductive phenotypes among meadow voles since males with good spatial ability also tended to have high dominance rank. This does not, however, preclude the existence of alternative tactics, such as a satellite tactic, used by males with poor spatial ability and low dominance rank. Males with good spatial ability and high dominance rank are likely to engage in an optimal combination of mate-guarding and mate-searching tactics. I did find that spatial-learning ability and speed decreased with increased population density, which suggests that a mate-searching phenotype might be density dependent among male meadow voles. Finally, spatial memory seems to be under different selective pressures than spatial-learning ability and speed because spatial memory was uncorrelated with male dominance rank and did not show density-dependent variation.

REFERENCES

Allen, G. L. 1999. Spatial abilities, cognitive maps, and wayfinding. In: *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes* (Ed. by R. G. Golledge), pp. 46-80. Baltimore, Maryland: The Johns Hopkins University Press.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Arak, A. 1984. Sneaky breeders. In: *Producers & Scroungers: Strategies of Exploitation and Parasitism* (Ed. by C. J. Barnard), pp. 154-194. New York: Chapman & Hall.

Barash, D. P. 1981. Mate guarding and gallivanting by male hoary marmots (*Marmota caligata*). *Behavioral Ecology and Sociobiology*, **9,** 187-193.

Barnard, C. J. & Luo, N. 2002. Acquisition of dominance status affects maze learning in mice. *Behavioural Processes,* **60,** 53-59.

Benus, R. F., Bohus, B., Koolhaas & van Oortmerssen, G. A. 1991. Heritable variation for aggression as a reflection of individual coping strategies. *Experientia*, **47,** 1008-1017.

Berard, J. D., Nurnberg, P., Epplen, J. T. & Schmidtke, J. 1994. Alternative reproductive tactics and reproductive success in male rhesus macaques. *Behaviour*, **129,** 177-199.

Berteaux, D., Dety, J. & Rengifo, J. B. 1999. Multiple paternity in meadow voles (*Microtus pennsylvanicus*): investigating the role of the female. *Behavioural Ecology and Sociobiology*, **45,** 283-291.

Boonstra, R. & Boag, P. T. 1992. Spring declines in Microtus pennsylvanicus and the role of steroid hormones. *Journal of Animal Ecology*, **61,** 339-352.

Boonstra, R. & Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology*, **52,** 757-780.

Boonstra, R., Hochachka, W. M. & Pavone, L. 1994. Heterozygosity, aggression, and population fluctuations in meadow voles (*Microtus pennsylvanicus*). *Evolution,* **48,** 1350-1363.

Brockmann, H. J. 2001. The evolution of alternative strategies and tactics. *Advances in the Study of Behavior*, **30,** 1-51.

Chitty, D. 1960. Population processes in the vole an their relevance to general theory. *Canadian Journal of Zoology*, **38,** 99-113.

Chitty, D. 1967. The natural selection of self-regulatory behavior in animal populations. *Proceedings of the Ecological Society of Australia,* **2,** 51-78.

Chitty, D. 1987. Social and local environments of the vole *Microtus townsendii*. *Canadian Journal of Zoology,* **65,** 2555-2566.

Christian, J. J. 1971. Fighting, maturity, and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy,* **52,** 556-567.

Colvin, D. V. 1973. Agonistic behaviour in male of five species of voles *Microtus*. *Animal Behaviour,* **21,** 471-480.

Cox, C. R. & Le Boeuf, B. J. 1977. Female incitation of male competition: a mechanism in sexual selection. *The American Naturalist,* **111,** 317-335.

Dagg, A. I. & Windsor, D. E. 1972. Swimming in northern terrestrial mammals. *Canadian Journal of Zoology,* **50,** 117-130.

Dewsbury, D. A. 1983. A comparative study of rodent social behavior in a seminatural enclosure. *Aggressive Behavior,* **9,** 207-215.

Dewsbury, D. A. 1990. Fathers and sons: genetic factors and social dominance in deer mice, *Peromyscus maniculatus*. *Animal Behaviour,* **5,** 59-66.

D'Hooge, R. & De Deyn, P. P. 2001. Applications of the Morris water maze in the study of learning and memory. *Brain Research Reviews*, **36,** 60-90.

Dominey, W. J. 1984. Alternative mating tactics and evolutionarily stable strategies. *American Zoologist,* **24,** 385-396.

Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour,* **125,** 283-313.

Drickamer, L. C. 1992. Oestrous female house mice discriminate dominant from subordinate males and sons of dominant from sons of subordinate males by odour cues. *Animal Behaviour,* **43,** 868-879.

Drickamer, L. C., Vandenbergh, J. G. & Colby, D. R. 1973. Predictors of dominance in male golden hamster (*Mesocricetus auratus*). *Animal Behaviour,* **21,** 557-563.

Dueser, R. D., Wilson, M. L. & Rose, R. K. 1981. Attributes of dispersing meadow voles in open-grid populations. *Acta Theriologica,* **26,** 139-162.

Edwards, D. A. & Rowe, F. A. 1975. Neural and endocrine control of aggressive behavior. In: *Hormonal Correlates of Behavior* (Ed. by Euthnow, B. E. & Sprotl, R. L.), pp. 275-303, New York: Plenum Press.

Galea, L. A. M., McEwen, B. S., 1999. Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience,* **89,** 955-964.

Galea, L.A.M., Ossenkopp, K.-P. & Kavaliers, M. 1994a. Performance (re-acquisition) of a water-maze task by adult meadow voles: effects of age of initial task acquisition and in utero environment (litter sex-ratio). *Behavioural Brain Research,* **63,** 177-185.

Galea, L.A.M., Ossenkopp, K.-P. & Kavaliers, M. 1994b. Developmental changes in spatial learning in the Morris water-maze in young meadow voles, *Microtus pennsylvanicus*. *Behavior and Brain Research,* **60,** 43-50.

Galea, L.A.M., Kavaliers, M., Ossenkopp, K.-P. & Hampson, E. 1995. Gonadal hormone levels and spatial learning performance in the Morris water maze in male and female meadow voles, *Microtus pennsylvanicus*. *Hormones and Behavior* **, 29,** 106-125.

Galea, L.A.M., Perrot-Sinal, T.S., Kavaliers, M., Ossenkopp, K.-P. 1999. Relations of hippocampal volume and dentate gyrus width to gonadal hormone levels in male and female meadow voles. *Brain Research,* **821,** 383-391.

Gaulin, S. J. C. & FitzGerald, R. W. 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist*, **127,** 74-88.

Gaulin, S. J. C. & FitzGerald, R. W. 1988. Home-range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy*, **69,** 311-319.

Gaulin, S. J. C. & FitzGerald, R. W. 1989. Sexual selection for spatial-learning ability. *Animal Behaviour*, **37,** 322-331.

Gaulin, S. J. C. & Hoffman, H. A. 1988. Evolution and development of sex differences in spatial ability. In: *Human Reproductive: a Darwinian Perspective* (Ed. by L. Betzig, M. B. Mulder, & P. Turke), pp. 7-152. New York: Cambridge University Press.

Gipps, J. H. W. 1982. The effects of testosterone and scopolamine HBr on aggressive behaviour of male voles, *Microtus townsendii*. *Canadian Journal of Zoology*, **60,** 946-950.

Greenfield, M. D. & Shelly, T. E. 1985. Alternative mating strategies in a desert grasshopper: evidence of density-dependence. *Animal Behaviour*, **33,** 1192-1210.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology and Evolution*, **11,** 92-98,

Hall, A. T., Woods, P. E. & Barrett, G. W. 1991. Population dynamics of the meadow vole (Microtus pennsylvanicus) in nutrient-enriched old-field communities. *Journal of Mammalogy,* **72,** 332-342.

Harper, S. J. & Batzli, G. O. 1997. Are staged dyadic encounters useful for studying aggressive behaviour of arvicoline rodents? *Canadian Journal Zoology,* **75,** 1051-1058.

Horne, T. J. & Ylönen, H. 1998. Heritabilities of dominance-related traits in male bank voles (*Clethrionomys glareolus*). *Evolution*, **52,** 894-899.

Huck, U. W. & Banks, E. M. 1982. Male dominance status, female choice and mating success in the brown lemming, *Lemmus trimucronatus*. *Animal Behaviour,* **30,** 665-675.

Huck, U. W., Banks, E. M. & Wang, S.-C. 1986. Behavioral and physiological correlates of aggressive dominance in male brown lemmings (*Lemmus sibiricus*). *Aggressive Behavior*, **12,** 139-148.

Isgor, C. & Sengelaub, D. R. 1998. Prenatal gonaldal steroids affect adult spatial behavior, CA1 and CA3 pyramidal cell morphology in rats. *Hormones and Behavior,* **34,** 183-198.

Jackson, T. P. 1999. The social organization and breeding system of Brants' whistling rat (*Parotomys brantsii*). *Journal of Zoology, London,* **247,** 323-331.

Jacobs, L. F., Gaulin, S. J., Sherry, D. F. & Hoffman, G. E. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Science USA*, **87,** 6349-6352.

Kavaliers, M., Eckel, L. A. & Ossenkopp, K.-P. 1993. Brief exposure to 60 Hz magnetic fields improves sexually dimorphic spatial learning performance in meadow vole, *Microtus pennsylvanicus*. *Journal of Comparative Physiology,* **173,** 241-248.

Koprowski, J. L. 1993a. Alternative reproductive tactics in male eastern gray squirrels: "making the best of a bad job". *Behavioral Ecology,* **4,** 165-171.

Koprowski, J. L. 1993b. Behavioral tactics, dominance, and copulatory success among male fox squirrels. *Ethology Ecology & Evolution,* **5,** 169-176.

Krebs, C. J. 1970. Microtus population biology: behavioral changes associated with the population cycle in *M. ochrogaster* and *M. pennsylvanicus*. *Ecology,* **51,** 34-52.

Krebs, C. J., Keller, B. L. & Tamarin, R. H. 1969. *Microtus* population biology: demographic changes in fluctuating populations of M. ochrogaster and M. pennsylvanicus in southern Indiana. *Ecology*, **50,** 587-607.

Lidicker, W. Z. 1973. Regulation of numbers in an island population of the California vole, a problem in community dynamics. *Ecological Monographs*, **43,** 271-302.

Lisk, R. D., Huck, U. W., Gore, A. C. & Armstrong, M. X. 1989. Mate choice, mate guarding and other mating tactics in golden hamsters maintained under seminatural conditions. *Behaviour*, **109,** 58-75.

Lucas, J. R. & Howard, R. D. 1995. On alternative reproductive tactics in anurans: dynamic games with density and frequency dependence. *The American Naturalist*, **146,** 365-397.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioural Ecology Sociobiology*, **7,** 65-71.

Mallory, F. F. & Clulow, F. V. 1977. Evidence of pregnancy failure in the wild meadow vole, *Microtus pennsylvanicus*. *Canadian Journal of Zoology*, **55,** 1-17.

Mathews, L. M. 2002. Tests of the mate-guarding hypothesis for social monogamy: does population density, sex ratio, or female synchrony affect behavior of male snapping shrimp (*Alpheus angulatus*)? *Behavioral Ecology and Sociobiology*, **51,** 426-432.

Meek L. R. & Lee, T. M. 1993. Prediction of fertility by mating latency and photoperiod in nulliparous and primiparous meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility*, **97,** 353-357.

Myers, J. H. & Krebs, C. J. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. *Ecological Monographs*, **41,** 53-78.

Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996. *Applied Linear Statistical Models.* 4th edn. Boston: WCB/McGraw-Hill.

Ormerod, B. K. & Galea, L. A. M. 2003. Reproductive status influences the survival but not production of new cells in the dentate gyrus of adult male meadow voles. *Neuroscience Letters*, **234,** 25-28.

Ostfeld, R. S. & Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76,** 521-532.

Parker, K. J., Phillips, K. M & Lee, T. M. 2001. Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour,* **61,** 1217-1226.

Randall, J. A. 1991. Mating strategies of a nocturnal, desert rodent (*Dipodomys spectabilis*). *Behavioral Ecology and Sociobiology,* **28,** 215-220.

Randall, J. A., Hekkala, E. R., Cooper, L. D. & Barfield, J. 2002. Familiarity and flexible mating strategies of a solitary rodent, *Dipodomys ingens*. *Animal Behaviour,* **64,** 11-21.

Rau, M. E. 1983. Establishment and maintenance of behavioural dominance in male mice infected with *Trichinella spiralis*. *Parasitology,* **86,** 319-322.

Redish, A. D. 1999. *Beyond the Cognitive Map: From Place Cells to Episodic Memory.* Massachusetts: The MIT Press.

Roof, R. L. & Havens, M. D. 1992. Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Research,* **572,** 310-313.

Rose R. K. 1979. Levels of wounding in the meadow vole *Microtus pennsylvanicus. Journal of Mammalogy,* **60,** 37-45.

Salo, A. L. & Dewsbury, D. A. 1995. Three experiments on mate choice in meadow voles (*Microtus pennsylvanicus*). *Journal of Comparative Psychology,* **109,** 42-46.

Schwagmeyer, P. L. 1988. Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *American Naturalist,* **131,** 885-892.

Schwagmeyer, P. L. 1994. Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology,* **98,** 265-276.

Schwagmeyer, P. L. & Parker, G. A. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour,* **35,** 1015-1025.

Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioural Ecology Sociobiology,* **19,** 359-364.

Shapiro, L. E. & Dewsbury, D. A. 1986. Male dominance, female choice and male copulatory behavior in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). *Behavioural Ecology Sociobiology,* **18,** 267-274.

Sherman, P. W. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. *Nature*, **338,** 418-420.

Sinervo, B. 2001a. Selection in local neighborhoods, the social environment and ecology of alternative strategies. In: *Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches* (Ed. by L. A. Dugatkin), pp. 191-226, Princeton, New Jersey: Princeton University Press.

Sinervo, B. 2001b. Runaway social games, genetic cycles driven by alternative male and female strategies, and the origin of morphs. *Genetica*, **112-113,** 417-434.

Sluyter, F., van Oormerssen, G. A., de Ruiter, J. H. & Koolhaas, J. M. 1996. Aggression in wild house mice: current state of affairs. *Behavior Genetics,* **26,** 489-496.

Solomon, N. G. & Jacquot, J. J. 2002. Characteristics of resident and wandering prairie voles, Microtus ochrogaster. *Canadian Journal of Zoology*, **80,** 951-955.

Stewart, C. A. & Morris, R. G. M. 1993. The watermaze. In: *Behavioral Neuroscience: A Practical Approach.* (Ed. by Sahgal, A.), pp. 107-122. New York: Oxford University Press.

Storey, A. E. & Snow, D. T. 1990. Postimplantation pregnancy disruptions in meadow voles: relationship to variation in male sexual and aggressive behavior. *Physiology and Behavior,* **47,** 19-25.

Storey, A. E., French, R. J. & Payne, R. 1995. Sperm competition and mate guarding in meadow voles (*Microtus pennsylvanicus*). *Ethology*, **101,** 265-279.

Turner, B. N. & Iverson, S. L. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. *Ecology,* **54,** 967-981.

Turner, B. N., Iverson, S. L. & Severson, K. 1980. Effects of castration on open-field behaviour and aggression in male meadow voles (*Microtus pennsylvanicus). Canadian Journal of Zoology,* **58,** 1927-1932.

Upchurch, M. & Wehner, J. M. 1988. Differences between inbred strains of mice in Morris water maze performance. *Behavior Genetics,* **18,** 55-68.

Upchurch, M. & Wehner, J. M. 1989. Inheritance of spatial learning ability in inbred mice: a classical genetic analysis. *Behavioral Neuroscience,* **103,** 1251-1258.

Van Oortmerssen, G. A. & Busser, J. 1989. Studies in wild house mice 3: disruptive selection on aggression as a possible force of evolution. In: *House Mouse Aggression: A Model for Understanding the Evolution of Social Behaviour* (Ed.

by :P. F. Brain, D. Mainardi & S. Parmigiani), pp. 87-117, New York, Harwood Academic Publishers.

Vom Saal, F. S. 1987. Perinatal testosterone exposure has opposite effects on adult intermale aggression and infanticide in mice. In: *House Mouse Aggression: A Model for Undertsding the Evolution of Social Behaviour*. (Ed. by P. F. Brain, D. Mainardi & S. Parmigiani), pp. 179-204, New York: Hardwood Academic Publishers.

Wagner, G. C., Beuving, L. J. & Hutchinson, R. R. 1979. Androgen-dependency of aggressive target-biting and paired fighting in male mice. *Physiology & Behavior*, **22,** 43-46.

Waltz, E. C. 1982. Alternative mating tactics and the law of diminishing returns: the satellite threshold model. *Behavioural Ecology and Sociobiology*, **10,** 75-83.

Waterman, J. M. 1998. Mating tactics of male Cape ground squirrels, *Xerus inauis*: consequences of year-round breeding. *Animal Behaviour*, **56,** 459-466.

Webster, A. B. & Brooks, R. J. 1981a. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62,** 738-751.

Webster, A. B. & Brooks, R. J. 1981b. Daily movements and short activity periods of free-ranging meadow voles *Microtus pennsylvanicus*. *Oikos*, **37,** 80-87.

Williams, C. L., Barnett, A. M. & W. H. Meck. 1990. Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, **104,** 84-97.

Yamamura, N. & Tsuji, N. 1989. Postcopulatory guarding strategy in a finite mating period. *Theoretical Population Biology*, **35,** 36-50.

Zielinski, W. J. & Vandenbergh, J. G. 1993. Testosterone and competitive ability in male house mice, *Mus musculus*: laboratory and field studies. *Animal Behaviour*, **45,** 873-891.

Table 1. Pearson correlation coefficients, with associated significance levels, among the behavioral measures obtained from the water maze and body mass for all males (*N*=237).

Variable	Acquisition path length[a]	Transfer path length[a]	Retention time	Acquisition trials	Thigmotaxis[b]	Body mass
Acquisition path length	—	*r*=0.50 *P*<0.0005	*r*=-0.30 *P*<0.0005	*r*=0.53 *P*<0.0005	*r*=0.47 *P*<0.0005	*r*=-0.064 *P*=0.33
Transfer path length		—	*r*=-0.32 *P*<0.0005	*r*=0.33 *P*<0.0005	*r*=0.44 *P*<0.0005	*r*=-0.12 *P*=0.076
Retention time			—	*r*=-0.17 *P*=0.011	*r*=-0.19 *P*=0.004	*r*=-0.038 *P*=0.57
Acquisition trials				—	*r*=0.36 *P*<0.0005	*r*=0.021 *P*=0.75
Thigmotaxis					—	*r*=-0.061 *P*=0.36
Body mass						—

[a] Path lengths were log transformed for all analyses.

[b] Percentage of time thigmotactic during final block of acquisition trials.

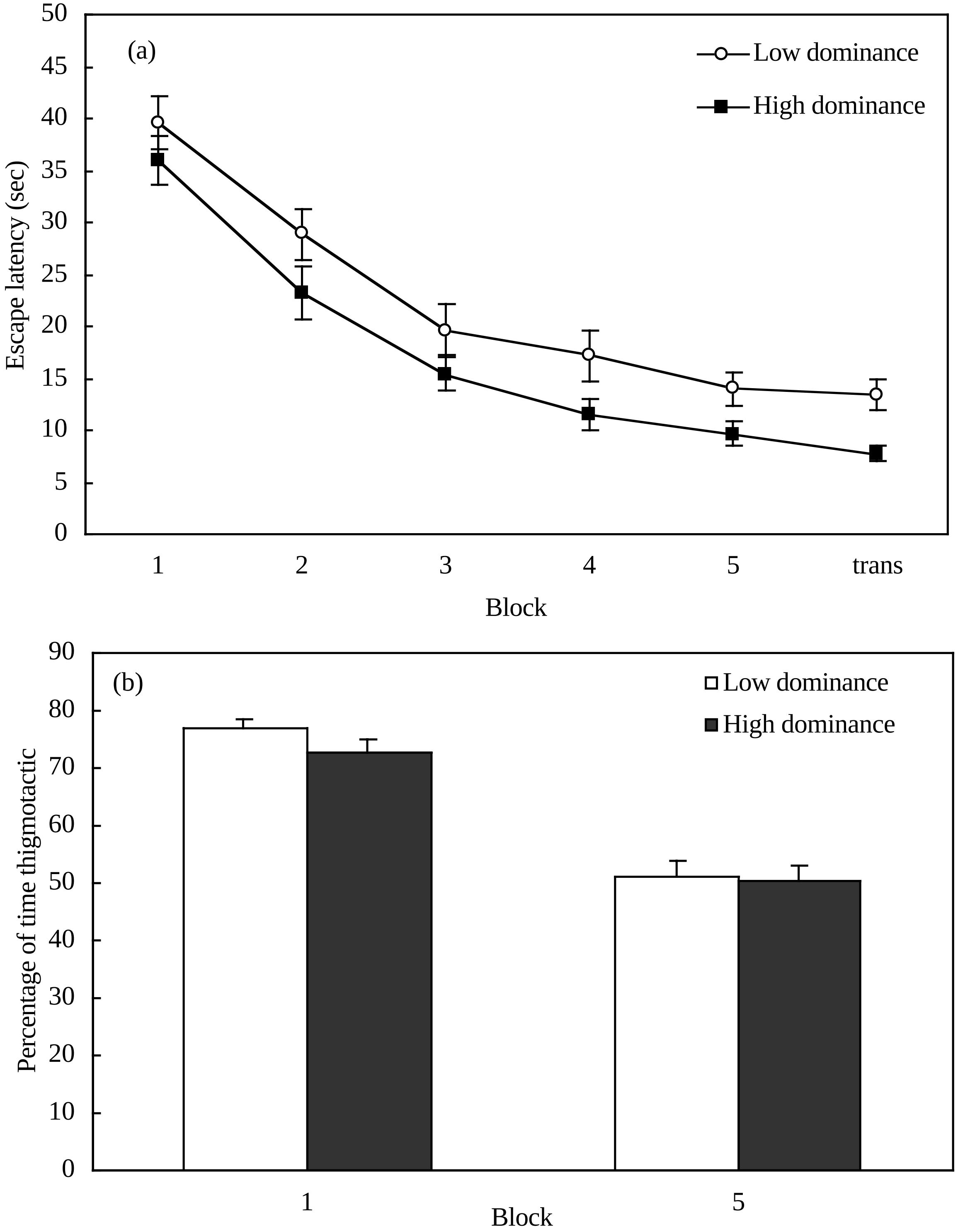


Figure 1. (a) Escape latencies over five blocks of acquisition trials and transfer trials for males with low (0-3) and high (4-7) ordinal dominance ranks. (b) Percentage of time spent thigmotactic (swimming in outer 50% of water maze) during blocks 1 and 5 of acquisition trials for males with low and high ordinal dominance ranks. All values are shown as $\overline{X}$ ±SE.

