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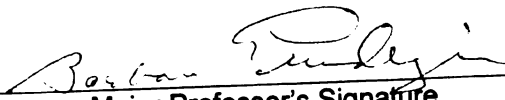
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PERSONALITY IN MICHIGAN'S *PEROMYSCUS*

By

Lauri L. Torgerson

A THESIS

Submitted to
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ABSTRACT

PERSONALITY IN MICHIGAN'S *PEROMYSCUS*

By

Lauri Lynn Torgerson

An emerging area of research investigates the ecological implications of repeatable individual differences in behavior. A personality is any behavior that is repeatable over time and across contexts. I examined inter- and intraspecific variation in personality in *Peromyscus leucopus noveboracensis*, the white-footed mouse, and *P. maniculatus gracilis*, the woodland deer mouse, as a mediator of coexistence and dispersal. I used open-field trials and principal component analysis to extract axes that describe activity, sociality, aggression, and location. I then used linear, generalized linear, and mixed effect models to reveal that *P. maniculatus* was more active and social than *P. leucopus*. In dyadic trials, sociality and aggression of the focal mouse were independent of the species of the opponent mouse. Analyses with raw variables indicated that both species approached heterospecifics more than conspecifics, and retreated from *P. maniculatus* more than from *P. leucopus*. Because extreme over-winter mortality left my study area almost vacant, I used behavioral axes to examine arrival date in dispersers. Early dispersers were more active, social, and submissive than late-season dispersers. Activity and sociality were also plastic over time, with the trend among all mice being to reduce activity and sociality as the season progressed. These studies illustrate that personality may be an axis of niche differentiation and is important in describing dispersal phenotypes in *Peromyscus*, thus illustrating the value of including personality in ecological studies.

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CHAPTER ONE

Introduction to *Peromyscus*, personality, coexistence and dispersal

Psychologists have long studied consistent individual differences in human behavior, or personalities (Allport 1937; Cattell 1946), and their impacts on an individual's place in society (Anderson et al. 2001; Goldberg 1972; Zhang and Arvey 2009). Until recently, ecologists and evolutionary biologists have regarded individual differences in animal behavior as noise. However, recent research has begun to examine the ecological and evolutionary implications of repeatable individual differences in behavior. These are termed temperaments (Réale et al. 2007), behavioral syndromes (Sih et al. 2004), or personalities (Dingemanse et al. 2003). For the purpose of this thesis, I will use the term personality to refer to any behavior that is repeatable over time and across contexts. Personalities can strongly influence community ecology, population dynamics, and landscape ecology (Réale et al. 2007), possibly lending insight into studies of coexistence and dispersal. This thesis seeks to examine the role of animal personality in species coexistence and dispersal in deer mice of the genus *Peromyscus*.

The white-footed mouse, *Peromyscus leucopus noveboracensis*, and the woodland deer mouse, *P. maniculatus gracilis*, live both allopatrically and sympatrically in the Great Lakes region and have experienced climate-induced geographic range changes and shifts in relative abundance in recent years (Myers et al. 2009). Since 1980, populations of *P. leucopus*, the more southern congener, have expanded northward and eastward from Wisconsin into the Upper Peninsula of Michigan and become sympatric with Michigan *P. maniculatus* populations. Coincident

declines in *P. maniculatus gracilis*, the northern congener, have been observed in the northern Lower Peninsula of Michigan (Myers et al. 2005; Myers et al. 2009).

In 2008, I live-trapped *P. leucopus* and *P. maniculatus gracilis* in the Pigeon River State Forest, MI with the goal of uncovering inter- and intraspecific variation in personality that might mediate species coexistence and explain recent geographic range shifts and shifts in relative abundance. My study area supported one resident mouse in early May, leaving a large area to be re-colonized. In the fall, the grid supported 40 residents. The extremely low spring abundance allowed me to examine how personality mediated dispersal over the course of the season.

Coexistence in *Peromyscus leucopus* and *P. maniculatus gracilis*

To coexist stably, sympatric species need to differentiate niche space in attributes such as their ecology or morphology (Gause 1934; Hardin 1960; MacArthur and Levins 1967). Among some sympatric species, differential use of microhabitat has been cited as enabling coexistence (Price and Kramer 1984). When microhabitat is not partitioned spatially, small mammals might still partition the microhabitat temporally (Haim and Rozenfeld 1993; Kotler et al. 1993). In mice of the genus *Peromyscus* that occupy the same microhabitat at the same time, coexistence is sometimes accomplished through food partitioning (Smartt 1978; Wolff et al. 1985). While time, space, or food partitioning are often sufficient to explain coexistence in small mammals, in cases where these axes are inadequate, we are unable to predict how the relative abundance of competing species will respond to the changing environment in which they live (Munkemuller et al. 2009).

Much research has examined the similarities and differences between *Peromyscus leucopus noveboracensis* and either *P. maniculatus gracilis* (the subspecies I studied) or a similar subspecies, *P. m. nubiterrae*, the cloudland deer mouse. *Peromyscus leucopus* and *P. maniculatus nubiterrae* have similar population ecologies and feeding habits (Wolff 1985a; Wolff et al. 1985), but some research has suggested that the two species exhibit differences in microhabitat use, nest use, and winter survivorship. One study showed that *Peromyscus leucopus* was active earlier in the night and when the weather was comparably warmer, more humid, and more overcast when compared with *P. m. gracilis* (Drickamer and Capone 1977). Another study suggested that *Peromyscus maniculatus gracilis* used larger nests, increased food hoarding behavior, and a greater use of torpor in winter (Pierce and Vogt 1993). Both mice prefer arboreal nests when in allopatry, but *P. leucopus* seemed to move to ground nests when sympatric with *P. m. nubiterrae* (Dooley and Dueser 1996). Coexistence of these two species has been partially attributed to interspecific differences in winter acclimatization paired with fluctuating environmental conditions, which allow *P. leucopus* to increase in relative abundance during summers and warm years and *P. maniculatus* to increase in relative abundance during winters and cold years (*P. m. gracilis*—Long 1996; *P. m. nubiterrae*—Wolff 1996). Despite a great deal of research on these species, niche axes that allow their coexistence remain largely unknown. This could be because morphology and ecology are not the primary niche axes in which these two coexisting species differentiate themselves and should thus lead us to examine personality as a potential axis of niche differentiation.