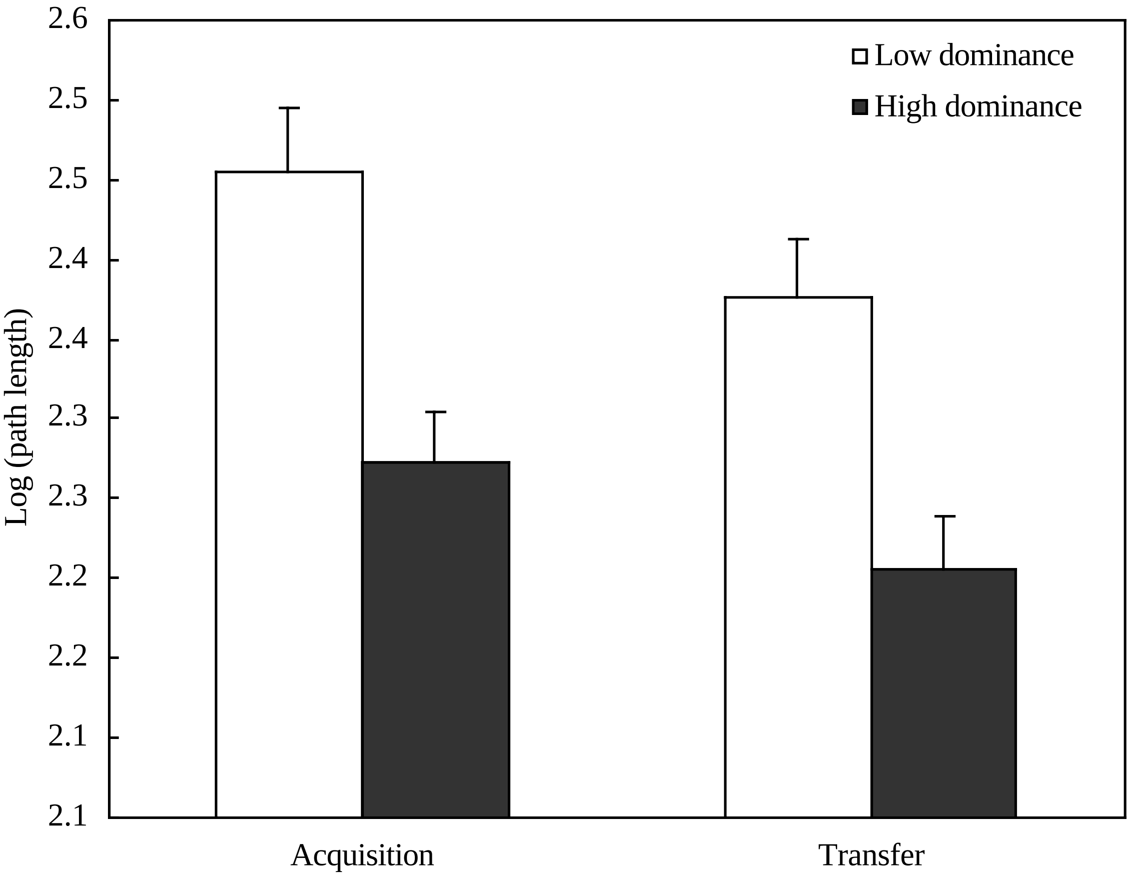


Figure 2. Comparisons ($\overline{X}$ ±SE) of voles with low (0-3) and high (4-7) ordinal dominance ranks for log transformed path lengths (cm) during block 5 of the acquisition trials and transfer trials.

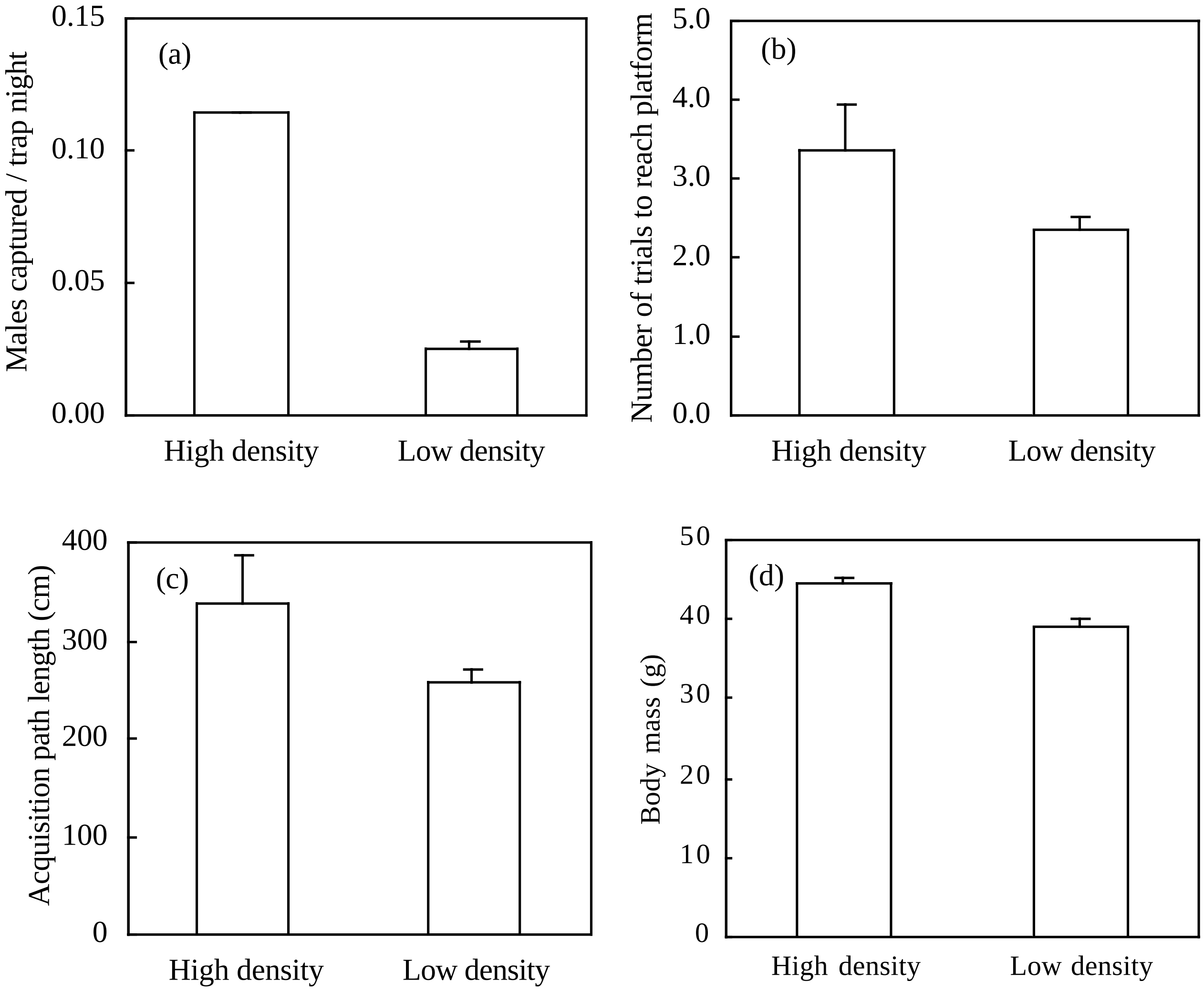


Figure 3. (a) Male population density during a period of high density (spring 2002) and the average male density for periods of relatively low density (spring 2000, spring 2001, Fall 2001, Fall 2002). The other graphs show corresponding differences in (b) number of acquisition trials needed to reach the platform, (c) path length during block 5 of the acquisition trials, and (d) body mass among male voles. All means are reported as $\overline{X}$ ±SE.

Chapter 3

RELATIVE IMPORTANCE OF MALE SPATIAL ABILITY AND DOMINANCE IN DETERMINING VISITATION TO FEMALES' NESTS AND HOME RANGE SIZE AMONG MEADOW VOLES

INTRODUCTION

One of Charles Darwin's many insights was the realization that there are multiple mechanisms by which selection can occur (Darwin 1871). Two mechanisms of intrasexual selection are contest competition and scramble competition (Andersson 1994). Contest competition involves direct aggressive interactions between males and selects for traits that improve an individual's ability to defeat opponents, such as large body size, weaponry, and threat signals. Scramble competition involves indirect competition between males and selects for traits that allow individuals to rapidly and accurately locate mates, such as improved spatial ability, mobility, and perceptual ability (Schwagmeyer 1994). Among mammals, females usually have greater parental investment than males, which leads to contest and scramble competition for access to females (Trivers 1972, Cunningham & Birkhead 1998).

Among many animals, particularly mammals, contest competition has been studied by examining dominance relationships among individuals. An individual is defined as dominant over another if it consistently wins agonistic interactions between the two individuals (Drews 1993). In many mammalian species, dominant males gain more copulations than subordinates, and there is some evidence that this leads to greater reproductive success for dominant males (Dewsbury 1982, Ellis 1995). Traits associated with dominance rank are also heritable among rodents (Dewsbury 1990; Sluyter et al. 1996; Horne & Ylönen 1998).

Spatial ability is a trait thought to be selected by scramble competition. Spatial ability is a complex trait that generally refers to the learning and memory of the position and relationship of the observer relative to environmental stimuli (Gaulin & Hoffman 1988; Allen 1999). Scramble competition has been hypothesized to favor better spatial ability by improving a male's ability to: (1) efficiently navigate between females, (2) relocate females as they become sexually receptive, and (3) avoid areas without receptive females (Gaulin & Hoffman 1988; Schwagmeyer 1994). Spatial ability is also heritable among rodents (Upchurch & Wehner 1988, 1989).

Few studies have examined the relative importance of scramble and contest competition in determining male reproductive success (Schwagmeyer & Woonter 1986; Able 1999). Meadow voles (*Microtus pennsylvanicus*) are well suited for such a study because evidence suggests that both scramble and contest competition occur in this species. Male ranges overlap those of multiple other males and multiple females, suggesting that there is the opportunity for both contest and scramble competition in the field (Madison 1980). Sexually mature males are attracted to the scent and congregate in the ranges of females in postpartum estrus (Madison 1980; Webster & Brooks 1981; Ferkin & Johnston 1995). Males seem to form stable dominance hierarchies, and inter-male aggression also peaks during the breeding season (Christian 1971; Turner & Iverson 1973; Tamarin 1977; Rose 1979; Boonstra & Rodd 1983). Males also expand their home ranges during the breeding season, presumably to search for mates (Webster & Brooks 1981; Boonstra & Rodd 1983). In contrast, females are territorial and their home ranges either remain the same size or shrink during the breeding season (Gaulin & FitzGerald 1989; Madison 1980; Madison & McShea 1987). I previously demonstrated that males with better spatial ability have larger home ranges and locate more females' nests (Chapter 1).

The first goal of this study was to determine the relative importance of spatial ability and dominance rank in determining male reproductive success. Specifically, I measured visitation to female nest boxes by males with known dominance rank and spatial ability in a field experiment similar to that described in Chapter 1. I previously demonstrated that males with better spatial ability have higher dominance rank, but this relationship was fairly weak (Chapter 2), and one of these traits may be a better predictor of male reproductive success than the other. I also found that males with better spatial ability did not achieve greater reproductive success (Chapter 1), which suggests that contest competition may be more important than scramble competition in determining male reproductive success.

The second goal of this study was to determine the relative importance of spatial ability and dominance rank in determining male range size. Among territorial species, a dominant individual might be better at deterring intruders and therefore be better able to maintain a larger home range than a subordinate. For example, Zielinski et al. (1992) found that dominant female house mice had larger home ranges than subordinates. However, male meadow voles are non-territorial, and it is less clear what role dominance would play in determining individual range size. Both levels of aggression and range size among males increase during the breeding season (Turner & Iverson 1973; Rose 1979; Gaulin & FitzGerald 1989; Boonstra et al. 1994). Ambrose (1973) found that dominant meadow voles exhibited smaller shifts in the location of their range centers, but dominants and subordinates showed no difference in range size. Similarly, two other studies found no relationship between aggression and range size among meadow voles during the breeding season (Krebs 1970; Turner and Iverson 1973). As predicted by Gaulin & FitzGerald (1986), I previously demonstrated that male meadow voles with better spatial ability have larger home ranges (Chapter 1). Therefore, I predicted that spatial ability would be a better predictor of range size than dominance rank.

I previously used a composite index to measure male spatial ability (Chapter 1). Because spatial-learning ability and spatial memory involve different neurological processes (Redish 1999; Kesner 2000; D’Hooge & De Deyn 2001; William et al. 2002), it is possible that sexual selection affects these components of spatial ability differently. Therefore, in this study, I examined spatial memory and two indices of spatial-learning ability separately for comparisons with male visitation to nests and home range sizes of males.

METHODS

Collection and Housing

Adult meadow voles were collected at Miami University’s Ecology Research Center (ERC) near Oxford, Ohio. Two batches of 40 voles were collected during October-December 2001 and April-May 2002. Voles were housed singly in clear polycarbonate cages (18 × 28 × 12 cm) at Miami University’s animal facility. The animal room was kept at 25°C on a cycle of 14 h light:10 h dark. Rodent chow (Lab Diet #5013) and water were provided ad libitum, and sunflower seeds and lettuce were provided as weekly supplements. Cotton Nestlets (Ancare, Bellmore, NY) and dried alfalfa were provided for bedding. All males were in captivity for approximately one month prior to behavioral testing. I also established a breeding colony from other animals collected at the ERC as a source of virgin females for experiments. Pups were weaned at 21 days and housed with same-sex litter-mates for an additional 20-30 days. Reproductive maturity was determined based on body mass (> 30 g) and conduction of the external genitalia: adult males had descended testes and adult females had perforate vaginas (Boonstra & Rodd 1983).

Water Maze Testing

The spatial ability of all males used in field experiments was tested using the water maze (Morris & Stewart 1993). A circular pool (70 cm diameter and 45 cm height) was filled with water to a depth of 15 cm and divided into four equal quadrants with string raised above the pool. A 7 cm diameter clear plastic platform submerged 1.5 cm below the surface was used as the goal. The water temperature averaged 20.0 °C, and the water was made opaque using non-toxic white paint. I taped three white note cards with black shapes drawn on them at evenly spaced intervals around the edge of the water maze as salient visual cues. Various objects around the room were kept in consistent locations during testing as distal visual cues. The observer stood approximately 1 m away from the site where the vole was released. Because each vole was released at four different locations around the maze, the observer was not a consistent visual cue. All trials were video recorded.

I followed a four-phase protocol (preliminary, acquisition, transfer, and retention), and the daily testing sequence of voles was randomized. All inter-trial intervals on the same day lasted 45 s, during which each vole was first dried off with a towel and then placed in a holding cage. During the preliminary phase, each male was introduced into the maze, allowed to swim for 60 s, and then placed on the platform for 15 s. Each vole was given three consecutive preliminary trials on the same day. The preliminary phase was conducted during one day in a separate room from all other testing and the note cards were not in place, so the voles were not acquiring the task during this phase.

During the acquisition phase (conducted 24 h after the preliminary phase), I recorded the time it took each vole to reach the platform (escape latency). For each vole, the platform was assigned to one of the four randomly chosen quadrants. The platform remained in the same quadrant for all trials involving a particular vole. Four possible release sites were designated at equidistant points around the pool. One release site was set aside for use during the transfer phase (see below). This site was counter-balanced such that half the voles had a release site that was closer to the platform than the other half (this was necessary because the platform was offset from the center of the pool). During the acquisition phase, I tested each vole on three consecutive trials per day for 5 blocks (days) of trials, such that each vole was introduced into the maze from the three different release sites in a random order each day. Any trial that lasted more than 60 s was terminated by placing the vole on the platform for 15 s and then removing it from the maze. Similarly, whenever a vole reached the platform, it was allowed to remain there for 15 s before ending the trial.

During the transfer phase (conducted 24 h after the last acquisition trial), I introduced each vole into the maze from the release site not used during the acquisition phase. Three consecutive trials at the same release site were conducted for each vole during this phase. Finally, during the retention phase (conducted 24 h after the transfer phase), the platform was removed from the maze and voles were released into the maze for 60 s from one of the three release sites used during acquisition trials. I recorded the time spent swimming in the quadrant where the platform had been.

My protocol resulted in three measures of spatial ability: (1) *acquisition path length* (average path length for block 5 of the acquisition trials), (2) *transfer path length* (average path length for the transfer trials), and (3) *retention time* (time spent in the target quadrant during the retention trials). Acquisition path length, and transfer path length provided different indices of spatial-learning ability, whereas retention time provided an index of spatial memory. I used both acquisition and transfer path lengths to measure spatial-learning ability because the transfer test required more complex navigational ability than did the acquisition test. Namely, performance during the acquisition trials required only learning a simple motor (praxic) response to locate the platform, whereas good performance during the transfer trials required more complex “route” or “locale” navigation (Redish 1999). Path length has been commonly used in past studies to assess spatial-learning ability, and retention time is a common measure of spatial memory (D’Hooge & De Deyn 2001).

I also measured the amount of time voles spent in the outer 50% of the water maze (within 10 cm of edge) to determine the percentage of time each male spent thigmotactic during blocks 1 and 5 of the acquisition trials. Past studies have suggested that high levels of thigmotaxis are indicative of high anxiety and/or low behavioral flexibility (Pleskacheva et al. 2000; Vyssotski et al. 2002).

Dominance Testing

Relative spatial ability was determined by ranking the males for each of the three measures of spatial ability and then determining a composite index of spatial ability (Chapter 1) based on the average of these ranks: (acquisition rank + transfer rank + retention rank) / 3. Males from the two collection batches were assigned to one of the four groups such that the variance in the spatial ability scores was high within each group. Specifically, the four males with the highest spatial ability scores were first assigned at random to each of four groups, then the four males with the lowest spatial ability scores were assigned at random to those four groups. This procedure was repeated until each of the four groups contained eight males. The eight males with relatively average spatial ability were not used for further experimentation. I conducted pairwise dominance trials among all males within a group of eight but not between groups. Thus, dominance data were collected for four groups of eight males from each of two batches of voles (64 males total).

I tested male dominance following methods similar to those used in past studies (Huck & Banks 1982; Shapiro & Dewsbury 1986; Harper & Batzli 1997). All tests were conducted indoors during the light part of the cycle in a circular Plexiglas arena (50 cm high, 60 cm diameter). A removable opaque partition was placed across the center of the arena at the start of each trial, and the voles were placed on either side of the partition for a 5 min habituation period. The tip of each male’s tail was marked with fluorescent powder for identification during trials (color was alternated for consecutive trials with each pair). I collected data from behind an opaque plastic sheet with a small opening for observation. I recorded the frequency of aggressive interactions during 15 min trials using all-occurrence sampling. The behaviors recorded were: threat, lunge, chase, box, and wrestle (Colvin 1973; Turner & Iverson 1973). "Chase" included cases in which one vole rapidly pursued the other as well as displacement behavior in which the aggressor moved toward a stationary vole causing it to retreat while the aggressor acquired the position of the retreating vole. I recorded threat behavior (rearing on hind-legs) only if the recipient responded by retreating or showing a submissive posture. This was done to avoid recording behaviors not clearly associated with the establishment of dominance. Because severe wounding never occurred, none of the trials had to be interrupted. A male was considered dominant if he exhibited more aggression towards his opponent than vice versa. Each pair was tested on repeated trials until the same individual was dominant in two trials. After testing, each vole was given an ordinal dominance rank (0-7) based on the number of other individuals he dominated. I also used average number of attacks per arena trial to measure relative male aggression.

Field Experiment

I conducted a field experiment from July-October, 2002 at the ERC following methods similar to those described in Chapter 1. The experiment was conducted in eight 32 × 32 m enclosures with 60 cm high, galvanized steel walls (Appendix 1). The size of the enclosures was chosen such that each enclosure was approximately as large as four female home ranges (Ostfeld et al. 1988; Jacquot 1999). A 1 m strip immediately inside and outside the enclosures was sprayed with herbicide and cleared of vegetation prior to starting the experiment. All eight enclosures were surrounded by an electric fence to prevent entry by terrestrial predators. I set up a 5 × 5 grid of Sherman live traps spaced at 5 m intervals and removed all small mammals from enclosures prior to starting the experiment. All voles used in the field experiment were lightly anesthetized with Isoflorane and injected with a passive integrated transponder (AVID, Norco, CA) for identification prior to release into the field enclosures.

Four lab-reared (F1 or F2) virgin females were used for each enclosure. The females were not closely related to each other or the males. To control the distribution of females and determine male visitation to female nests, each female was housed in a nest box. Each wooden box (40 × 40 × 10 cm) had a one-way door that allowed males to enter and mate but prevented voles from leaving. Within each enclosure, four nest boxes with females were arranged in a square (25 × 25 m) such that each box was near a corner of the enclosure (7.5 m from edge). Each box was supplied ad libitum with water and the same rodent chow that voles received in the lab as well as alfalfa for bedding.

One day after the nest boxes with females were placed in the enclosures, I released four males into each enclosure. The males for each enclosure were taken from the groups of 8 males used for dominance testing, and I assigned voles to enclosures such that the variance in both dominance rank and spatial ability was high within each enclosure. At this time, the doors to the nest boxes were blocked to prevent male entry. Following a four-day acclimation period, I trapped for eight days to obtain home range data and determine male survivorship. A second release was conducted to replace males that had disappeared, followed by another 4 days of acclimation and 8 days of trapping.

After the second release, only one male survived in one of the enclosures, and the experiment was discontinued for that enclosure. The final number of males within each of the other enclosures varied somewhat ($\overline{X}$ ±SE=3.6±0.8, range=3-5). Vole densities within the enclosures ($\overline{X}$ ±SE=84.4±8.9 ha^{-1}) were equivalent to that of a natural population during the increasing or declining phase of the population cycle (Krebs 1970; Ostfeld & Canham 1995). I unblocked the doors to the nest boxes in early August. Trapping was continued within enclosures two nights per week throughout the experiment to monitor male survivorship and to update male home range locations on a weekly basis. The experiment lasted for 56 days after the very first male entered a nest box.

To minimize the possibility that males were entering boxes to obtain food rather than mates, I planted the enclosures with clover and seven feeding stations were evenly distributed between nest boxes and replenished with rodent chow regularly. I also trained males to enter nest boxes in the laboratory prior to releasing them into enclosures to minimize individual differences in the propensity to enter nest boxes. All males used in the field experiment had entered a nest box containing a female twice during one-hour training trials.

Each nest box was checked twice daily, approximately one hour after dawn and one hour before dusk, for the presence of males. Each male found in a box was identified and released at a random grid point within his home range. I checked the females once per week for pregnancy by palpation and brought pregnant females back to the animal housing facility to rear pups. I replaced pregnant females 1-2 days prior to parturition with another lab-reared virgin female to avoid infanticide by males (Storey et al. 1994).

Statistical Analysis

For the males used in the field experiment, repeated measures ANOVA was used to test changes in escape latency (time to reach the platform) over the five blocks of acquisition trials and the transfer trials. A paired *t* test was used to compare the percentage of time thigmotactic during block 1 and block 5 of the acquisition trials.

All of the measures obtained from the water maze and paired arena trials were considered as predictor variables for nest box visitation. Two measures of visitation were analyzed: total number of nest box visits, and number of visits to each male's most frequently visited nest box. I did not analyze the number of different nest boxes visited because 56% of males visited all four nest boxes within their enclosures, creating low variability for this measure. Analysis of covariance (ANCOVA) was used to compare the predictor variables to nest-box visitation, with enclosure as a random factor. Acquisition path length, transfer path length, and retention time were all analyzed in the same model because they each measured components of spatial ability, whereas thigmotaxis, dominance rank, and average attacks per trial were analyzed individually. I chose to analyze thigmotaxis separately from the other water-maze variables because thigmotaxis is generally interpreted as an index of anxiety rather than spatial ability, and it makes interpretation of partial regression coefficients difficult because it is correlated with the other water-maze variables (Chapter 2).

For males that visited all four boxes within their enclosures, I analyzed the relationship between percentage of visits to the most frequently visited nest box and each of the predictor variables. For these analyses, I compiled data from the enclosures and used linear regressions rather than ANCOVA due to low sample size (N=14). I expected males with better spatial ability to make fewer visits to any one nest box.

Home range data were complied and analyzed using Ranges V (Kenward & Hodder 1996). Some of the standard measures of range size (i.e., convex polygons, maximum range length) were strongly correlated with the number of captures, complicating further analyses (Stickel 1954). However, average distance from each capture site to the geometric range center (Slade & Russel 1998) was not correlated with number of captures when only males with at least 5 captures were considered (Simple linear regression: r^2=0.049, $F_{1,20}$=1.02, P=0.32). Initially, I analyzed the spatial ability and dominance rank data separately using ANCOVA. Because both the spatial ability variables and dominance rank proved to be significant predictors of range size, I conducted another ANCOVA that included the spatial ability variables and dominance rank as covariates to tease apart the relative importance of these variables in predicting range size.

All path length and escape latency data were log transformed to meet analysis assumptions (Neter et al. 1996). I report standardized partial regression coefficients (β) for each covariate used with ANCOVA (Neter et al. 1996). All analyses were conducted using SPSS 11.0. A significance level of α=0.05 was used for all tests, and all data are presented as $\overline{X}\pm$SE.

Ethical Note

Spatial ability was measured using the Morris water maze, which involved exposing voles to an aversive stimulus, cold water. I attempted to minimize the amount of stress that voles experienced by limiting trials to a maximum of 60 s and drying voles after each trial. The water maze has been previously used extensively with meadow voles (e.g., Galea et al. 1995; Kavaliers et al. 1993), and meadow voles are also excellent swimmers (Dagg & Windsor 1972). The dominance trials also exposed males to potential injury, but no cases of noticeable wounding occurred. Similar methods have been used successfully in previous studies involving meadow voles (e.g., Colvin 1973; Turner & Iverson 1973).

RESULTS

Escape latencies differed among the five blocks of acquisition trials (Fig. 1; Repeated Measures ANOVA: $F_{5,20}=29.38$, $P<0.0005$), with significant differences among all blocks (all $P < 0.02$) except blocks 4, 5, and the transfer trials. Voles also exhibited a significant difference in the percentage of time thigmotactic between blocks 1 and 5 (block 1: 72.0±2.9; block 5: 50.7±2.6; Paired *t* test: $t_{24}=7.37$, $P<0.0005$).

Nest Box Visitation

The first male entered a nest box on the first day that the nest boxes were opened. During the 3584 box checks (2 checks/day × 56 days × 32 boxes) conducted, 1016 instances of male visitation to nest boxes occurred. Three males never entered a nest box. Five males disappeared prior to the end of the experiment, but they were all present within the enclosures for about half of the experiment (32.6±8.0 days). Therefore, all males had sufficient time to visit nest boxes and no males were excluded from data analyses.

Spatial ability was a good predictor of the total number of nest box visits (Table 1). Acquisition path length was negatively correlated with total number of nest box visits, indicating that males with better spatial-learning ability visited more nest boxes. Similarly, males with better spatial memory (retention time) visited more nest boxes. In contrast, transfer path length was positively correlated with total number of nest box visits, indicating that males that were better at learning this relatively complex spatial task visited fewer nest boxes. Total number of nest box visits was unrelated to percentage of time thigmotactic during the final block of acquisition trials (ANCOVA: β=-0.26, $F_{1,17}$=1.40, P=0.25).

Number of visits to the most frequently visited nest box showed results similar to those obtained for total number of visits to nest boxes (Table 1). Males that made more visits to their most frequently visited nest boxes also had better spatial memory and better spatial-learning ability, as measured by acquisition path length. In contrast, males that performed better in the transfer task made fewer visits to their most frequently visited nest boxes. Number of visits to the most frequently visited nest box was unrelated to the percentage of time thigmotactic during the final block of acquisition trials (ANCOVA: β=-0.18, $F_{1,17}$=0.49, P=0.50).

In contrast to the spatial ability variables, dominance rank was not correlated with total number of nest box visits (ANCOVA: β=-0.23, $F_{1,17}$=1.39, P=0.26). Average number of attacks per trial was also not correlated with total number of nest box visits (ANCOVA: β=0.0062, $F_{1,17}$=0.70, P=0.79). Number of visits to the most frequently visited nest box was also not correlated with dominance rank (ANCOVA: β=-0.14,

$F_{1,17}$=0.36, P=0.56) or average number of attacks per trial (ANCOVA: β=0.10, $F_{1,17}$=0.15, P=0.70).

Fourteen males (56%) visited all four nest boxes within their enclosures and only three males (12%) did not visit any nest boxes. Considering only males that visited all four nest boxes within their enclosures, the percentage of visits to the most frequently visited nest box was positively correlated with transfer path length (Fig. 2; R^2=0.29, $F_{1,12}$=4.81, P=0.049). This indicates that males that performed poorly during the transfer trials were likely to visit the same nest box repeatedly. In contrast, the other spatial ability variables, thigmotaxis, dominance rank, and average attacks per trial were not correlated with percentage of visits to the most frequently visited nest box (Simple linear regressions: all P>0.20). A multiple regression with all three spatial ability variables was also not significant (Multiple regression: R^2=0.32, $F_{3,10}$=1.58, P=0.26).

Home Range Size

Males' home range sizes were significantly correlated with transfer performance and spatial memory but not with acquisition performance (Table 2). Males with better spatial-learning ability, as measured by the transfer task, had larger home ranges. In contrast, males with better spatial memory had smaller home ranges. Average distance to range center was not correlated with the percentage of time thigmotactic during the final block of acquisition trials (ANCOVA: β=-0.35, $F_{1,14}$=2.97, P=0.11).

Males with higher dominance ranks had significantly greater average distances to their range centers (ANCOVA: β=0.48, $F_{1,14}$=7.56, P=0.016). However, dominance rank was not a significant predictor of range size independent of its correlated effects with spatial ability (Table 2). This means that the significant correlation between dominance rank and range size was primarily due to the fact that dominance rank was correlated with spatial-learning ability and spatial memory. In contrast, transfer path length remained significantly correlated with range size independent of correlated effects with dominance rank (Table 2). Retention time remained only marginally significant when analyzed in combination with dominance rank (Table 2). Average distance to range center was not correlated with the average number of attacks per trial (ANCOVA: $\beta=0.43$, $F_{1,14}=2.90$, $P=0.11$).

DISCUSSION

Nest Box Visitation

Spatial ability was a better predictor of visitation to females' nests by males than was dominance rank or aggression. Dominance rank and relative aggression of males were not related to the total number of nest box visits or number of visits to each male's most frequently visited nest box. Males with better spatial-learning ability (acquisition), and better spatial memory (retention) made more visits to nest boxes overall and made more visits to their most frequently visited nest boxes. Hence, the acquisition and retention data are consistent with my previous finding that males with better spatial ability visit more females' nests (Chapter 1). Males with better spatial-learning ability were probably better at learning the location of nests and males with better spatial memory were probably better at relocating nests. I also previously found that males that visited a particular female more frequently obtained a reproductive advantage (Chapter 1).

I previously found that male meadow voles with good spatial ability did not achieve greater reproductive success than males with poor spatial ability (Chapter 1). One explanation for this finding was that some males with high dominance rank were preventing males with high spatial ability and relatively low dominance rank from mating by either actively chasing them away or inhibiting them with scent marks (Turner & Iverson 1973; Boonstra & Rodd 1983; Johnston et al. 1997; Luque-Larena et al. 2001). My current results suggest that this explanation is unlikely because males with higher dominance rank did not make more visits to their most frequently visited nest boxes. Although I cannot eliminate the possibility that males were aggressively deterring rivals outside the nest boxes, it appears that contest competition was not counter-acting the benefits gained through scramble competition. Therefore, other explanations are needed to explain the fact that males with better spatial ability do not seem to achieve greater reproductive success (Chapter 1). Females may preferentially mate with males based on traits that are not related to spatial ability. One possible trait is major-histocompatability complex (MHC) phenotypes, which females can detect using olfactory cues from males' urine (Plante et al. 1991; Penn & Potts 1999).

In laboratory experiments involving competitive mating trials with meadow voles, Storey et al. (1995) found that dominant males tended to engage in post-copulatory mate guarding which resulted in higher reproductive success than that achieved by subordinate males. Therefore, I was surprised to find that males that were more aggressive or that had higher dominance ranks did not make more visits to their most frequently visited nest box. This result may be due in part to the fact that males with higher dominance rank tend to also perform better at the transfer task (Chapter 2), and transfer task performance was negatively correlated with rates of visitation to nest boxes. However, I did not observe a negative relationship between dominance rank and nest box visitation. Therefore, males with high dominance ranks may have been engaging in a combination of mate-guarding and mate-searching strategies, which led to no relationship between dominance rank and nest box visitation.

Although each of my three measures of spatial ability was predictive of the total number of nests visited, the correlations were not all in the same direction. In particular, my two measures of spatial-learning ability provided contradictory results: males that performed better at the acquisition task visited more nest boxes, whereas males that performed better at the transfer task visited fewer nest boxes. The differences between these results may be because the transfer task requires more complex navigational ability than does the acquisition task. The acquisition task requires only “praxic” navigation, whereas the transfer task requires “route” or “locale” navigation (Redish 1999). Praxic navigation involves learning a constant motor response to locate the platform. Although voles using praxic navigation could efficiently learn the location of the hidden platform over the five blocks of acquisition trials, their ability to locate the platform would be disrupted by release at a new starting point during the transfer task. In contrast, route navigation involves learning a series of subgoals in which each direction becomes associated with a particular sensory view. Finally, locale navigation involves learning the location of a point relative to a constellation of spatial cues and involves the formation of a cognitive map (O’Keefe & Nadel 1978; Redish 1999). For males using route or locale navigation, release at a novel starting location during the transfer task would be unlikely to disrupt their ability to locate the platform. Therefore, my results suggest that males using praxic navigation visit more nest boxes, whereas males using more complex modes of navigation visit fewer nest boxes. Perhaps praxic navigation is all that males need to relocate nest boxes. This idea is supported by the fact that voles build discrete runways between nesting sights, which are likely to simplify navigation between points within a male's home range (Wolff 1985; Harper & Batzli 1996).

It remains unclear, however, why males that were better at more complex modes of navigation visited fewer nest boxes. Males with good performance at the transfer task may have been searching more extensively for mates, leaving them with less time for repeat visits to the same nest box. I previously demonstrated that as males visit more nests, they devote fewer visits to any one nest (Chapter 1). Thus, males that performed well at the transfer task may have engaged in a mate-searching strategy, while the males that performed well at the acquisition task may have engaged in a mate-guarding strategy (Van Oormerssen, & Busser 1989; Storey et al. 1995; Bauer et al. 2001). In support of this idea, males that performed well at the transfer task made fewer visits to their most frequently visited nest boxes, suggesting they were less likely to guard their mates. There is also considerable neuroanatomical evidence that different types of navigation involve different parts of the brain (Jarrad 1993; McDonald & White 1993; Redish 1999; Kesner 2000; D'Hooge & De Deyn 2001). Interestingly, rats with hippocampal lesions cannot learn spatial tasks but are better able to learn reinforced stimulus-response associations, suggesting a trade-off between spatial learning and appetitive learning (McDonald & White 1993). This may explain why males that performed well at the transfer task did not repeatedly visit the same female since such behavior is likely to involve appetitive learning. Thus, males that were better at more complex modes of navigation, and possibly having associated neurological differences, seem to devote more time to searching for new females rather than repeatedly visiting the same female.

I previously found that males that were more thigmotactic visited fewer females' nests, which suggested that males with higher levels of anxiety were poorer at locating nests (Chapter 1). In the current study, thigmotaxis was not related to nest visitation. This discrepancy may be because thigmotaxis seems to be indicative of multiple behavioral traits. Thigmotaxis may be indicative of high levels of anxiety (Champagne et al. 2002) or poor spatial-learning ability (Lipp & Wolfer 1998), both of which would be expected to lead to reduced rates of nest visitation. Alternatively, thigmotaxis might be indicative of low levels of behavioral flexibility (Vyssotski et al. 2002) and therefore associated with the tendency to visit the same nest box repeatedly. Given these three different interpretations of thigmotactic behavior, its utility as a behavioral assay seems limited.

Home Range Size

The only variable measured that was positively correlated with range size was one of the measures of spatial learning ability (transfer path length). Although males with higher dominance rank did have larger home ranges, this seems to have been because males with higher dominance rank also tend to have better spatial-learning ability. In contrast, males that performed better during the transfer phase had larger home ranges independent of correlations with dominance rank. The other measure of spatial-learning ability (acquisition path length) was not a significant predictor of range size. Interestingly, males with better spatial memory tended to have smaller home ranges.

These results lend support to the hypothesis that spatial-learning ability is selected through scramble competition for mates (Gaulin & FitzGerald 1986; Chapter 1). The larger ranges of males with better spatial-learning ability seems to lead to more encounters with more different females (Chapter 1). In contrast, males with poor spatial-learning ability may gain higher reproductive success by concentrating their ranging behavior near a single female rather than expanding their ranges in search of more females. I previously found that males that visited a particular female more frequently were more likely to successfully reproduce with that female (Chapter 1). Therefore, males may optimize their rates of visitation to females' nests based on their spatial ability.

My finding that males with higher dominance rank also have larger home ranges is supported by other studies that have shown that increased male range size during the breeding season coincides with increased levels of male aggression (Turner & Iverson 1973; Rose 1979; Gaulin & FitzGerald 1989; Boonstra et al. 1994). However, two studies found no relationship between aggression and range size among meadow voles (Krebs 1970; Turner & Iverson 1973). This discrepancy may be due to the fact that my study used an ordinal dominance rank while the two previous studies developed a composite index of aggression. Although a relatively coarse index, ordinal dominance rank may be a more accurate measure of individual differences than indices that assign weight to different aggressive behaviors without a biological reason to do so (Drews 1993). It should also be noted that I found no significant relationship between average number of attacks per trial and home range size, illustrating that dominance rank and aggression are not exactly the same behavioral traits.

Males with higher dominance rank did not, however, have larger ranges independent of the correlations between the spatial ability variables and dominance rank. Males with higher dominance rank have better spatial-learning ability, but not better spatial memory (Chapter 2). This suggests that traits associated with high dominance rank could be selected as a correlated effect of selection favoring good spatial-learning ability. However, I did not find that dominant males made more nest box visits than subordinates, suggesting that dominant males were not benefiting from increased range size. Presumably, this is because dominance rank and spatial ability are only weakly correlated among meadow voles (Chapter 2). Although both spatial ability and dominance rank have been shown to be heritable (Upchurch & Wehner 1988, 1989; Dewsbury 1990; Sluyter et al. 1996; Horne & Ylönen 1998), the quantitative genetics of spatial ability and dominance rank should be examined further to determine how selection might act upon these traits simultaneously. The physiological link between dominance and spatial ability is likely to involve the influence of testosterone upon the brain (Turner et al. 1980; Williams et al. 1990; Zielinski & Vandenbergh 1993; Sluyter et al. 1996; Galea & McEwen 1999; Galea et al. 1999).

These results refine my previous finding that males with better spatial ability, as measured by a composite index, had larger home ranges (Chapter 1). As with nest-box visitation, the different measures of spatial ability showed different relationships with range size, and this may be indicative of the modes of navigation employed by meadow voles during their natural ranging behavior (Redish 1999). The fact that acquisition path length was not correlated with range size supports my previous contention that simple praxic navigation may not be used by meadow voles that are ranging widely. Males with better performance during the transfer phase had larger home ranges, suggesting that the more complex navigational abilities of these males allowed them to range more widely. Finally, males with better spatial memory may have had smaller home ranges because they were repeatedly visiting the same female. Perhaps males with good spatial memory were better able to remember and relocate a nest box after being released at a random point within their home ranges. Males with poor spatial memory may have roamed at random after being released from a nest box, resulting in a larger home range. These results highlight the fact that spatial ability is a complex trait and that not all measures obtained from the Morris water maze are measuring the same neurological processes (Allen 1999; D’Hooge & De Deyn 2001).

In summary, my results showed that some measures of spatial ability were better predictors of frequency of male visitation to female nests, and presumably reproductive success, than was dominance rank. This suggests that among meadow voles scramble competition for mates is a more important selective pressure than contest competition for mates. I also found an apparent trade-off between increased range size and the frequency visitation to any one female’s nest. My results further suggest that males that are better at more complex modes of navigation are more likely to engage in a mate-searching strategy, whereas males with good praxic navigational ability and good spatial memory are more likely to engage in a mate-guarding strategy.

REFERENCES

Able, D. J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioural Ecology and Socioibiology,* **46,** 423-428.

Allen, G. L. 1999. Spatial abilities, cognitive maps, and wayfinding. In: *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes* (Ed. by R. G. Golledge), pp. 46-80. Baltimore, Maryland: The Johns Hopkins University Press.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Ambrose, H. W. 1973. An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus*. *Journal of Mammalogy,* **54,** 79-110.

Bauer, R. T. & Abdalla, J. H. 2001. Male mating tactics in the shrimp *Palaemonetes pugio* (Decapoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology,* **107,** 185-199.

Bernasconi-Guastalla, S., Wolfer, D. P. & Lipp, H.-P. 1994. Hippocampal mossy fibers and swimming navigation in mice: correlations with size and left-right asymmetries. *Hippocampus,* **4,** 53-64.

Berteaux, D., Dety, J. & Rengifo, J. B. 1999. Multiple paternity in meadow voles (*Microtus pennsylvanicus*): investigating the role of the female. *Behavioural Ecology and Sociobiology,* **45,** 283-291.

Boonstra, R. & Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology,* **52,** 757-780.

Boonstra, R., Hochachka, W. M. & Pavone, L. 1994. Heterozygosity, aggression, and population fluctuations in meadow voles (*Microtus pennsylvanicus*). *Evolution,* **48,** 1350-1363.

Brockmann, H. J. 2001. The evolution of alternative strategies and tactics. *Advances in the Study of Behavior,* **30,** 1-51

Christian, J. J. 1971. Fighting, maturity, and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy,* **52,** 556-567.

Colvin, D. V. 1973. Agonistic behaviour in male of five species of voles *Microtus*. *Animal Behaviour,* **21,** 471-480.

Conrad, C. D., Galea, L. A., Kuroda, Y. & McEwen, B. S. 1996. Chronic stress impairs rat spatial memory on the Y maze, and the effect is blocked by tianeptine pretreatment. *Behavioral Neuroscience,* **110,** 1321-1334.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour*, **56,** 1311-1321.

Dagg, A. I. & Windsor, D. E. 1972. Swimming in northern terrestrial mammals. *Canadian Journal of Zoology,* **50,** 117-130.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex.* Princeton, New Jersey: Princeton University Press.

Dewsbury, D. A. 1990. Fathers and sons: genetic factors and social dominance in deer mice, *Peromyscus maniculatus*. *Animal Behaviour,* **5,** 59-66.

Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Quarterly Review of Biology*, **57,** 135-159.

Dewsbury, D. A. 1983. A comparative study of rodent social behavior in a seminatural enclosure. *Aggressive Behavior,* **9,** 207-215.

D'Hooge, R. & De Deyn, P. P. 2001. Applications of the Morris water maze in the study of learning and memory. *Brain Research Reviews,* **36,** 60-90.

Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour,* **125,** 283-313.

Drickamer, L. C., Vandenbergh, J. G. & Colby, D. R. 1973. Predictors of dominance in male golden hamster (*Mesocricetus auratus*). *Animal Behaviour,* **21,** 557-563.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Etholology and Sociobiology,* **16,** 257-333.

Ferkin, M. H. & Johnston, R. E. 1995. Effects of pregnancy, lactation and postpartum oestrus on odour signals and the attraction to odours in female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour,* **49,** 1211-1217.

Galea, L.A.M., Kavaliers, M., Ossenkopp, K.-P. & Hampson, E. 1995. Gonadal hormone levels and spatial learning performance in the Morris water maze in male and female meadow voles, *Microtus pennsylvanicus*. *Hormones and Behavior* **, 29,** 106-125.

Galea, L. A. M., McEwen, B. S., 1999. Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience,* **89,** 955-964.

Galea, L.A.M., Perrot-Sinal, T.S., Kavaliers, M., Ossenkopp, K.-P. 1999. Relations of hippocampal volume and dentate gyrus width to gonadal hormone levels in male and female meadow voles. *Brain Research,* **821,** 383-391.

Gaulin, S. J. C. & FitzGerald, R. W. 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *American Naturalist,* **127,** 74-88.

Gaulin, S. J. C. & FitzGerald, R. W. 1988. Home-range size as a predictor of mating systems in *Microtus*. *Journal of Mammalogy*, **69,** 311-319.

Gaulin, S. J. C. & FitzGerald, R. W. 1989. Sexual selection for spatial-learning ability. *Animal Behaviour,* **37,** 322-331.

Gaulin, S. J. C. & Hoffman, H. A. 1988. Evolution and development of sex differences in spatial ability. In: *Human Reproductive: a Darwinian Perspective* (Ed. by L. Betzig, M. B. Mulder, & P. Turke), pp. 7-152. New York: Cambridge University Press.

Gross, M. R. 1996. Alternative reproductive strategies and tactics: diversity within the sexes. *Trends in Ecology and Evolution*, **11,** 92-98.

Harper, S. J. & Batzli, G. O. 1997. Are staged dyadic encounters useful for studying aggressive behaviour of arvicoline rodents? *Canadian Journal Zoology,* **75,** 1051-1058.

Horne, T. J. & Ylönen, H. Heritabilities of dominance-related traits in male bank voles (*Clethrionomys glareolus*). *Evolution*, **52,** 894-899.

Huck, U. W. & Banks, E. M. 1982. Male dominance status, female choice and mating success in the brown lemming, *Lemmus trimucronatus*. *Animal Behaviour,* **30,** 665-675.

Huck, U. W., Banks, E. M. & Wang, S.-C. 1986. Behavioral and physiological correlates of aggressive dominance in male brown lemmings (*Lemmus sibiricus*). *Aggressive Behavior*, **12,** 139-148.

Jacobs, L. F., Gaulin, S. J., Sherry, D. F. & Hoffman, G. E. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Science USA,* **87,** 6349-6352.

Jarrard, L. E. 1993. On the role of the hippocampus in learning and memory in the rat. *Behavioral and Neural Biology,* **60,** 9-26.

Joseph, R. 1979. Effects of rearing and sex on maze learning and competitive exploration in rats. *The Journal of Psychology,* **101,** 37-43.

Kavaliers, M. & Colwell, D. D. 1995. Reduced spatial learning in mice infected with the nematode, *Heligmosomoides polygyrus*. *Parasitology*, **110,** 591-597.

Kavaliers, M., Eckel, L. A. & Ossenkopp, K.-P. 1993. Brief exposure to 60 Hz magnetic fields improves sexually dimorphic spatial learning performance in meadow vole, *Microtus pennsylvanicus*. *Journal of Comparative Physiology*, **173,** 241-248.

Kavaliers, M., Colwell, D. D. & Galea, L. A. M. 1995. Parasite infection impairs spatial learning in mice. *Animal Behaviour,* **50,** 223-229.

Kesner, R. P. 2000. Behavioral analysis of the contribution of the hippocampus and parietal cortex to the processing of information: interactions and dissociations. *Hippocampus,* **10,** 483-490.

Krebs, C. J. 1970. *Microtus* population biology: behavioral changes associated with the population cycle in *M. ochrogaster* and *M. pennsylvanicus*. *Ecology,* **51,** 34-52.

Lipp, H.-P. & Wolfer, D. P. 1998. Genetically modified mice and cognition. *Current Opinions in Neurobiology,* **8,** 272-280.

Luque-Larena, J. J., López, P., Gosálbez, J. 2001. Scent matching modulates space use and agonistic behaviour between male snow voles, *Chionomys nivalis*. *Animal Behaviour,* **62,** 1089-1095.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioural Ecology Sociobiology*, **7,** 65-71.

Madison, D. M. & McShea, W. J. 1987. Seasonal changes in reproductive tolerance, spacing, and social organization in meadow voles: a microtine model. *American Zoologist*, **27,** 899-908.

McDonald, R. J. & White, N. M. 1993. A triple dissociation of memory systems: hippocampus, amygdala, and dorsal striatum. *Behavioral Neuroscience*, **107,** 3-22.

Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution,* **52,** 8-18.

Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. 1996. *Applied Linear Statistical Models.* 4th edn. Boston: WCB/McGraw-Hill.

Nyborg, H. 1983. Spatial ability in men and women: review and new theory. *Advances in Behavior Research and Theory,* **5,** 89-140.

O'Keefe, J. & Nadel, L. 1978. *The Hippocampus as a Cognitive Map.* Oxford: Oxford University Press.

Olton, D. S. 1982. Spatially organized behaviors of animals: behavioral and neurological studies. In: *Spatial Abilities: Development and Physiological Foundations* (Ed. by M. Potegal), pp. 335-361, New York: Academic Press.

Ostfeld, R. S. & Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76,** 521-532.

Plante, Y., Boag, P. T., White, B. N. & Boonstra, R. 1991. Highly polymorphic genetic markers in meadow voles (Microtus pennsylvanicus) revealed by a murine major histocompatibility complex (MHC) probe. *Canadian Journal of Zoology*, **69,** 213-220.

Penn, D. J. & Potts, W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist*, **153,** 145-164.

Rau, M. E. 1983. Establishment and maintenance of behavioural dominance in male mice infected with *Trichinella spiralis*. *Parasitology*, **86,** 319-322.

Redish, A. D. 1999. *Beyond the Cognitive Map: From Place Cells to Episodic Memory.* Massachusetts: The MIT Press.

Rose R. K. 1979. Levels of wounding in the meadow vole *Microtus pennsylvanicus. Journal of Mammalogy*, **60,**37-45.

Schwagmeyer, P. L. 1988. Scramble-competition polygyny in an asocial mammal: male mobility and mating success. *American Naturalist*, **131,** 885-892.

Schwagmeyer, P. L. 1994. Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology*, **98,** 265-276.

Schwagmeyer, P. L. & Parker, G. A. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour,* **35,** 1015-1025.

Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioural Ecology and Sociobiology*, **19,** 359-364.

Shapiro, L. E. & Dewsbury, D. A. 1986. Male dominance, female choice and male copulatory behavior in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). *Behavioural Ecology Sociobiology*, **18,** 267-274.

Sinervo, B. 2001. Selection in local neighborhoods, the social environment and ecology of alternative strategies. In: *Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches* (Ed. by L. A. Dugatkin), pp. 191-226, Princeton, New Jersey: Princeton University Press.

Slade, N. A. & Russel, L. A. 1998. Distances as indices to movements and home-range szie from trapping records of small mammals. *Journal of Mammalogy*, **79,** 346-351.

Sluyter, F., van Oormerssen, G. A., de Ruiter, J. H. & Koolhaas, J. M. 1996. Aggression in wild house mice: current state of affairs. *Behavior Genetics*, **26,** 489-496.

Stickel, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy*, **35,** 1-15.

Stewart, C. A. & Morris, R. G. M. 1993. The watermaze. In: *Behavioral Neuroscience: A Practical Approach.* (Ed. by Sahgal, A.), pp. 107-122. New York: Oxford University Press.

Storey, A. E., Bradbury, C. G. & Joyce, T. L. 1994. Nest attendance in male meadow voles: the role of the female in regulating male interactions with pups. *Animal Behaviour*, **47,** 1037-1046.

Storey, A. E., French, R. J. & Payne, R. 1995. Sperm competition and mate guarding in meadow voles (*Microtus pennsylvanicus*). *Ethology*, **101,** 265-279.

Tamarin, R. H. 1977. Reproduction in the island beach vole, *Microtus brewerei,* and the mainland meadow vole, *Microtus pennsylvanicus,* in southeastern Massachusetts. *Journal of Mammalogy*, **58,** 536-548.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136-179, Chicago: Aldine.

Turner, B. N. & Iverson, S. L. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. *Ecology,* **54,** 967-981.

Turner, B. N., Iverson, S. L. & Severson, K. 1980. Effects of castration on open-field behaviour and aggression in male meadow voles (*Microtus pennsylvanicus).* *Canadian Journal of Zoology,* **58,** 1927-1932.

Upchurch, M. & Wehner, J. M. 1988. Differences between inbred strains of mice in Morris water maze performance. *Behavior Genetics,* **18,** 55-68.

Upchurch, M. & Wehner, J. M. 1989. Inheritance of spatial learning ability in inbred mice: a classical genetic analysis. *Behavioral Neuroscience,* **103,** 1251-1258.

Van Oormerssen, G. A. & Busser, J. 1989. Studies in wild house mice 3: disruptive selection on aggression as a possible force of evolution. In: *House Mouse Aggression: A Model for Understanding the Evolution of Social Behaviour* (Ed.

by :P. F. Brain, D. Mainardi & S. Parmigiani), pp. 87-117, New York, Harwood Academic Publishers.

Vom Saal, F. S. 1987. Perinatal testosterone exposure has opposite effects on adult intermale aggression and infanticide in mice. In: *House Mouse Aggression: A Model for Undertsding the Evolution of Social Behaviour*. (Ed. by P. F. Brain, D. Mainardi & S. Parmigiani), pp. 179-204, New York: Hardwood Academic Publishers.

Vyssotski, A. L, Dell'Omo, G., Poletaeva, I. I., Vyssotski, D. L, Minichiello, L., Klein, R., Wolfer, D. P. & Lipp, H.-P. 2002. Long-term monitoring of hippocampus-dependent behavior in naturalistic settings: mutant mice lacking neuortrophin receptor TrkB in the forebrain show spatial learning but impaired behavioral flexibility. *Hippocampus,* **12,** 27-38.

Wagner, G. C., Beuving, L. J. & Hutchinson, R. R. 1979. Androgen-dependency of aggressive target-biting and paired fighting in male mice. *Physiology & Behavior,* **22,** 43-46.

Webster, A. B. & Brooks, R. J. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy*, **62,** 738-751.

Tyler, W. J., Alonso, M., Bramham, C. R. & Pozzo-Miller, L. D. 2002. From acquisition to consolidation: on the role of brain-derived neurotrophic factor signaling in hippocampal-dependent learning. *Learning and Memory,* **9,** 224-237.

Williams, C. L., Barnett, A. M. & W. H. Meck. 1990. Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience*, **104,** 84-97.

Wolff, J. O. 1985. Behavior. In: *Biology of New World Microtus*. (Ed. by R. H. Tamarin), pp. 340-366, Boston: The American Society of Mammalogists.

Würbel, H. 2001. Ideal homes? Housing effects on rodent brain and behaviour. *Trends in Neuroscience,* **24,** 207-211.

Zielinski, W. J. & Vandenbergh, J. G. 1993. Testosterone and competitive ability in male house mice, *Mus musculus*: laboratory and field studies. *Animal Behaviour*, **45,** 873-891.

Zielinski, W. J., vom Saal, F. S. & Vandenbergh, J. G. 1992. The effect of intrauterine position on the survival, reproduction and home range size of female house mice (*Mus musculus*). *Behavioural Ecology and Sociobiology,* **30,** 185-191.

Table 1. ANCOVA for two measures of nest box visitation with performance during the three phases of water maze testing as covariates and enclosure as a random factor.

Variables	β*	*F*	*df*	*P*
Total number of nest box visits				
Log (block 5 path length)	-0.47	5.83	1,15	0.029
Log (transfer path length)	0.81	14.05	1,15	0.002
Retention time	0.51	7.75	1,15	0.014
Enclosure effect		3.30	6,15	0.028
Number of visits to most frequently visited nest box				
Log (block 5 path length)	-0.64	9.97	1,15	0.007
Log (transfer path length)	1.00	20.06	1,15	<0.0005
Retention time	0.50	6.88	1,15	0.019
Enclosure effect		1.49	6,15	0.25

*Standardized partial regression coefficients.

Table 2. Two ANCOVA's for average distance to range center (males with at least 5 captures) with enclosure as a random factor, performance during the three phases of water maze testing as covariates for the first analysis, and dominance rank as an additional covariate for the second analysis.

Variables	β*	*F*	*df*	*P*
Average distance to range center				
Log (block 5 path length)	0.0039	0.0004	1,12	0.98
Log (transfer path length)	-0.68	10.95	1,12	0.006
Retention time	-0.46	6.48	1,12	0.026
Average distance to range center				
Log (block 5 path length)	-0.015	0.006	1,11	0.94
Log (transfer path length)	-0.72	7.09	1,11	0.022
Retention time	-0.49	4.07	1,11	0.069
Dominance rank	-0.057	0.054	6,11	0.82
Enclosure effect		3.91	6,11	0.024

*Standardized partial regression coefficients.

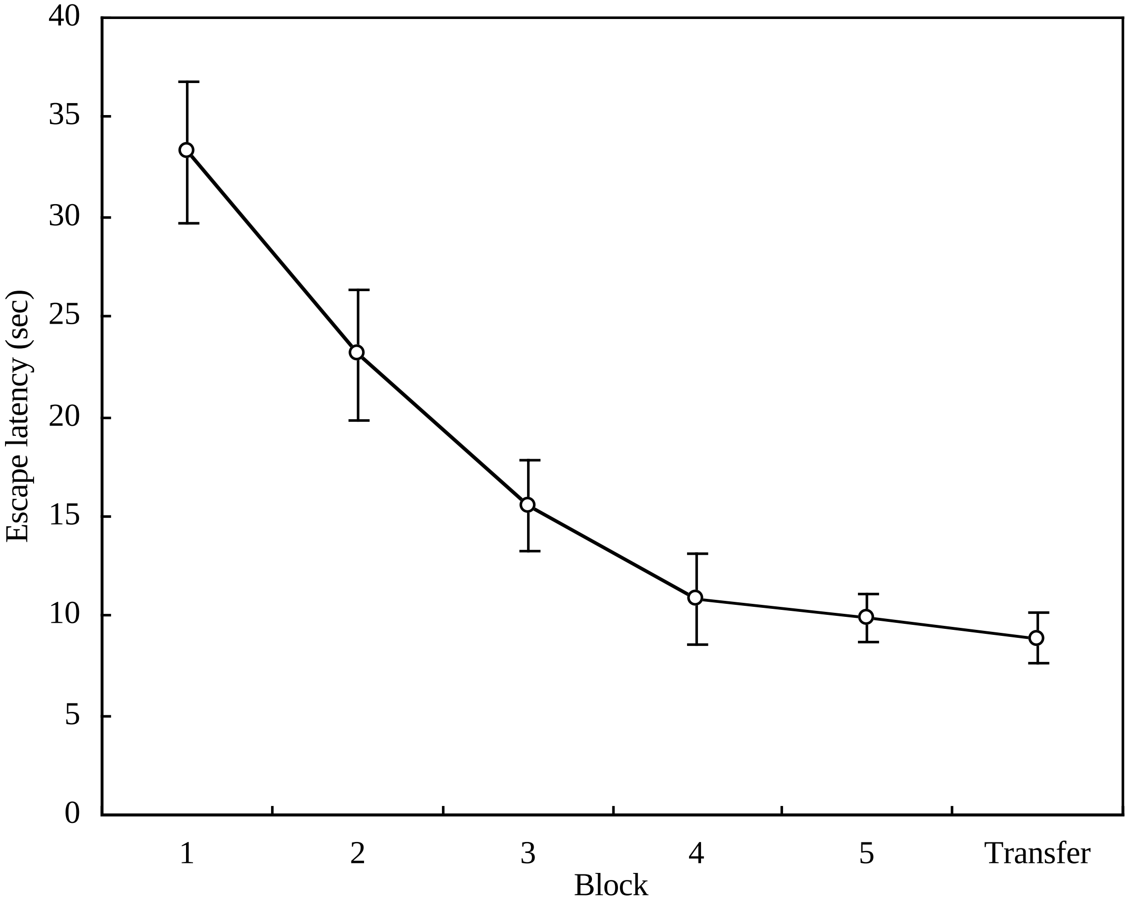


Figure 1. Escape latencies to reach the platform over five blocks of water maze acquisition trials and the transfer trials ($\overline{X}$ ±SE).

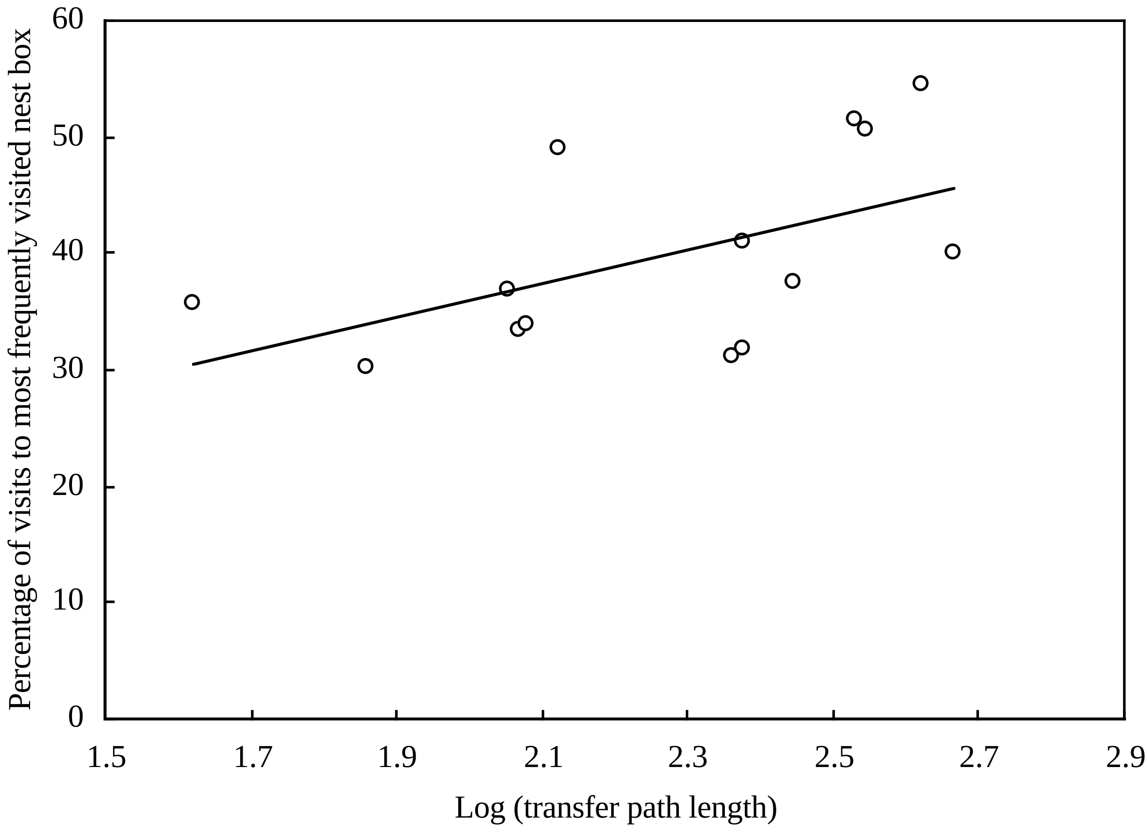


Figure 2. Linear regression of the percentage of visits by males to their most frequently visited nest boxes against path length (cm) during water maze transfer trials (log transformed). Only males that visited all four nest boxes within enclosures are included (*N*=14).

Chapter 4

FEMALE CHOICE BASED ON MALE SPATIAL ABILITY AND DOMINANCE RANK AMONG MEADOW VOLES

INTRODUCTION

Although sexual selection can lead to dramatic differences in morphology and behavior within and among species, surprisingly little is known about how different mechanisms of sexual selection contribute to the evolution of traits (Andersson 1994; Cunningham & Birkhead 1998). Intersexual selection can either oppose, complement, or be neutral with respect to the direction of intrasexual selection upon a trait (Moore & Moore 1999; Sih et al. 2002). Intrasexual selection can be divided into scramble competition and contest competition for mates (Andersson 1994; Murphy 1998). Scramble competition favors traits that increase an individual's ability to rapidly and accurately locate mates, whereas contest competition favors traits that increase an individual's ability to guard a mate and fight off rivals. An increasing number of studies have attempted to determine the relative importance of intrasexual and intersexual selection (e.g., Moore 1990; Howard et al. 1997; Sih et al. 2002), but few studies have examined female choice for male traits that are selected by scramble competition (Able 1999).

Among mammals, females usually have a higher parental investment than males, and this differential seems to result in selection for male-male competition and female choosiness for mates (Trivers 1972). Females of many mammalian species have been found to preferentially mate with dominant males and presumably gain indirect benefits for their offspring (Dewsbury 1982; Ellis 1995). The offspring of dominant males could have greater fitness either because dominance is linked to other traits that improve survivorship or because the sons of dominant males have superior mating success due to female choice or male-male competition (Weatherhead & Robertson 1979). Because dominant males are by definition superior at contest competition (Drews 1993), intersexual and intrasexual selection might be expected to favor a complementary suite of traits. Many male traits have been shown to serve a dual purpose as signals to potential mates and signals to ward off rivals (Berglund et al. 1996).

However, females may not always benefit from mating with a dominant male (Qvarnström & Forsgren 1998). Some studies have demonstrated that females will choose mates based on a variety of traits other than dominance rank (Lenington 1983; Meikle et al. 1995; Penn & Potts 1999). I was interested in determining whether females might be choosing mates based on their spatial ability, a trait believed to be selected for by scramble competition (Gaulin & FitzGerald 1986; Schwegmeyer 1994). Considerable evidence suggests that spatial ability is a trait favored by scramble competition among meadow voles, with males that have better spatial ability being able to locate more potential mates (Gaulin & FitzGerald 1986, 1989; Jacobs et al. 1990; Galea et al. 1994; Chapter 1). However, contest competition for mates also occurs among male meadow voles (Turner & Iverson 1973; Boonstra & Rodd 1983; Storey et al. 1995). Thus, a female might make mating decisions based on male spatial ability, dominance rank, or both of these traits. If spatial ability is a better predictor of male reproductive success than dominance rank, then a female would gain more benefits for her male offspring if she made mate-choice decisions based on spatial ability rather than dominance rank. I previously demonstrated that male meadow voles with higher dominance rank also tend to have better spatial ability (Chapter 2), but females may still be choosing mates based on one of these traits and not the other.

Female meadow voles show mate preferences in the laboratory and have the opportunity to exhibit mate choice in the field. Studies with captive animals have shown that females prefer to mate with familiar rather than unfamiliar males (Salo & Dewsbury 1995, Parker et al. 2001) and non-siblings rather than siblings (Bollinger et al. 1991, 1993). In the field, females also preferentially mate with males that visit their nests more frequently than other males (Chapter 1). No previous studies have demonstrated that female meadow voles preferentially mate with dominant males, but female odor preferences suggest that this is likely (Ferkin et al. 1992; Ferkin & Johnston 1993). Females have the opportunity for mate choice in the field because each female's home range is likely to be overlapped by the ranges of multiple males (Madison 1980; Webster & Brooks 1981).

The goal of this study was to determine the relative influence of male spatial ability and dominance rank upon female preferences. Although dominant males tend to also have higher spatial ability than subordinate male meadow voles, this is not always the case (Chapter 2). In this study, I took advantage of the variability in the relationship between dominance rank and spatial ability by allowing females to chose between males that varied in their relative spatial ability and dominance rank.

METHODS

Collection and Housing

Forty adult male meadow voles were collected at Miami University's Ecology Research Center (ERC) near Oxford, Ohio. Voles were housed singly in clear polycarbonate cages (18×28×12 cm) at Miami University's animal facility. Reproductive maturity was determined based on body mass (> 30 g) and conduction of the external genitalia: adult males had descended testes and adult females had perforate vaginas (Boonstra & Rodd 1983). Voles were maintained at 21°C on a cycle of 14 h light:10 h dark (lights on at 0800 hours). Rodent chow (Lab Diet #5013, PMI Nutrition International, Brentwood, MD) and water were provided ad libitum, and sunflower seeds and lettuce were provided as weekly supplements. Cotton Nestlets (Ancare, Bellmore, NY) and dried alfalfa were provided for bedding. All males experienced a summer light cycle for approximately two months prior to behavioral testing and had descended testes during behavioral testing. The voles were weighed after each set of behavioral tests to monitor their health.

Water Maze Testing

The spatial ability of all 40 males was tested using the water maze (Stewart & Morris 1993). A circular pool (90 cm diameter and 45 cm height) was filled with water to a depth of 15 cm and divided into four equal quadrants with string raised above the pool. A 7 cm diameter clear plastic platform submerged 1.5 cm below the surface was used as the goal. The water temperature averaged 20.0 °C, and the water was made opaque using non-toxic white paint. I taped three white note cards with black shapes drawn on them at evenly spaced intervals around the edge of the water maze as additional visual cues. Various objects around the room were kept in consistent locations during testing as distal visual cues. The observer stood approximately 1 m away from the site where the vole was released. Because each vole was released at four different locations around the maze, the observer was not a consistent visual cue. All trials were video recorded from above.

As in my previous studies (Chapters 1-3), I followed a four-phase protocol (preliminary, acquisition, transfer, and retention), and randomized the daily testing sequence of voles. All inter-trial intervals on the same day were 45 s, during which each vole was first dried off with a towel and then placed in a holding cage. During the preliminary phase, each male was introduced into the maze, allowed to swim for 60 s, and then placed on the platform for 15 s. Each vole was given three consecutive preliminary trials on the same day. The preliminary phase was conducted during one day in a separate room from all other testing and the note cards were not in place, so the voles were not acquiring the task during this phase.

During the acquisition phase (conducted 24 h after the preliminary phase), I recorded the time it took each vole to reach the platform (escape latency). For each vole, the platform was assigned to one of the four randomly chosen quadrants. The platform remained in the same quadrant for all trials involving a particular vole. Four possible release sites were designated at equidistant points around the pool. One release site was set aside for each vole to use during the transfer phase (see below). The location of this site was counter-balanced such that half the voles had a release site that was closer to the platform than the other half (this was necessary because the platform was offset from the center of the pool). During the acquisition phase, I tested each vole on three consecutive trials per day for 5 blocks (days) of trials, such that each vole was introduced into the maze from the three different release sites in a random order each day. Any trial that lasted 60 s was terminated by placing the vole on the platform for 15 s and then removing it from the maze. Similarly, whenever a vole reached the platform, it was allowed to remain there for 15 s before ending the trial.

During the transfer phase (conducted 24 h after the last acquisition trial), I introduced each vole into the maze from the release site not used during the acquisition phase. This phase measured the voles' ability to transfer what they had learned during the acquisition phase to a novel context. Three consecutive trials at the same release site were conducted for each vole during this phase. Finally, during the retention phase (conducted 24 h after the transfer phase), the platform was removed from the maze and voles were released into the maze for 60 s from one of the three release sites used during their acquisition trials. From video recordings, I determined path lengths for block 5 of the acquisition trials and the transfer trials and time spent swimming in the quadrant where the platform had previously been during the retention trials.

My protocol resulted in two measures of spatial-learning ability (average path lengths during the final block of acquisition trials and during the transfer trials) and one measure of spatial memory (time in the target quadrant during the retention phase). Path length has been commonly used in past studies to assess spatial-learning ability, and retention time is a common measure of spatial memory (D'Hooge & De Deyn 2001). To categorize males based on their spatial ability, I used a composite index: spatial ability score = (acquisition rank + transfer rank + retention rank) / 3.

Dominance Testing

Following water-maze testing, I tested males for their relative dominance rank following methods similar to those described in my previous studies (Chapter 2, 3). All tests were conducted indoors during the light part of the cycle in a circular Plexiglas arena (50 cm high, 60 cm diameter). A removable opaque partition was placed across the center of the arena at the start of each trial, and a male was placed on either side of the partition for a 5 min habituation period. The tip of each male’s tail was marked with fluorescent powder for identification during trials (color was alternated for consecutive trials). Data were collected from behind a plastic sheet with a small opening for observation. I recorded the frequency of all aggressive interactions (threat, lunge, chase, box, and wrestle) during 15 min trials using all-occurrence sampling. A male was considered the winner of a particular trial if he exhibited more aggression towards his opponent than vice versa. A male was considered to be dominant to another male if he won two out of three trials.

My goal for dominance testing was to obtain 10 pairs of males to be used for Experiment 1 (good spatial ability and low dominance rank versus poor spatial ability and high dominance rank) and 10 pairs to be used for Experiment 2 (good spatial ability and high dominance rank versus poor spatial ability and low dominance rank). This was done using two rounds of dominance testing. For the first round, the males used for dominance trials were chosen such that the difference in spatial ability scores between males within each pair was maximized for all 20 pairs (i.e., males that had relatively good spatial ability were paired with males that had relatively poor spatial ability). After the first round of testing, eight males fit the criteria for use in Experiment 1, and no further dominance testing was conducted with these males. The remaining males were re-paired such that the difference in spatial ability within a pair was again maximized. Two pairs of males from the second round of testing fit the criteria for use in Experiment 1. The remaining ten pairs were used for Experiment 2.

Female Choice Experiments

Female-choice trials were conducted using methods similar to Parker et al. (2001). Fourteen adult, virgin, lab-reared (F2 or F3) females were used for each of the two experiments. No two females were closely related to each other, and no female was closely related to any of the males. For the first experiment, each female was given a choice between a male with good spatial ability and low dominance rank and a male with poor spatial ability and high dominance rank. For the second experiment, each female was given a choice between a male with good spatial ability and high dominance rank and a male with poor spatial ability and low dominance rank. Ten different pairs of males were used for each experiment, and four pairs were reused with a second female to increase my sample size. At least one week elapsed between trials for the male pairs that were used a second time. I did not consider repeated tests with the same males to be pseudo-replication because the males represented my experimental stimulus, and each female was an independent sampling unit (Berteux et al. 1999).

The clear Plexiglas choice apparatus consisted of three adjacent chambers (20 × 20 × 20 cm each) that were each supplied with food and water ad libitum and a cotton Nestlet (Ancare, Bellmore, NY). Males were collared with plastic cable-ties just prior to being placed in the apparatus. I placed a collared male, counter-balanced for treatment, into each of the side chambers and a female in the center chamber for each trial. The chambers were divided by wire mesh for three days, which allowed olfactory and visual communication between the female and the two males, but prevented most physical contact. This period was used to habituate voles to the apparatus and induce estrus in the females (Meek & Lee 1993). One day prior to starting data collection, I tethered males using wire fishing leader, with one end attached to their collars with a swivel clip and the other end attached to the lid of the chamber. Just prior to starting data collection, I replaced the wire mesh with Plexiglas dividers that had 3 cm diameter holes at the base. Males were able to move freely within their own chambers but unable to enter the neutral chamber or the other male's chamber, whereas females were able to move freely among all three chambers. All interactions within the apparatus were video-recorded in time-lapse (1 s / 30 s) for 24 h. Voles experienced a long-day light cycle (14 h light:10 h dark) during testing, and red lights on a timer were used to observe voles during the dark phase. The recordings were analyzed for frequency and duration of visitation as well as for any observable copulations. The female's entire body had to pass through the hole in a divider between chambers to be scored as a visit. I cleaned the testing apparatus thoroughly between trials. Because few copulations were observed, duration and frequency of visitation were used as my primary indices of mate preference. Previous experiments with prairie voles and brown lemmings have demonstrated a positive relationship between duration of visitation and number of copulations (Huck & Banks 1982; Wolff et al. 2002).

Statistical Analysis

For both experiments, I calculated the average proportion of visits each female made to each of the two males. I also calculated the average proportion of time each female spent with each of the two males. The differences between these proportions were determined using Wilcoxon signed-rank tests (Sokal & Rohlf 1995).

Contingency tests were used for each experiment to determine if the proportion of visits to the two male treatments depended upon the side of the apparatus that they were on. I did not control for male body mass during the experiments. Therefore, I compiled the data for the two experiments and compared the body mass of the preferred male, based on frequency and duration of visitation, to the body mass of the other male using paired *t* tests. All statistical tests were conducted using SPSS 11.0 at a significance level of α=0.05.

Ethical Note

Spatial ability was measured using the Morris water maze, which involved exposing voles to an aversive stimulus, cold water. I attempted to minimize the amount of stress that voles experienced by limiting trials to a maximum of 60 s and drying voles after each trial. The water maze has been used extensively with meadow voles (e.g., Galea et al. 1995; Kavaliers et al. 1998), and meadow voles are also excellent swimmers (Dagg & Windsor 1972).

No cases of severe wounding were observed during dominance testing, and males engaged in few aggressive acts per 15 min trial ($\overline{X}$ ±SE= 4.7±0.6). Tethering males may have been somewhat stressful, but this is currently the best method available for separating intersexual selection from intrasexual selection. I carefully monitored each male's health (behavior and condition of pelage) during the female-choice trials, and discontinued trials when a male was in noticeably poor condition. I found that the males exhibited normal social interactions with females while they were tethered. Other studies have also found no detrimental effects from tethering meadow voles (Berteaux et al. 1999; Parker et al. 2001).

RESULTS

Experiment 1

Females visited males with good spatial ability and low dominance rank more often than males with poor spatial ability and high dominance rank (Fig. 1; Wilcoxon signed-rank test: T=11, N=14, P<0.005). Similarly, females spent more time with the male that had good spatial ability and low dominance rank (Fig. 1; Wilcoxon signed-rank test: T=18, N=14, P<0.025). Two females were each observed copulating once and one female was observed copulating twice with the same male. All four copulations were with males that were visited more frequently and for the longer duration.

The difference in the duration of visitation between males from the two treatments and the difference in the frequency of visitation between the males from the two treatments were not significantly correlated (Spearman rank correlation: r_s=0.36, N=14, P=0.20), indicating that the male that a female visited more frequently was not necessarily the male with whom she spent more time. Female preference was not dependent upon the side of the apparatus that males were on, regardless of whether preference was determined using frequency of visits (χ_1^2 =0.64, NS) or duration of visitation (χ_1^2 =0.043, NS).

Experiment 2

Females tended to visit males with good spatial ability and high dominance rank more frequently than males with poor spatial ability and low dominance rank, but this preference was not statistically significant (Fig. 2; Wilcoxon signed-rank test: *T*=27, *N*=14, NS). Females also spent more time with males that had good spatial ability and high dominance rank, but this preference was also not statistically significant (Fig. 2; Wilcoxon signed-rank test: *T*=34, *N*=14, NS). Three females were each observed copulating twice. Two of these females copulated with both males, and the other female copulated twice with the male that she visited more frequently and for the longer duration.

The difference in the duration of visitation to males from the two treatments and the difference in the frequency of visitation to males from the two treatments was positively correlated (Spearman rank correlation: r_s=0.63, *N*=14, *P*=0.016), indicating that the male that a female visited more frequently tended to also be the male with whom she spent more time. Female preference was not dependent upon the side of the apparatus that males were on, regardless of whether preference was determined using frequency of visits (χ_1^2 =0.035, NS) or duration of visitation (χ_1^2 =0.0094, NS).

Using the combined data for the two experiments, males that were visited more frequently did not have greater body mass than the less frequently visited males (Paired *t* test: t_{27}=0.26, *P*=0.80). Similarly, males that were visited longer did not have greater body mass than the males that were visited for a shorter period of time (Paired *t* test: t_{27}=0.03, *P*=0.98).

DISCUSSION

In Experiment 1, females visited males with good spatial ability and low dominance rank more often and for a longer time period than males with poor spatial ability and high dominance rank. This suggests that male spatial ability is a better predictor of female mate preferences than is male dominance rank. In Experiment 2, females showed no significant preference between males with good spatial ability and high dominance rank and males with poor spatial ability and low dominance rank. This suggests that the perceived benefits of mating with a male with good spatial ability may have been counteracted by the perceived costs of mating with males with high dominance rank. Although the results of Experiment 1 might be interpreted as a female preference for males with low dominance rank rather than a preference based on spatial ability, this was probably not the case because females in Experiment 2 did not show a preference for males with lower dominance rank.

Reproductively active male meadow voles out-perform females in both complex mazes (Gaulin & FitzGerald 1986, 1989) and water mazes (Kavaliers et al. 1993, 1998). I previously demonstrated that males with good spatial ability have larger home ranges and locate more females in the field (Chapters 1 & 3). Thus, sex differences in spatial ability among meadow voles may be the result of both female choice and scramble competition. Some previous studies have also found that intersexual and intrasexual selection can have complementary effects upon male traits (Ligon et al. 1990; Berglund et al. 1996; Hagelin 2002), but these studies investigated traits associated with contest competition rather than scramble competition. Able (1999) found that scramble competition favored male salamanders with wider tails for increased mobility, but females showed no mating preference based on male tail depth. In some species, including meadow voles, scramble competition seems to be more important than contest competition in determining male reproductive success (Schwagmeyer & Woontner 1986; Bauer & Abdalla 2001). Because spatial ability is heritable (Upchurch & Wehner 1988, 1989), females that mate with males that have better spatial ability are likely to gain indirect fitness benefits for their male offspring. The male offspring of sires with good spatial ability would be better able to locate mates and would be favored by female choice. These indirect benefits might be particularly important during periods of low population density when mates become more difficult to locate (Chapter 2). Okasanen et al. (1999) demonstrated that male reproductive success was heritable among bank voles, but this was most likely due to female choice and contest competition rather than scramble competition because matings occurred under laboratory conditions.

This is the first demonstration of female choice based on male spatial ability. Spatial ability is a particularly interesting behavioral trait because its underlying neural mechanisms are relatively well understood among rodents (O’Keefe & Nadel 1978; Redish 1999; D’Hooge & De Deyn 2001). Brain regions associated with spatial learning and memory are sexually dimorphic among meadow voles. Males tend to have a larger hippocampus than females (Jacobs et al. 1990; Galea et al. 1999), and males have more dendritic arborization in the parietal and prefrontal cortex than do females (Kavaliers et al. 1998). Although it has been hypothesized that these sex differences in brain morphology are the result of scramble competition for mates (Gaulin & FitzGerald 1986; Jacobs et al. 1990), my current results suggest that they may also be the result of female mating preferences for males with better spatial ability. These results are comparable to those obtained from studies with birds that have shown that female choice can influence the evolution of the song control nucleus (HVc) in males. Among warblers, the relative volume of the HVc is correlated with song complexity (Székely et al. 1996; Airey et al. 2000a), and females show a mating preference for males with larger repertoires (Hasselquist et al. 1996; Airey et al. 2000b). Because the brain is a metabolically costly organ, behavioral traits associated with mental competency may provide females in a variety of species with an honest signal of male quality (Jacobs 1996; Miller 2000).

Females did not show a preference for males with high dominance rank compared to males with low dominance rank. This was somewhat surprising considering that in numerous other rodent species females prefer to socialize and mate with higher ranking males (Dewsbury 1981; Huck et al. 1986; Lisk et al. 1989; Evsikov et al. 1994; Horne & Ylönen 1996; Kruczek 1997). However, among montane voles (*Microtus montanus*), which have a similar social organization to that of meadow voles, females do not show a mating preference for dominant males over subordinates (Shapiro & Dewsbury 1986). Studies with a wide range of other taxa have also shown that contest competition for mates and female choice do not always select for the same traits (Moore 1990; Sorrenson & Derrickson 1994; Cremer & Greenfield 1998; Howard et al. 1997; Sih et al. 2002), which is probably because the costs of mating with a dominant male sometimes outweigh the benefits. Females could incur direct costs in the form of increased risk of injury by associating with a more aggressive dominant male, as is the case among Japanese macaques (Soltis et al. 1997). It has also been hypothesized that females might incur indirect costs by mating with a dominant male (Qvarnström & Forsgren 1998). For example, highly aggressive male offspring might have reduced survivorship because they expose themselves to increased risk of injury during intersexual conflict or increased risk of predation. In combination, female choice and contest competition among meadow voles could result in stabilizing selection for traits associated with dominance rank. A comparable situation occurs among cockroaches in which females prefer pheromones produced by subordinate males (Moore & Moore 1999).

Besides potential indirect benefits, females might also gain direct benefits by avoiding males with high dominance rank. Although male meadow voles exhibit less paternal behavior than other vole species (McGuire & Novak 1984), they do somtimes help females care for their offspring, particularly late in the breeding season (Storey et al. 1994; Parker & Lee 2002). Paternal care leads to increased weight gain by offspring, which could lead to greater offspring fitness (Storey & Snow 1987). Parker & Lee (2001) demonstrated that male meadow voles switch from being aggressive toward pups to being paternal after 24 h of cohabitation with a female, and this switch from aggressive to paternal behavior seems to be due to an increase in arginine vassopressin (AVP) in the brain. However, they also found that some males that were aggressive before intracerebroventricular injections of AVP remained non-paternal after injections.

Therefore, females may be avoiding the costs of mating with males that have low paternal ability by avoiding males with high dominance rank.

My results demonstrate that female meadow voles show preferences based on male spatial ability, but the mechanism for female perception of male spatial ability remains unknown. The underlying mechanism may involve testosterone levels because testosterone seems to have activational effects on male spatial ability. Specifically, males with higher testosterone levels have larger overall hippocampal volumes (Galea & McEwen 1999; Galea et al. 1999) and testosterone promotes the survival of new cells in the dentate gyrus (Ormerod & Galea 2003). Furthermore, females use olfactory cues to distinguish between males based on their testosterone levels (Ferkin et al. 1992, 1994; Ferkin & Johnston 1993; Leonard et al. 2001). Females may therefore determine a male's relative spatial ability using olfactory cues correlated with testosterone level.

Female preferences for males with an optimal level of testosterone may be the mechanism for female preferences for males based on both spatial ability and dominance rank. Evidence suggests that males with higher dominance rank have higher levels of testosterone (Christian 1971; Turner & Iverson 1973; Rose 1979; Turner et al. 1980; Galea & McEwen 1999). Therefore, if females simply preferred males with higher testosterone levels, one would predict that they should prefer males with high dominance rank and high spatial ability. I found that females preferred males with relatively good spatial ability and low dominance rank, which suggests that males with high dominance rank but low spatial ability may have a testosterone level higher than that preferred by females. Studies with humans have shown that there is an optimal level of circulating testosterone for performance of spatial tasks, with high levels of testosterone causing reduced spatial ability (Nyborg 1983; Gouchie & Kimura 1991; Moffat & Hampson 1996). Female meadow voles seem to prefer the scents of males with an intermediate level of testosterone (Ferkin et al. 1994), which may correspond with a preference for males with good spatial ability and low dominance rank.

I previously found that male meadow voles with better spatial ability are better able to locate female nests (Chapter 1), and my current results suggest that females prefer to mate with males with better spatial ability. This suggests that males with better spatial ability should have a strong reprodutive advantage, but I previously found that males with better spatial ability did not achieve significantly higher reproductive success (Chapter 1). There are a number of explanations for this discrepancy. My current results suggest that females do not always preferentially mate with males that have both relatively high dominance rank and high spatial ability. The preferred male is likely to depend upon which other males are available, which means that the reproductive success of a male with high spatial ability will be determined to some degree by the relative spatial ability and dominance rank of neighboring males (Greene et al. 2000; Sinervo 2001).

I was surprised to find that only 21.4% (6/28) of the females copulated during the 24 h trials. Using a similar experimental design, Berteaux et al. (1999) found that 74.4% of females copulated. This difference may have been because the males used by Berteuax et al (1999) were captive-reared and the males that I used were wild-caught. I chose to use wild males due to the detrimental effects of laboratory rearing upon spatial ability (Walker-Sands 1995; Würbel 2001; Schrijver et al. 2002), but wild voles may have experienced more stress during female-choice testing than animals accustomed to living in captivity. In spite of the fact that few of my females copulated, frequency and duration of visitation seemed to provide an accurate estimate of mate preferences. Four females mated exclusively with the male that they visited more frequently and for the longer duration, two females mated with both males, and no females mated exclusively with the male that they visited less frequently or for a shorter duration. This supports other studies that have shown that males visited for longer periods obtain more copulations (Huck & Banks 1982; Wolff et al. 2002).

In summary, I found that female meadow voles prefer males with relatively good spatial ability and low dominance rank. This suggests that both inter-male scramble competition and female mate choice favor males with better spatial ability. In contrast, the effects of inter-male contest competition and female choice on male traits associated with dominance rank seem to oppose one another. Female detection of male testosterone level is a possible mechanism for mating preferences based on spatial ability and dominance rank. I further hypothesize that females prefer males with an optimal level of testosterone rather than males with higher or lower than average testosterone levels. My results highlight the importance of considering the effects of multiple mechanisms of sexual selection before drawing conclusions about the intensity and direction of selection upon a trait.

REFERENCES

Able, D. J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioural Ecology and Socioibiology*, **46,** 423-428.

Airey, D.C., Buchanan, K.L., Székely, T., Catchpole, C.K. & DeVoogd, T.J. 2000a. Song, sexual selection and a song control nucleus (HVc) in the brains of European sedge warblers. *Journal of Neurobiology*, 44, 1-6

Airey, D.C., Castillo-Juarez, H., Casella, G., Pollak, E.J. & DeVoogd, T.J. 2000b. Variation in the volume of zebra finch song nuclei is heritable: developmental and evolutionary implications. *Proceedings of the Royal Society of London B.*, **267,** 2099-2104.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Bauer, R. T. & Abdalla, J. H. 2001. Male mating tactics in the shrimp *Palaemonetes pugio* (Decopoda, Caridea): precopulatory mate guarding vs. pure searching. *Ethology*, **107,** 185-199.

Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, **58,** 385-399.

Berteaux, D., Dety, J. & Rengifo, J. B. 1999. Multiple paternity in meadow voles (*Microtus pennsylvanicus*): investigating the role of the female. *Behavioural Ecology and Sociobiology*, **45,** 283-291.

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

Bollinger, E. K., Harper, S. J., Kramer & Barrett, G. W. 1991. Avoidance of inbreeding in the meadow vole (*Microtus pennsylvanicus*). *Journal of Mammalogy*, **72,** 419-421.

Boonstra, R. & Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology*, **52,** 757-780.

Boonstra, R., Xia, X. & Pavone, L. 1993. Mating system of the meadow vole, *Microtus pennsylvanicus*. *Behavioral Ecology*, **4,** 83-89.

Christian, J. J. 1971. Fighting, maturity, and population density in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **52,** 556-567.

Cremer, S. & Greenfield, M. D. 1998. Partitioning the components of sexual selection: attractiveness and agonistic behaviour in male wax moths, *Achroia grisella* (Lepidoptera: Pyralidae). *Ethology*, **104,** 1-9.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour*, **56,** 1311-1321.

Dewsbury, D. A. 1981. Social dominance, copulatory behavior, and differential reproduction in deer mice (*Peromyscus leucopus*). *Journal of Comparative Physiological Psychology*, **95,** 880-895.

Dewsbury, D. A. 1982. Dominance rank, copulatory behavior, and differential reproduction. *Quarterly Review of Biology,* **57,** 135-159.

D'Hooge, R. & De Deyn, P. P. 2001. Applications of the Morris water maze in the study of learning and memory. *Brain Research Reviews,* **36,** 60-90.

Drews, C. 1993. The concept and definition of dominance in animal behaviour. *Behaviour,* **125,** 283-313.

Ellis, L. 1995. Dominance and reproductive success among nonhuman animals: a cross-species comparison. *Etholology and Sociobiology,* **16,** 257-333.

Evsikov, V. I., Nazarova & Potapov., M. A. 1994. Female odor choice, male social rank, and sex ratio in the water vole. *Advances in Biosciences,* **93,** 303-307.

Ferkin, M. H. & Johnston, R. E. 1993. Roles of gonadal hormones in control of five sexually attractive odors of meadow voles (*Microtus pennsylvanicus*). *Hormones and Behaviour,* **27,** 523-538.

Ferkin, M. H., Gorman, M. R. & Zucker, I. 1992. Influence of gonadal hormones on odours emitted by male meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility,* **95,** 729-736.

Ferkin, M. H., Sorokin, E. S., Renfroe, M. W. & Johnston, R. E. 1994. Attractiveness of male odors to females varies directly with plasma testosterone concentration in meadow voles. *Physiology & Behavior,* **55,** 347-353.

Galea, L. A. M., McEwen, B. S., 1999. Sex and seasonal differences in the rate of cell proliferation in the dentate gyrus of adult wild meadow voles. *Neuroscience,* **89,** 955-964.

Galea, L.A.M., Ossenkopp, K.-P. & Kavaliers, M. 1994. Developmental changes in spatial learning in the Morris water-maze in young meadow voles, *Microtus pennsylvanicus*. *Behavior and Brain Research,* **60,** 43-50.

Galea, L.A.M., Perrot-Sinal, T.S., Kavaliers, M., Ossenkopp, K.-P. 1999. Relations of hippocampal volume and dentate gyrus width to gonadal hormone levels in male and female meadow voles. *Brain Research,* **821,** 383-391.

Gaulin, S. J. C. & FitzGerald, R. W. 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *The American Naturalist,* **127,** 74-88.

Gaulin, S. J. C. & FitzGerald, R. W. 1989. Sexual selection for spatial-learning ability. *Animal Behaviour,* **37,** 322-331.

Gouchie, C. & Kimura, D. 1991. The relationship between testosterone levels and cognitive ability patterns. *Psychoneuroendocrinology,* **16,** 323-334.

Greene, E., Lyon, B. E., Muehter, V. R., Ratcliffe, L., Oliver, S. J. & Boag, P. T. 2000. Disruptive sexual selection for plumage coloration in a passerine bird. *Nature,* **407,** 1000-1003.

Hagelin, J. C. 2002. The kinds of traits involved in male-male competition: a comparison of plumage, behavior, and body size in quail. *Behavioral Ecology,* **13,** 32-41.

Hasselquist, D., Bensch, S. & von Schantz, T. 1996. Correlation between male song reperoire, extra-pair paternity and offspring survival in the great reed warbler. *Nature,* **381,** 229-232.

Horne, T. J. & Ylönen, H. 1996. Female bank voles (*Clethrionomys glareolus*) prefer dominant males: but what if there is no choice? *Behavioral Ecology and Sociobiology,* **38,** 401-405.

Howard, R. D., Moorman, R. S. & Whiteman, H. H. 1997. Differential effects of mate competition and mate choice on eastern tiger salamanders. *Animal Behaviour,* **53,** 1345-1356.

Huck, U. W. & Banks, E. M. 1982. Male dominance status, female choice and mating success in the brown lemming, *Lemmus trimucronatus*. *Animal Behaviour,* **30,** 665-675.

Huck, U. W., Banks, E. M. & Wang, S-C. 1986. Behavioral and physiological correlates of aggressive dominance in male brown lemmings (*Lemmus sibiricus*). *Aggressive Behavior,* **12,** 139-148.

Jacobs, L. F., Gaulin, S. J., Sherry, D. F. & Hoffman, G. E. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Science USA,* **87,** 6349-6352.

Jacobs, L.F. 1996. Sexual selection and the brain. *Trends in Ecology and Evolution,* **11,** 82-86.

Kavaliers, M., Ossenkopp, K.-P., Galea, L. A. M. & Kolb, B. 1998. Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Research,* **810,** 41-47.

Kruczek, M. 1997. Male rank and female choice in the bank vole, *Clethrionomys glareolus*. *Behavioral Processes* **40,** 171-176.

Lenington, S. 1983. Social preferences for partners carrying ‘good genes’ in wild house mice. *Animal Behaviour*, **31,** 325-333.

Leonard, S. T., Ferkin, M. H. & Johnson, M. M. 2001. The response of meadow voles to an over-mark in which the two donors differ in gonadal hormone status. *Animal Behaviour*, **62,** 1172-1177.

Ligon, J. D., Thornhill, R., Zuk, M. & Johnson, K. 1990. Male-male competition, ornamentation and the role of testosterone in sexual selection in red jungle fowl. *Animal Behaviour*, **40,** 367-373.

Lisk, R. D., U. W. Huck, Gore, A. C. & Armstrong, M. X. 1989. Mate choice, mate guarding and other mating tactics in golden hamsters maintained under seminatural conditions. *Behaviour*, **109,** 58-75.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioural Ecology Sociobiology,* **7,** 65-71.

McGuire, B. & Novak, M. 1984. A comparison of maternal behavior in the meadow vole (*Microtus pennsylvanicus*), prairie vole (*M. ochrogaster*) and pine vole (*M. pinetorum*). *Animal Behaviour*, 32, 1132-1141.

Meek. L. R. & Lee, T. M. 1993. Prediction of fertility by mating latency and photoperiod in nulliparous and primiparous meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility*, **97,** 353-357.

Meikle, D. B., Kruper, J. H. & Browning, C. R. 1995. Adult male house mice born to undernourished mothers are unattractive to oestrous females. *Animal Behaviour*, **50,** 753-758.

Miller, G. 2000. *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. Anchor Books: New York.

Moffat, S. D. & Hampson, E. 1996. A curvilinear relationship between testosterone and spatial cognition in humans: possible influence of hand preference. *Psychoneuroendocrinology*, **21,** 323-337.

Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. *Evolution*, **44,** 315-331.

Moore, A. J. & Moore, P. J. 1999. Balancing sexual selection through opposing mate choice and male competition. *Proceedings of the Royal Society of London Series B*, **266,** 711-716.

Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution*, **52,** 8-18.

Nyborg, H. 1983. Spatial ability in men and women: review and new theory. *Advances in Behavior Research and Theory*, **5,** 89-140.

O'Keefe, J. & Nadel, L. 1978. *The Hippocampus as a Cognitive Map.* Oxford: Oxford University Press.

Oksanen, T. A., Alatalo, R. V., Horne, T. J., Koskela, E., Mappes, J. & Mappes, T. 1999. Maternal effort and male quality in the bank vole, *Clethrionomys glareolus*. *Proceedings of the Royal Society of London, Series B*, **266,** 1495-1499.

Ormerod, B. K. & Galea, L. A. M. 2003. Reproductive status influences the survival but not production of new cells in the dentate gyrus of adult male meadow voles. *Neuroscience Letters*, **234,** 25-28.

Parker, K. J. & Lee, T. M. 2001. Central vasopressin administration regulates the onset of facultative paternal behavior in *Microtus pennsylvanicus* (Meadow voles). *Hormones and Behavior,* **39,** 285-294.

Parker, K. J. & Lee, T. M. 2002. Interaction of photoperiod and testes development is associated with paternal care in *Microtus pennsylvanicus* (meadow vole). *Physiology and Behavior*, **75,** 91-95.

Parker, K. J., Phillips, K. M & Lee, T. M. 2001. Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour,* **61,** 1217-1226.

Penn, D. J. & Potts, W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist*, **153,** 145-164.

Qvarnström, A. & Forsgren, E. 1998. Should females prefer dominant males? *Trends in Ecology and Evolution,* **13,** 498-501.

Redish, A. D. 1999. *Beyond the Cognitive Map: From Place Cells to Episodic Memory.* Massachusetts: The MIT Press.

Rose R. K. 1979. Levels of wounding in the meadow vole *Microtus pennsylvanicus. Journal of Mammalogy*, **60,**37-45.

Salo, A. L. & Dewsbury, D. A. 1995. Three experiments on mate choice in meadow voles (*Microtus pennsylvanicus*). *Journal of Comparative Psychology,* **109,** 42-46.

Schrijver, N. C. A., Baher, N. I., Weiss, I. C. & H. Würbel. 2002. Dissociable effects of isolation rearing and environmental enrichment on exploration, spatial learning and HPA activity in adult rats. *Pharmacology, Biochemistry and Behavior,* **73,** 209-224.

Schwagmeyer, P. L. 1994. Competitive mate searching in thirteen-lined ground squirrels (Mammalia, Sciuridae): potential roles of spatial memory. *Ethology*, **98,** 265-276.

Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioural Ecology Sociobiology*, **19,** 359-364.

Shapiro, L. E. & Dewsbury, D. A. 1986. Male dominance, female choice and male copulatory behavior in two species of voles (*Microtus ochrogaster* and *Microtus montanus*). *Behavioral Ecology and Sociobiology*, **18,** 267-274.

Sih, A. Lauer, M. & Krupa, J. J. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. *Animal Behaviour*, **63,** 1079-1089.

Sinervo, B. 2001. Selection in local neighborhoods, the social environment and ecology of alternative strategies. In: *Model Systems in Behavioral Ecology: Integrating Conceptual, Theoretical, and Empirical Approaches* (Ed. by L. A. Dugatkin), pp. 191-226, Princeton, New Jersey: Princeton University Press.

Sokal, R. R. & Rohlf, F. J. 1995. *Biometry: the Principles and Practice of Statistics in Biological Research*. 3rd edn. New York: W. H. Freeman and Company.

Soltis, J. Mitsunaga, F., Shimizu, K., Yanagihara, Y. & Nozaki, M. 1997. Sexual selection in Japanese macaques I: female mate choice or male sexual coercion? *Animal Behaviour*, **54,** 725-736.

Sorenson, L. G. & Derrickson, S. R. 1994. Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology*, **35,** 389-400.

Stewart, C. A. & Morris, R. G. M. 1993. The watermaze. In: *Behavioral Neuroscience: A Practical Approach.* (Ed. by Sahgal, A.), pp. 107-122. New York: Oxford University Press.

Storey, A. E. & Snow, D. T. 1987. Male identity and enclosure size affect paternal attendance of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, **35,** 411-419.

Storey, A. E., Bradbury, C. G. & Joyce, T. L. 1994. Nest attendance in male meadow voles: the role of the female in regulating male interactions. *Animal Behaviour*, **47,** 1037-1046.

Storey, A. E., French, R. J. & Payne, R. 1995. Sperm competition and mate guarding in meadow voles (*Microtus pennsylvanicus*). *Ethology,* **101,** 265-279.

Székely, T., Catchpole, C.K., DeVoogd, A., Marchl, Z. & DeVoogd, T.J. 1996. Evolutionary changes in a song control area of the brain (HVC) are associated with evolutionary changes in song repertoire among European warblers (Sylviidae). *Proceedings of the Royal Society of London B,* **263,** 607-610.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136-179. Chicago: Aldine.

Turner, B. N. & Iverson, S. L. 1973. The annual cycle of aggression in male *Microtus pennsylvanicus*, and its relation to population parameters. *Ecology,* **54,** 967-981.

Turner, B. N., Iverson, S. L. & Severson, K. 1980. Effects of castration on open-field behaviour and aggression in male meadow voles (*Microtus pennsylvanicus). Canadian Journal of Zoology,* **58,** 1927-1932.

Upchurch, M. & Wehner, J. M. 1988. Differences between inbred strains of mice in Morris water maze performance. *Behavior Genetics,* **18,** 55-68.

Upchurch, M. & Wehner, J. M. 1989. Inheritance of spatial learning ability in inbred mice: a classical genetic analysis. *Behavioral Neuroscience,* **103,** 1251-1258.

Walker-Sands, R. L. 1995. Sex differences in the development of spatial behavior in montane voles: experimental and hormonal influences. Ph.D. thesis, University of North Carolina at Greensboro.

Weatherhead, P. J. & Robertson R. J. 1979. Offspring quality and the polygyny threshold: "the sexy son hypothesis". *The American Naturalist,* **113,** 201-208.

Webster, A. B. & Brooks, R. J. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy,* **62,** 738-751.

Wolff, J. O., Mech, S. G., Dunlap, A. S. & Hodges, K. E. 2002. Multi-male mating by paired and unpaired female prairie voles (*Microtus ochrogaster*). *Behaviour,* **139,** 1147-1160.

Würbel, H. 2001. Ideal homes? Housing effects on rodent brain and behaviour. *Trends in Neuroscience,* **24,** 207-211.

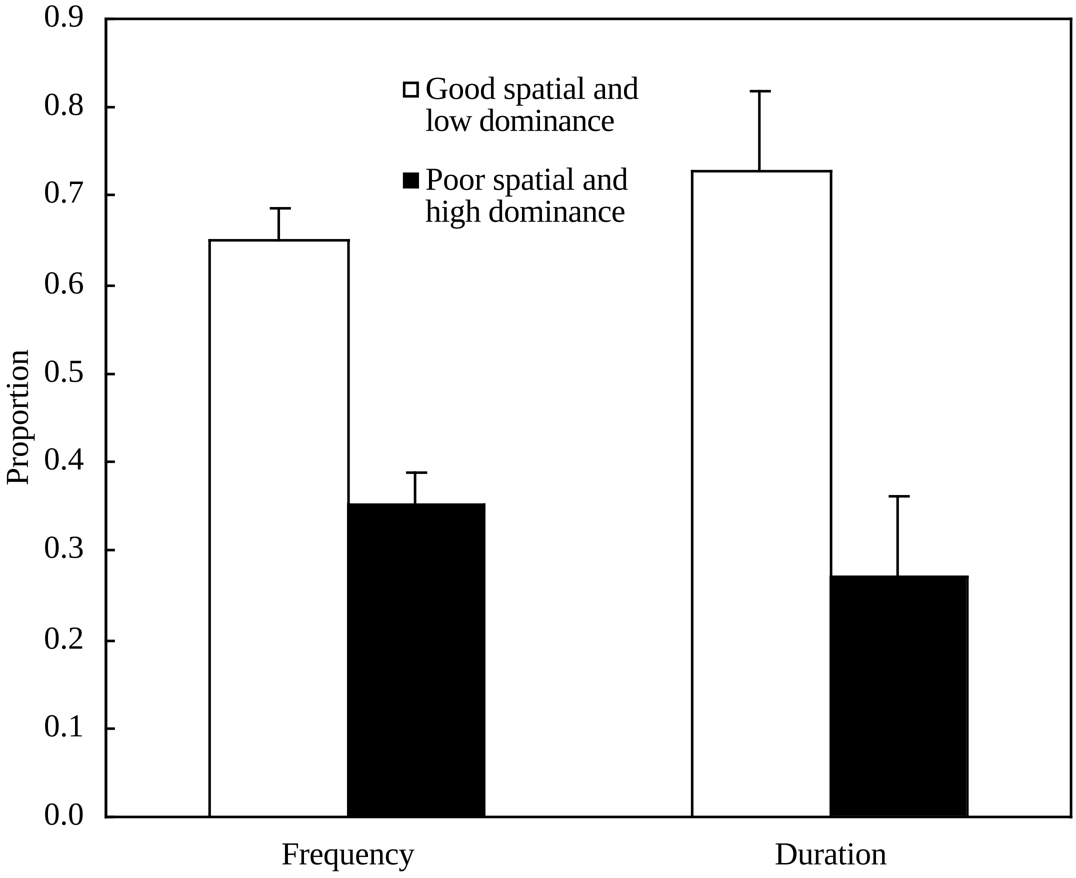


Figure 1. Proportion of visits (frequency) and proportion of visitation time (duration) for females visiting males with good spatial ability and low dominance rank or males with poor spatial ability and high dominance rank. All values are shown as $\overline{X}$ ±SE.

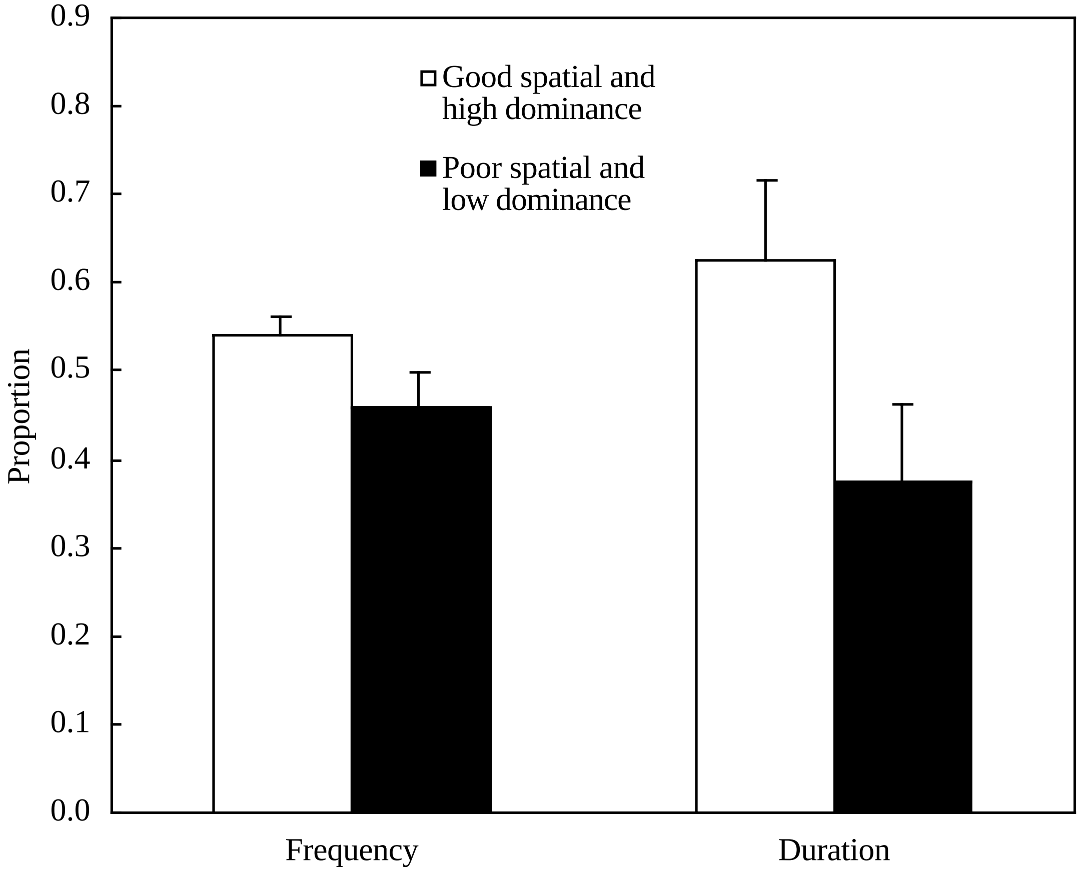


Figure 2. Proportion of visits (frequency) and proportion of visitation time (duration) for females visiting males with good spatial ability and high dominance rank or males with poor spatial ability and low dominance rank. All values are shown as $\overline{X}$ ±SE.

GENERAL DISCUSSION

Summary

My experiments provided insights into the relative strength of different mechanisms of sexual selection acting upon spatial ability and traits associated with dominance rank among male meadow voles (Fig. 1). Males with better spatial ability visited more different nest boxes and made more visits to their most frequently visited nest boxes (Chapter 1). However, the different measures of spatial ability were not all correlated with nest box visitation in the same way (Chapter 3). Males with better spatial-learning ability, as measured by an acquisition task, and with better spatial memory visited more nest boxes overall and made more visits to their most frequently visited nest boxes. In contrast, males that performed well at a transfer task, which measured more complex navigational ability, visited fewer nest boxes and made fewer visits to their most frequently visited nest boxes. Although the trends were in the expected direction, males with better spatial ability did not sire more litters or more pups than males with poor spatial ability (Chapter 1). Thus, the paternity data suggest that the strength of intrasexual selection by scramble competition acting upon spatial ability may be fairly weak, but males with better spatial ability were better able to locate and relocate females' nests. The strength of selection by scramble competition may be strongest during periods of low population density. In support of this hypothesis, I found that males had poorer spatial-learning ability and spatial-learning speed during a period of high population density (Chapter 2).

Males with better spatial ability seemed to encounter more females because they were ranging more widely. My composite index of spatial ability was positively correlated with male home range size (Chapter 1). However, as with nest visitation, not all measures of spatial ability were correlated with home range size in the same way (Chapter 3). Spatial-learning ability, as measured by the acquisition task, was not correlated with male range size. More complex spatial-learning ability, as measured by the transfer task, was positively correlated with range size. Spatial memory was negatively correlated with range size. These results suggest that males with strengths in different components of spatial ability may use alternative mating strategies. Males good at complex navigational tasks seemed to use a mate-searching strategy, while males with good spatial memory repeatedly visited the same female, which suggests they were using a mate-guarding strategy.

Males that were more aggressive and had higher dominance rank also tended to have better spatial-learning ability, which indicated that there is not a trade-off between these behaviors (Chapter 2). The correlation between male dominance rank and spatial ability was not, however, strong enough to give males with higher dominance rank an advantage in terms of locating female nests (Chapter 3). Males with higher dominance rank did not visit more females' nests overall and they did not make more visits to their most frequently visited nest boxes. Male aggression, as measured by average number of attacks per arena trial, was also not related to nest visitation. Thus, males with higher dominance rank did not seem to be more likely to engage in a mate guarding strategy.

Females preferred males with good spatial ability and low dominance rank over males with poor spatial ability and high dominance rank (Chapter 4). Females also showed no preference between males with good spatial ability and high dominance rank and males with poor spatial ability and low dominance rank (Chapter 4). These results suggest that females prefer males with good spatial ability and may avoid males with high dominance rank. Females seemed to exert some degree of choice in the field, preferentially mating with males that visited them more often (Chapter 1). Both female choice and scramble competition seem to favor males with better spatial ability: males with better spatial ability located more females in the field and were preferred by females in the laboratory. In contrast I found no clear advantages of higher dominance rank: dominant males did not visit more females in the field and were not preferred by females in the laboratory. Therefore, selection by contest competition may be counter-acted by scramble competition and female choice. To confirm that this is the case, future studies should examine the relationship between dominance rank and reproductive success.

Spatial Ability and Reproductive Success

Numerous studies conducted with meadow vole populations from diverse parts of their geographic range have shown that males have larger home ranges than females during the breeding season (Ambrose 1973; Madison 1980; Dueser et al. 1981; Webster & Brooks 1981; Boonstra & Rodd 1983; Gaulin & FitzGerald 1986, 1989; Ostfeld et al. 1988; Sheridan & Tamarin 1988; Ostfeld & Canham 1995; Bowers et al. 1996; Fortier & Tamarin 1998; Jacquot 1999). Numerous studies have also shown that males have better spatial ability than females (Gaulin & FitzGerald 1986, 1989; Kavaliers et al. 1993, 1998; Galea et al. 1995, 2002). Brain regions associated with spatial ability are sexually dimorphic in meadow voles (Jacobs et al. 1990; Kavaliers et al. 1998; Galea et al. 1999).

My experiments demonstrated that males with better spatial ability had larger home ranges and visit more females' nests (Chapters 1 and 3). Furthermore, males that made more visits to nest boxes had higher reproductive success (Chapter 1). All of these results support Gaulin & FitzGerald's (1986) hypothesis that spatial ability is a sexually selected trait among meadow voles. However, the results of Chapter 1 left me with a conundrum: males with better spatial ability did not achieve greater reproductive success.

In subsequent chapters, I tested and rejected a number of explanations for why males with better spatial ability were not achieving greater reproductive success. There was no evidence of a trade-off between spatial ability and dominance rank (Chapters 2 and 3), and females preferred males with better spatial ability (Chapter 4). Perhaps the most plausible explanation remaining, as suggested in Chapter 1, is that males with better spatial ability did not achieve greater reproductive success because of the schedule used to remove males from nest boxes. Males were forced to remain in nest boxes for up to 12 hours, which could have prevented them from visiting as many females as they would have under more natural conditions. I may have also occasionally removed males from nest boxes too soon, preventing them from inducing estrus and obtaining a successful mating. These problems could be alleviated in future studies by using nest boxes that allow males to come and go but prevent females from leaving. Vyssotski et al. (2002) described feeding stations with mechanical doors that were opened using antennae that read passive transponders implanted in mice. The door closed after the mouse entered the feeding station and opened again when the mouse approached the door. This system keeps track of which mice have entered the feeding stations, controlling how often each individual is fed. Similar doors could be installed on nest boxes for use in the field. Alternatively, experiments could be conducted in which voles are allowed to range freely within enclosures, and the paternity of all offspring born within the enclosures could be determined. The disadvantage of this design is that male visitation to nests would be difficult to monitor and maternity would be less certain, making paternity considerably more difficult to assess.

Meadow Vole Mating System

Meadow voles are often assumed to be promiscuous or polygamous rather than monogamous (e.g., Gaulin & FitzGerlad 1989; Jacobs et al. 1990), but there seems to be limited evidence for this assumption. Getz (1972) seldom captured the same male-female pairs together and concluded that there was “no indication of formalized social structure within the meadow vole population”. Madison (1980) found that males’ daily ranges overlapped those of multiple females and concluded that males engaged in opportunistic matings with multiple females. Although these two studies provided indirect evidence for promiscuity among meadow voles, neither of them provided data on nest cohabitation or paternity. I found that males tended to repeatedly visit particular nest boxes, suggesting that they had mating preferences. Compiling the data from the two field experiments (Chapters 1 and 3) reveals a significant difference between the number of visits males made to their most frequently visited nest boxes and that expected if males had distributed their visitation evenly among the nests boxes that they visited (Fig. 2; $\chi^2_{53}=919.25$, $P<0.001$). Hence, males exhibited more mate fidelity than would be expected if they had been mating at random.

I identified the sire for 38 litters, and observed only 2 cases (5.3%) of multiple paternity (Chapter 1). Boonstra et al. (1993) assessed the paternity of 78 wild-caught meadow vole litters using two polymorphic allozymes: 11 of the litters showed evidence of multiple paternity. Using these data and a population genetics model, Boonstra et al. (1993) concluded that 33% of meadow vole litters from their population exhibited multiple paternity. One explanation for this difference is that I housed females in nest boxes, which could have reduced the rate of multiple paternity. Another possibility is that my estimate of multiple paternity may have been more accurate because I used microsatellites to assign paternity to every pup, whereas Boonstra et al. (1993) used allozymes to infer multiple paternity. My results suggest that a large proportion of meadow vole litters are sired by a single male, but this interpretation should be confirmed by assessing paternity for a population under more natural conditions.

As described in Chapter 4, meadow voles are also less paternal than other vole species which suggests they are more promiscuous (Wilson 1982; McGuire & Novak 1984; Gruder-Adams & Getz 1985). However, there is also clear evidence that male meadow voles exhibit facultative paternal behavior. Males show a social preference for females with whom they are more familiar and direct more aggression towards females with whom they are less familiar (Parker et al. 2001). In both of my field experiments, I also found evidence for male preferences for certain females (Fig. 2). A male could reduce the likelihood of pregnancy disruption by remaining near his mate (Storey & Snow 1990; Storey 1994, 1996). Males also remain with pups when the female is away from the nest, which provides potential thermoregulatory benefits to the offspring (Storey & Snow 1987; Parker & Lee 2002). Furthermore, males have been shown to guard the nest against other males that are potentially infanticidal (Storey et al. 1994). These results provide clear evidence of a “pair bond” if a pair bond is defined as a prolonged interaction between a male and a female that involves paternal care (Wickler & Seibt 1983). The apparent paternal behavior of meadow voles could also be interpreted as mate guarding. The only distinction between pair bonding and mate guarding seems to be the motivation of the male, which would be difficult to determine. Regardless, male meadow voles seem to be more paternal and more monogamous than was originally assumed.

Human Spatial Ability

A sex difference in spatial ability is among the most well documented psychological differences between men and women (Newcombe 1982; Nyborg 1983; Gaulin & Hoffman 1988; Silverman & Eals 1992; Sherry & Hampson 1997; Hampson 2000). Men tend to perform better than women on tasks involving mental rotation, judgments about moving objects, and geographical knowledge. Testosterone has positive organizational and activational effects upon spatial ability (Christiansen & Knussmann 1987; Jannowsky et al. 1994; Kimura & Hampson 1994), which has led some researchers to suggest that sex differences in spatial ability relate to inter-male competition for mates (Sherry & Hampson 1997). Male superiority at spatial tasks among meadow voles is often cited as evidence that sexual selection may be the ultimate cause of differences in spatial ability in humans (Gaulin 1995; Hampson 1995; Sherry & Hampson 1997; Dabbs et al. 1998; Hampson et al. 1998; Moffat et al. 1998; Beatty 2002; Jones et al. 2003). As with voles, it has been suggested that primitive men could have increased the number of women that they encountered by increasing their range sizes, and this would lead to increased reproductive success (Sherry & Hampson 1997; Jones et al. 2003).

My results provide further support for the hypothesis that sexual selection may lead to male superiority at some spatial tasks. However, not all measures of spatial ability gave me the same conclusion. Male meadow voles better at complex navigation ranged more widely, but made fewer visits to females' nests. This suggests that there may have also been opportunity costs for primitive humans: individuals spending time looking for new mates would have less time to spend with any one mate. I also found that males with better spatial memory seemed to be better at relocating a female's nest, and females were more likely to mate with males that visited them more frequently (Chapters 1 and 3). This suggests that there might be reproductive advantages gained from good spatial memory even in monogamous individuals. For example, a primitive man who spent much of the day hunting for food might have been better able to find his way home if he had better spatial memory. Some researchers have suggested that sex differences in spatial ability among humans are the result of sex differences in foraging habits (Silverman & Eals 1992; Geary 1996, 1998; Sherry & Hampson 1997), but the emphasis of this theory has been on tracking prey and using projectile weapons. An important additional benefit of good spatial ability for a male hunter may be the ability to find his way home to his mate.

It has also been suggested that the evolution of human intelligence is partly due to assortative mating based on mental abilities (Miller 2000; Madden 2001). My results provide the first evidence for female choice based on a cognitive trait in a rodent (Chapter 4). I suggested that the mechanism for this preference may involve female preferences for males with optimal testosterone levels (Ferkin et al. 1994). Female preferences for men with better spatial ability, and perhaps optimal testosterone levels, could partially explain the evolutionary origins of sex differences in spatial ability among humans. The meadow vole is an ideal species for further investigations of the evolution of sex differences in spatial ability because of the extensive body of past research on their population ecology and because of recent advances in our understanding of their neurobiology.

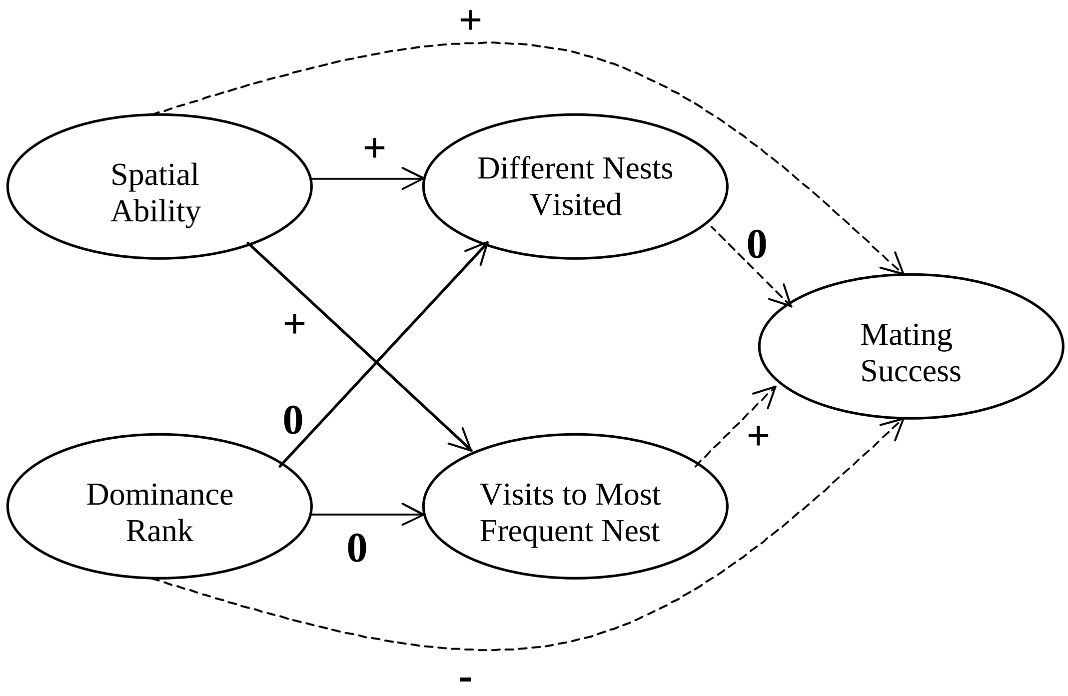


Figure 1. Diagram summarizing the results of Chapters 1-4. Dashed arrows represent female choice and solid arrows represent male-male competition. A “+” indicates a significant positive relationship, a “-“ indicates a significant negative relationship, and “0” indicates no relationship. The two outer arrows indicate female preferences for males regardless of the nature of nest visitation (Chapter 4).

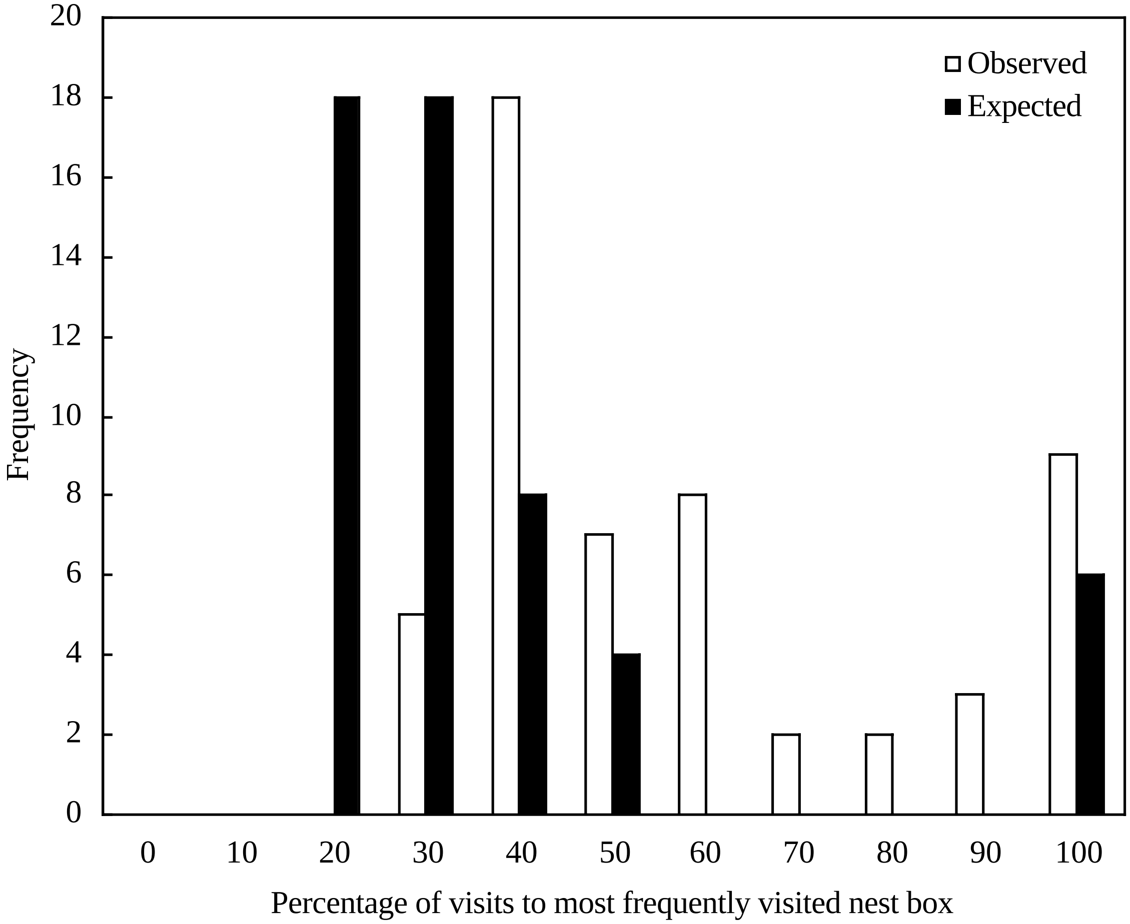


Figure 2. Frequency histograms comparing the observed percentage of visits by males to their most frequently visited nest boxes to that expected if males visited nest boxes evenly. Data from the 2001 and 2002 field experiments were compiled for this comparison.

References
for General Introduction and Discussion

Able, D. J. 1999. Scramble competition selects for greater tailfin size in male red-spotted newts (Amphibia: Salamandridae). *Behavioural Ecology and Socioibiology*, **46,** 423-428.

Ambrose, H. W., III. 1972. Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtus pennsylvanicus*. *Journal of Mammalogy*, **53,** 909-912.

Ambrose, H. W., III. 1973. An experimental study of some factors affecting the spatial and temporal activity of *Microtus pennsylvanicus*. *Journal of Mammalogy*, **54,** 79-110.

Anderson S. 1985. Taxonomy and systematics. In: *Biology of New World Microtus*. (Ed. by R. H. Tamarin), pp. 52-81.

Andersson, M. 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.

Beatty, W. W. 2002. Sex differences in geographical knowledge: driving experience is not essential. *Journal of the International Neuropsychological Society,* **8,** 804-810.

Beer, J. R. & MacLeod, C. F. 1961. Seasonal reproduction in the meadow vole. *Journal of Mammalogy,* **42,** 483-489.

Boonstra, R. & Rodd, F. H. 1983. Regulation of breeding density in *Microtus pennsylvanicus*. *Journal of Animal Ecology,* **52,** 757-780.

Boonstra, R., Xia, X. & Pavone, L. 1993. Mating system of the meadow vole, *Microtus pennsylvanicus*. *Behavioral Ecology*, **4,** 83-89.

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

Bradbury, J. W. & Daview, N. B. 1987. Relative roles of intra- and intersexual selection. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 143-163. New York: John Wiley & Sons Ltd.

Christiansen, K. & Knussman, R. 1987. Sex Hormone and cognitive functioning in men. *Neuropsychobiology,* **18,** 27-36.

Cremer, S. & Greenfield, M. D. 1998. Partitioning the components of sexual selection: attractiveness and agonistic behaviour in male wax moths, *Achroia grisella* (Lepidoptera: Pyralidae). Ethology, **104,** 1-9.

Cunningham, E. J. A. & Birkhead, T. R. 1998. Sex roles and sexual selection. *Animal Behaviour,* **56,** 1311-1321.

Dabbs, J. M., Chang, E. L., Strong, R. A. & Milun, R. 1998. Spatial ability, navigation strategy, and geographic knowledge in men and women. *Evolution and Human Behavior,* **19,** 89-98.

Darwin, C. 1871. *The Descent of Man, and Selection in Relation to Sex.* Princeton, New Jersey: Princeton University Press.

Dewsbury, D. A. 1981. An exercise in the prediction of monogamy in the field from laboratory data on 42 species of muroid rodents. *The Biologist,* **63,** 138-162.

Dieterich, R. A. & Preston, D. J. 1977. The meadow vole (*Mictrotus pennsylvanicus*) as a laboratory animal. *Laboratory Animal Science*, **27,** 494-499.

Droney, D. C. 1992. Sexual selection in a leking Hawaiian *Drasophila*: the roles of male competition and female choice in male mating success. *Animal Behaiour*., **44,** 1007-1020.

Dueser, R. D., Wilson, M. L. & Rose, R. K. 1981. Attributes of dispersion meadow voles in open-grid populations. *Acta Theriologica*, **26,** 139-162.

Ebensperger, L. A. 1998. Do female rodents use promiscuity to prevent male infanticide? Ethology Ecology and Evolution, **10,** 129-141.

Ferkin, M. H., Sorokin, E. S., Renfroe, M. W. & Johnston, R. E. 1994. Attractiveness of male odors to females varies directly with plasma testosterone concentration in meadow voles. *Physiology & Behavior*, **55,** 347-353.

Fortier, G. M., Erskine, M. S. & Tamarin, R. H. 1996. Hormonal correlates of receptivity in female meadow voles, *Microtus pennsylvanicus*. *Journal of Mammalogy*, **77,** 404-406.

Galea, L. A. M., Kavaliers, M., Ossenkopp, K.-P. & Hampson, E. 1995. Gonadal hormone levels and spatial learning performance in the Morris water maze in male and female meadow voles, *Microtus pennsylvanicus*. *Hormones and Behavior* **29,** 106-125.

Galea, L. A. M., Perrot-Sinal, T. S., Kavaliers, M. & Ossenkopp, K.-P. 1999. Relations of hippocampal volume and dentate gyrus width to gonadal hormone levels in male and female meadow voles. *Brain Research*, **821,** 383-391.

Galea, L. A. M., Lee, T. T.-Y., Kostaras, X., Sidhu, J. A. & Barr, A. M. 2002. High levels of estradiol impair spatial performance in the Morris water maze and increase 'depressive-like' behaviors in female meadow voles. *Physiology & Behavior*, **77,** 217-225.

Gaulin, S. J. C. 1995. Does evolutionary theory predict sex differences in the brain? *The Cognitive Neurosciences*, **80,** 1211-1225.

Gaulin, S. J. C. & FitzGerald, R. W. 1986. Sex differences in spatial ability: an evolutionary hypothesis and test. *The American Naturalist*, **127,** 74-88.

Gaulin, S. J. C. & FitzGerald, R. W. 1989. Sexual selection for spatial-learning ability. *Animal Behaviour*, **37,** 322-331.

Gaulin, S. J. C. & Hoffman, H. A. 1988. Evolution and development of sex differences in spatial ability. In: *Human Reproductive Behaviour: A Darwinian Perspective* (Ed. by L. Betzig, M. B. Mulder, & P. Turke), pp. 7-152. New York: Cambridge University Press.

Geary, D. C. 1996. Sexual selection and sex differences in mathematical abilities. *Behavioral and Brain Sciences*, **19,** 229-284.

Geary, D. C. 1998. Sexual selection, the division of labor, and the evolution of sex differences. *Behavioral and Brain Science*, **21,** 444-448

Getz, L. L. 1972. Social structure and aggressive behavior in a population of *Microtus pennsylvanicus*. *Journal of Mammalogy*, **53,** 310-317.

Gray, G. D. & Dewsbury, D. A. 1975. A quantitative description of the copulatory behaviour of meadow voles (*Microtus pennsylvanicus*). *Animal Behaviour*, **23,** 261-267.

Gray, G. D., Kenney, A. M. & D. A. Dewsbury. 1977. Adaptive significance of the copulatory behavior pattern of male meadow voles (*Microtus pennsylvanicus*) in relation to induction of ovulation and implantation in females. *Journal of Comparative Physiological Psychology*, **91,** 1308-1319.

Gruder-Adams, S. & Getz, L. L. 1985. Comparison of the mating system and paternal behavior in *Microtus ochrogaster* and *M. pennsylvanicus*. *Journal of Mammalogy*, **66,** 165-167.

Hamilton, W. J., Jr. 1941. Reproduction of the field mouse *Microtus pennsylvanicus* (Ord). 237, *Cornell University Agricultural Experiment Station Memoirs*, **237,** 1-23

Hampson, E. 1995. Spatial cognition in humans: Possible modulation by androgens and estrogens. *Journal of Psychiatry and Neuroscience,* **20,** 397-404.

Hampson, E. 2000. Sexual differences of spatial functions in humans. In: *Sexual Differentiation of the Brain* (Ed. by A. Matsumoto), pp. 279-300. New York: CRC Press.

Hampson, E., Rovet, J. F. & Altmann, D. 1998. Spatial reasoning in children with congenital adrenal hyperplasia due to 21-hydroxylase deficiency. *Developmental Neuropsychology,* **14,** 299-320.

Howard, R. D., Moorman, R. S. & Whiteman, H. H. 1997. Differential effects of mate competition and mate choice on eastern tiger salamanders. *Animal Behaviour*, **53,** 1345-1356.

Jacobs, L. F., Gaulin, S. J., Sherry, D. F. & Hoffman, G. E. 1990. Evolution of spatial cognition: sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Science, USA*, **87,** 6349-6352.

Jacquot, J. J. 1999. Use of space and movement of two vole species in response to habitat quality. Ph.D. thesis, Miami University.

Janowsky, J. S., Oviatt, S. K. & Orwoll, E. S. 1994. Testosterone influences spatial cognition in older men. *Behavioral Neuroscience*, **108,** 325-332.

Jones, C. A., Braithwaite, V. A. & Healy, S. D. 2003. The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, **117,** 403-411.

Kavaliers, M., Eckel, L. A. & Ossenkopp, K.-P. 1993. Brief exposure to 60 Hz magnetic fields improves sexually dimorphic spatial learning performance in meadow voles, *Microtus pennsylvanicus*. *Journal of Comparative Physiology A*, **173,** 241-248.

Kavaliers, M., Ossenkopp, K.-P., Galea, L. A. M. & Kolb, B. 1998. Sex differences in spatial learning and prefrontal and parietal cortical dendritic morphology in the meadow vole, *Microtus pennsylvanicus*. *Brain Research*, **810,** 41-47.

Kimura, D. & Hampson, E. 1994. Cognitive pattern in men and women is influenced by fluctuations in sex hormones. *Current Directions in Psychological Science,* **3,** 57-61.

Klein, S. L. & Nelson, R. J. 1998. Sex and species differences in cell-mediated immune responses in voles. *Canadian Journal of Zoology*, **76,** 1394-1398.

Klein, S. L. & Nelson, R. J. 1999. Social interactions unmask sex differences in humoral immunity in voles. *Animal Behaviour*, **57,** 603-610.

Koeppl, J. W. 1985. Zoogeography. In: *Biology of New World Microtus.* (Ed. by R. H. Tamarin), pp. 84-115.

Lee, C. & Horvath, D. J. 1969. Management of the meadow vole (*Microtus pennsylvanicus*). *Laboratory Animal Care,* **19,** 88-91.

Lee, C., Horvath, D. J., Metcalfe, R. W. & Inskeep, E. K. 1970. Ovulation in *Microtus pennsylvanicus* in a laboratory environment. *Laboratory Animal Care,* **20,** 1098-1102.

Madden, J. 2001. Sex, bowers and brains. *Proceedings of the Royal Society of London, Series B,* **268**, 833-838.

Madison, D. M. 1980. Space use and social structure in meadow voles, *Microtus pennsylvanicus*. *Behavioral Ecology Sociobiology,* **7,** 65-71.

Madison, D. M., FitzGerald, R. W. & McShea, W. J. 1984. Dynamics of social nesting in overwintering meadow voles (*Microtus pennsylvanicus*): possible consequences for population cycling. *Behavioral Ecology Sociobiology,* **15,** 9-17.

McGuire, B. & Novak, M. 1984. A comparison of maternal behavior in the meadow vole (*Microtus pennsylvanicus*), prairie vole (*M. ochrogaster*) and pine vole (*M. pinetorum*). *Animal Behaviour,* **32,** 1132-1141.

Meek, L. R. & Lee, T. M. 1993a. Female meadow voles have a preferred mating pattern predicted by photoperiod, which influences fertility. *Physiology and Behavior,* **54,** 1201-1210.

Meek. L. R. & Lee, T. M. 1993b. Prediction of fertility by mating latency and photoperiod in nulliparous and primiparous meadow voles (*Microtus pennsylvanicus*). *Journal of Reproduction and Fertility,* **97,** 353-357.

Meek, L. R. & Lee, T. M. 1994. Luteinizing hormone and prolactin in mated female meadow voles housed in long and short day lengths. *Biology of Reproduction,* **51,** 725-730.

Miller, G. 2000. *The Mating Mind: How Sexual Choice Shaped the Evolution of Human Nature*. Anchor Books: New York.

Moffat, S. D., Hampson, E. & Hatzipantelis, M. 1998. Navigation in a “virtual” maze: sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behavior,* **19,** 73-87.

Moore, A. J. 1990. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. *Evolution,* **44,** 315-331.

Moore, A. J. & Moore, P. J. 1999. Balancing sexual selection through opposing mate choice and male competition. *Proceedings of the Royal Society of London Series B*, **266,** 711-716.

Morrison, P., dieterich, R. & Preston, D. 1976. Breeding and reproduction of fifteen wild rodents maintained as laboratory colonies. *Laboratory Animal Science*, **26,** 237-243.

Murphy, C. G. 1998. Interaction-independent sexual selection and the mechanisms of sexual selection. *Evolution*, **52,** 8-18.

Newcombe, N. 1982. Sex-related differences in spatial ability: problems and gaps in current approaches. In: *Spatial Abilities: Development and Physiological Foundations* (Ed. by M. Potegal), pp. 223-250. New York: Academic Press.

Norrdahl, K. & Korpimäki, E. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? *Ecology*, **79,** 226-232.

Nyborg, H. 1983. Spatial ability in men and women: review and new theory. *Advances in Behavior Research and Theory*, **5,** 89-140.

Ostfeld, R. S. & Canham, C. D. 1995. Density-dependent processes in meadow voles: an experimental approach. *Ecology*, **76,** 521-532.

Ostfeld, R. S., Pugh, S. R., Seamon, J. O. & Tamarin, R. H. 1988. Space use and reproductive success in a population of meadow voles. *Journal of Animal Ecology,* **57**, 385-394.

Parker, G. A. 2000. Scramble in behaivour and ecology. *Philosophical Transactions of the Royal Society of London, Series B,* **355,** 1637-1645.

Parker, K. J. & Lee, T. M. 2001. Central vasopressin administration regulates the onset of facultative paternal behavior in *Microtus pennsylvanicus* (Meadow voles). *Hormones and Behavior,* **39,** 285-294.

Parker, K. J. & Lee, T. M. 2002. Interaction of photoperiod and testes development is associated with paternal care in *Microtus pennsylvanicus* (meadow vole). *Physiology and Behavior,* **75,** 91-95.

Parker, K. J., Phillips, K. M & Lee, T. M. 2001. Development of selective partner preferences in captive male and female meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour*, **61,** 1217-1226.

Penn, D. J. & Potts, W. K. 1999. The evolution of mating preferences and major histocompatibility complex genes. *The American Naturalist*, **153,** 145-164.

Plante, Y., Boag, P. T., White, B. N. & Boonstra, R. 1991. Highly polymorphic genetic markers in meadow voles (*Microtus pennsylvanicus*) revealed by a murine major histocompatibility complex (MHC) probe. *Canadian Journal of Zoology*, **69,** 213-220.

Pugh, S. R., Ostfeld, R. S., Tamarin, R. H. 1993. Reproductive asynchrony and its potential role in the mating system of meadow voles. *Acta Theriologica*, **38,** 263-271.

Salo, A. L. & Dewsbury, D. A. 1995. Three experiments on mate choice in meadow voles (*Microtus pennsylvanicus*). *Journal of Comparative Psychology,* **109,** 42-46.

Schwagmeyer, P. L. & Parker, G. A. 1987. Queuing for mates in thirteen-lined ground squirrels. *Animal Behaviour*, **35,** 1015-1025.

Schwagmeyer, P. L. & Woontner, S. J. 1986. Scramble competition polygyny in thirteen-lined ground squirrels: the relative contributions of overt conflict and competitive mate searching. *Behavioural Ecology Sociobiology*, **19,** 359-364.

Sih, A. Lauer, M. & Krupa, J. J. 2002. Path analysis and the relative importance of male-female conflict, female choice and male-male competition in water striders. *Animal Behaviour*, **63,** 1079-1089.

Sheridan, M. & Tamarin, R. H. 1988. Space use, longevity, and reproductive success in meadow voles. *Behavioral Ecology and Sociobiology,* **22,** 85-90.

Sherry, D. F. & E. Hampson. 1997. Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends in Cognitive Science*, **1,** 50-56.

Silverman, I. & Eals, M. 1992. Sex differences in spatial abilities: Evolutionary theory and data. In: *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (Ed. by J. H. Barkow, L. Cosmides & J. Tooby), New York: Oxford University Press.

Sorenson, L. G. & Derrickson, S. R. 1994. Sexual selection in the northern pintail (*Anas acuta*): the importance of female choice versus male-male competition in the evolution of sexually-selected traits. *Behavioral Ecology and Sociobiology,* **35,** 389-400.

Storey, A. E. 1994. Pre-implantation pregnancy disruption in female meadow voles *Microtus pennsylvanicus* (Rodentia: Muridae): Male competition or female mate choice? *Ethology*, **98,** 89-100.

Storey, A. E. 1996. Behavioral interactions increase pregnancy blocking by unfamiliar male meadow voles. *Physiology and Behavior,* **60,** 1093-1098.

Storey, A. E. & Snow, D. T. 1987. Male identity and enclosure size affect paternal attendance of meadow voles, *Microtus pennsylvanicus*. *Animal Behaviour,* **35,** 411-419.

Storey, A. E. & Snow, D. T. 1990. Postimplantation pregnancy disruptions in meadow voles: relationship to variation in male sexual and aggressive behavior. *Physiology and Behavior,* **47,** 19-25.

Storey, A. E., Bradbury, C. G. & Joyce, T. L. 1994. Nest attendance in male meadow voles: the role of the female in regulating male interactions. *Animal Behaviour,* **47,** 1037-1046.

Tamarin, R. H. 1977. Demography of the beach vole (*Microtus breweri*) and the meadow vole (*Microtus pennsylvanicus*) in southeastern Massachusetts. *Ecology,* **58,** 1310-1321.

Thomas, P. 1988. An experimental analysis of the sexual selection, resource competition, and exploitation as a resource hypotheses for infanticidal behavior in meadow voles, *Microtus pennsylvanicus*. Masters thesis, Villanova University.

Trivers, R. L. 1972. Parental investment and sexual selection. In: *Sexual Selection and the Descent of Man* (Ed. by B. Campbell), pp. 136-179, Chicago: Aldine.

Vyssotski, A. L, Dell'Omo, G., Poletaeva, I. I., Vyssotski, D. L, Minichiello, L., Klein, R., Wolfer, D. P. & Lipp, H.-P. 2002. Long-term monitoring of hippocampus-dependent behavior in naturalistic settings: mutant mice lacking neuortrophin receptor TrkB in the forebrain show spatial learning but impaired behavioral flexibility. *Hippocampus,* **12,** 27-38.

Walker, E. P. 1999.*Walker's Mammals of the World*. 6th edn. Baltimore: The Johns Hopkins University Press.

Webster, A. B. & Brooks, R. J. 1981. Social behavior of *Microtus pennsylvanicus* in relation to seasonal changes in demography. *Journal of Mammalogy,* **62,** 738-751.

Wickler, W. & Seibt, U. 1983. Monogamy: an ambiguous concept. In: Mate Choice (Ed. by P. Bateson), pp. 33-50. New York: Cambridge University Press.

Wiley, R. H. & Poston, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. *Evolution,* **50,** 1371-1381.

Wilson, S. C. 1982. Parent-young contact in prairie and meadow vole. *Journal of Mammalogy,* **63,** 300-305.

Yamamura, N. & Tsuji, N. 1989. Postcopulatory guarding strategy in a finite mating period. *Theoretical Population Biology*, **35,** 36-50.

Appendix 1: Enclosure Maps

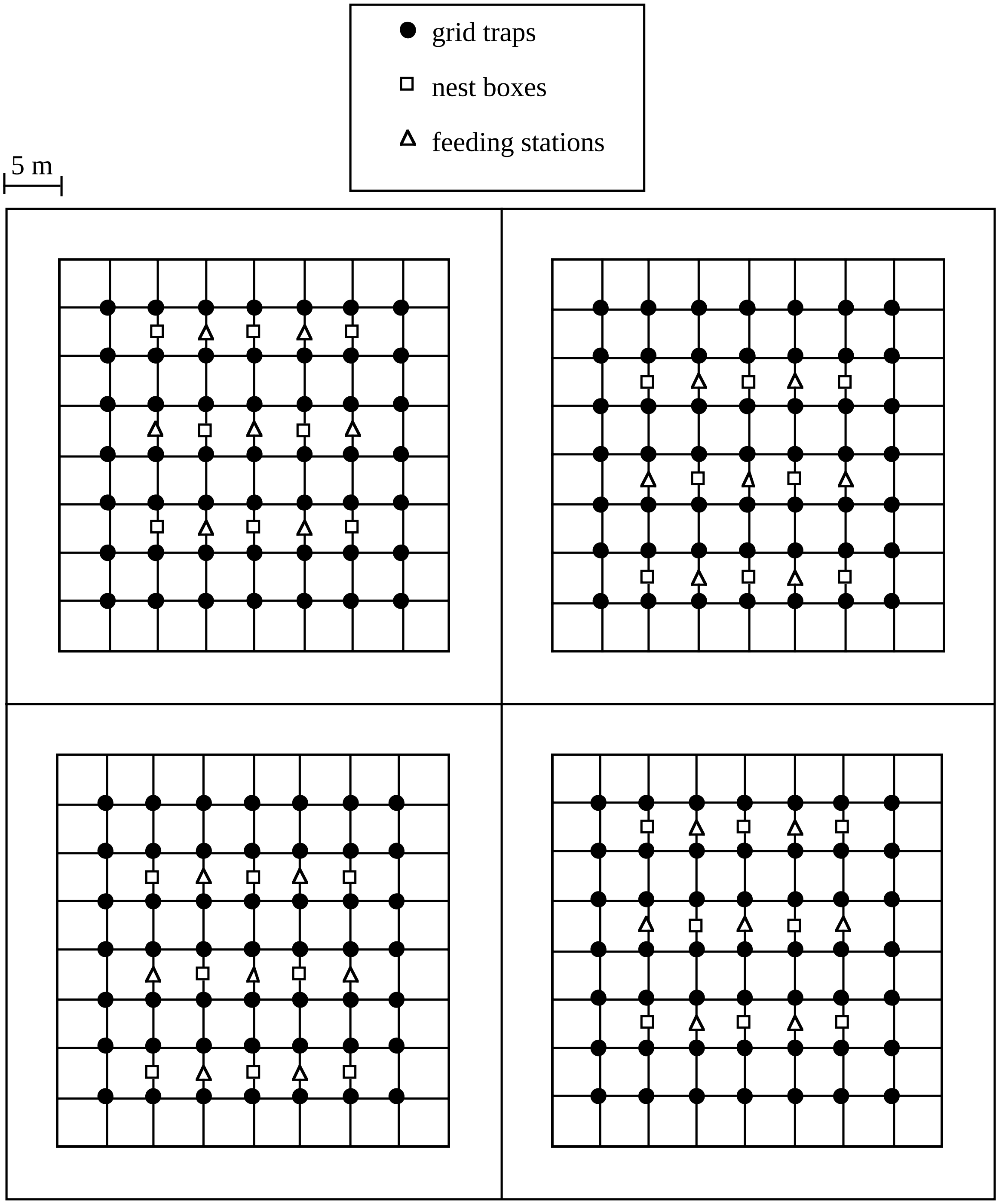


Figure 1. Map of 40 × 40 m enclosures used for experiments described in Chapter 1. The outer lines represent 50 cm high plastic fencing. A 5 m strip was mowed between the trapping grids and the fencing and another 5 m strip was mowed around the outer fence. All four enclosures were surrounded by an electric fence.

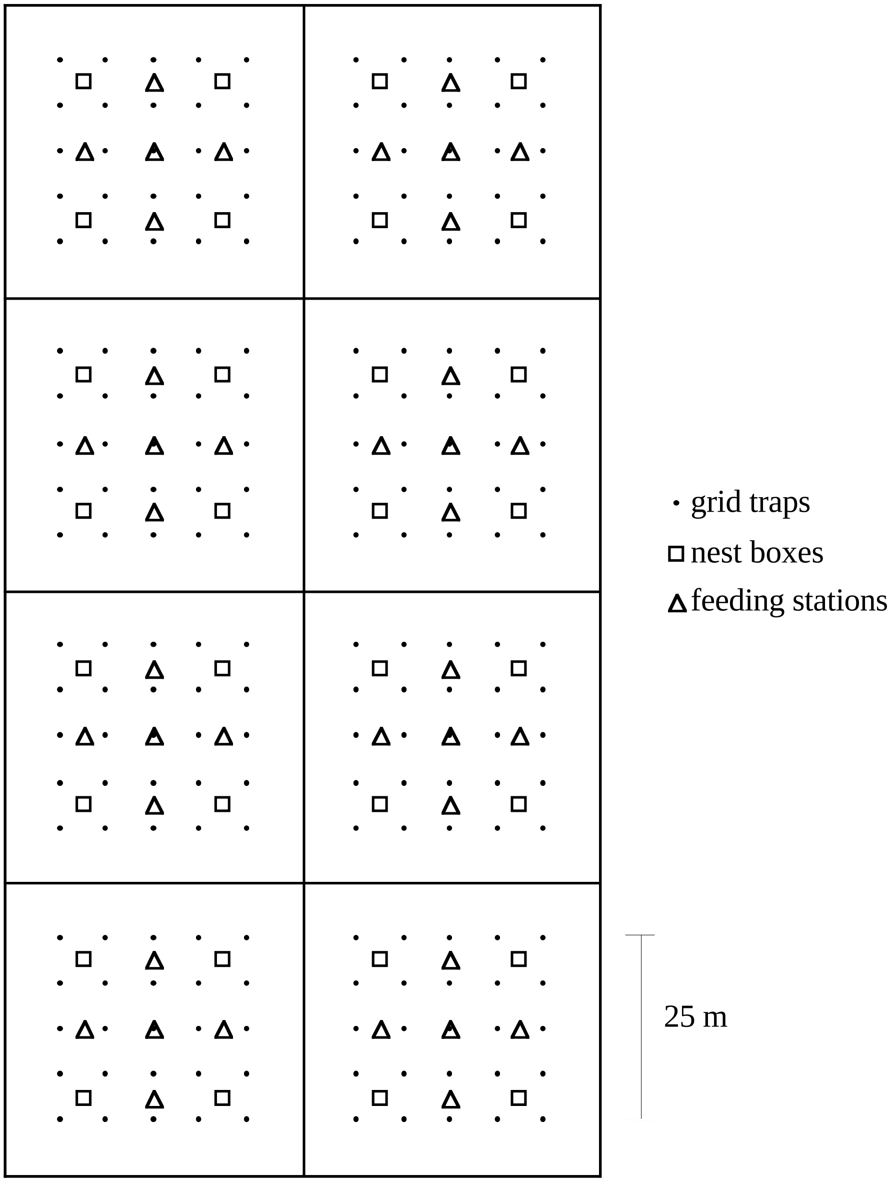


Figure 2. Map of eight 32 × 32 m enclosures used for experiment described in Chapter 3. The black lines represent 60 cm high, 20 gauge, galvanized steel walls. Vegetation was removed from a 1 m strip on either side of the walls. All eight enclosures were surrounded by an electric fence.

Appendix 2: Sample Paternity Gel

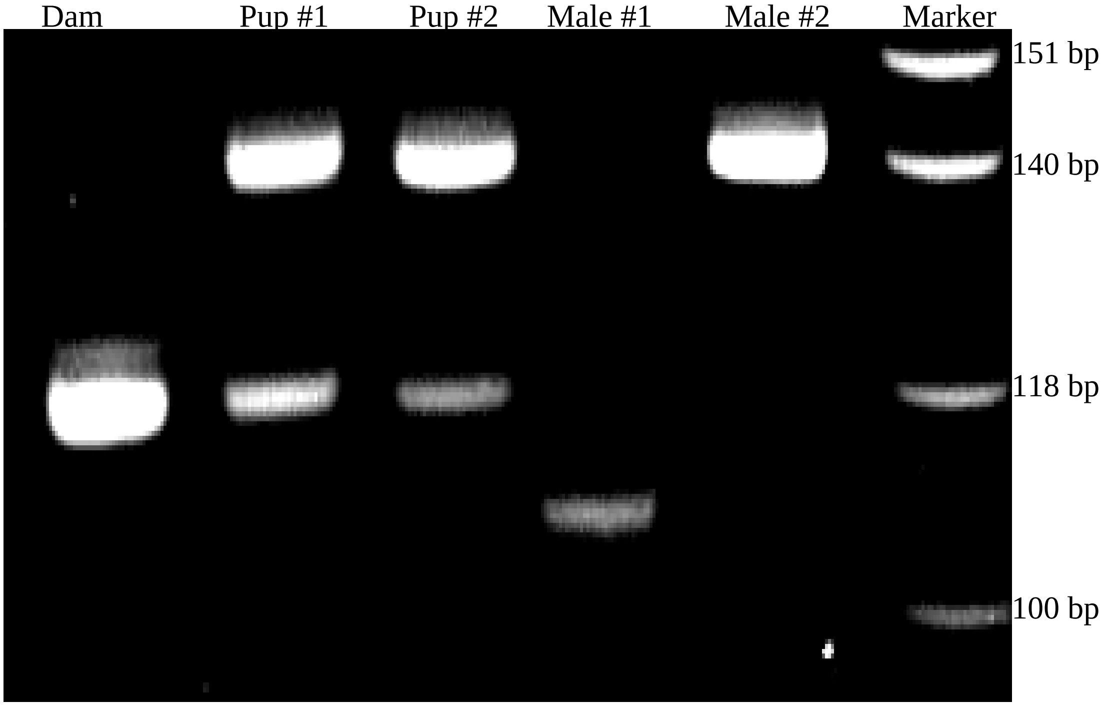


Figure 1. Example of an 8% acrylamide gel used for paternity determination for Experiment 2 described in Chapter 1. The first five lanes contain vole DNA amplified using a microsatellite primer (MSMM3, Ishibashi et al. 1999) and the final lane contains a molecular marker (ϕX174 DNA/*Hin*f I, Promega) with associated numbers of base pairs at the right. The female is a homozygote for a 115 bp allele that is also possessed by each of her pups. The pups are both heterozygotes with a 140 bp allele that must have been inherited from the sire. The two males shown visited the female's nest box 19-23 days prior to parturition, and were therefore both potential sires of the pups. Male #1 is a homozygote for a 110 bp allele that excludes him at the sire of the two pups. Male #2 possesses the 140 bp allele, making him the sire of the two pups.