Dispersal

Much is already known about dispersal in *P. leucopus* and *P. maniculatus*. Two types of dispersers have been identified, colonists and non-colonists. Colonists are adult mice that disperse into habitat that has experienced extreme winter mortality early in the spring, while non-colonizing late-season dispersers disperse into an already populated area (Krohne et al. 1984). Among all dispersers, males disperse more often and farther than females (Jacquot and Vessey 1995; Krohne et al. 1984). On the contrary, if one considers only colonist dispersers, females disperse slightly more often than males, and are adults (Jacquot and Vessey 1995; Krohne et al. 1984). While much is known about what ages and sexes are most likely to disperse, less is known about what actually drives certain individuals to disperse. I propose that personality may be a motivating force behind dispersal.

The decision to disperse is affected by external factors like inbreeding risk and competition, and internal phenotypic factors like physiology, morphology, life history, and behavior (Clobert et al. 2009). Inter-individual variation in personality axes, including sociality, aggression, exploration, and boldness, has been linked to dispersal in several vertebrate species and may lend insight into the question of what personality phenotypes are most likely to colonize de-populated habitats (Cote and Clobert 2007; Cote et al. 2010; Dingemanse et al. 2003; Duckworth and Badyaev 2007).

Sample sizes in study

In 2008, I live-trapped *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* in the Pigeon River State Forest. I trapped 142 mice a total of 622 times. Twenty-eight of these mice were *P. leucopus* and 44 were *P. maniculatus*. Because they

were not used in open-field behavioral trials, I did not identify the species of the remaining 70 mice. To investigate the following hypotheses, I performed open-field behavioral trials designed to extract behavioral axes on 40 *P. maniculatus* individuals and 18 *P. leucopus* individuals. I also performed dyadic trials on 17 *P. maniculatus* individuals and 12 *P. leucopus* individuals.

Hypotheses and Predictions

In Chapter 2, I used behavioral variables extracted from videos of open-field trials to examine inter- and intraspecific variation in *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis*. I tested the prediction that *P. maniculatus* would be more active than *P. leucopus* and that activity level would be correlated across contexts to form a personality.

In Chapter 3, I used three of the four behavioral axes (activity, sociality, and aggression) that were uncovered in Chapter 2 to create linear models and mixed effects linear models that described the behavioral phenotypes of mice that dispersed onto my grid throughout the season. To determine if plasticity had any effect on the relationship between personality and arrival date, I also examined the effects of plasticity and habituation on these personality axes.

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CHAPTER TWO

Inter- and intraspecific variation in the personality of sympatric *Peromyscus*

INTRODUCTION

Ecologists have long been fascinated by how two or more similar species are able to persist in sympatry. To coexist stably, sympatric species need to differentiate niche space in attributes such as their ecology or morphology (Gause 1934; Hardin 1960; MacArthur and Levins 1967). Among some sympatric species in California, such as deer mice (*Peromyscus maniculatus*), cactus mice (*P. eremicus*), agile kangaroo rats (*Dipodomys agilis*), and desert woodrats (*Neotoma lepida*), differential use of microhabitat has been cited as enabling coexistence (Price and Kramer 1984). When microhabitat is not partitioned spatially, small mammals such as spiny mice (genus *Acomys*) and sand dune gerbils (genus *Gerbillus*) partition the microhabitat temporally (Haim and Rozenfeld 1993; Kotler et al. 1993). In mice of the genus *Peromyscus* that occupy the same microhabitat at the same time, coexistence is sometimes accomplished through food partitioning (Smartt 1978; Wolff et al. 1985). While time, space, or food partitioning are often sufficient to explain coexistence in small mammals, in cases where these axes are inadequate, we are unable to predict how species will respond to the changing environment in which they live (Munkemuller et al. 2009).

Deer mice of the genus *Peromyscus* are widespread across North America and are being affected by the shifting environment produced by climate change (Moritz et al. 2008; Myers et al. 2009). Many of these species are recently diverged (Weber and Hoekstra 2009), are ecologically and morphologically similar, and live sympatrically

(Barry et al. 1990; Drickamer 1990; Wolff 1996). The white-footed mouse, *Peromyscus leucopus noveboracensis*, and the woodland deer mouse, *P. maniculatus gracilis*, live both allopatrically and sympatrically in the Great Lakes region and have experienced climate-induced changes in recent years (Myers et al. 2009). Since 1980, populations of *P. leucopus*, the more southern congener, have expanded northward and eastward from Wisconsin and become sympatric with previously allopatric *P. maniculatus* populations in Michigan's Upper Peninsula. Coincident declines in *P. maniculatus gracilis*, the northern congener, have been observed in southern parts of its range (Myers et al. 2005; Myers et al. 2009).

An abundance of research has examined the similarities and differences between *Peromyscus leucopus noveboracensis* and either *P. maniculatus gracilis* (the subspecies I studied) or a similar subspecies, *P. m. nubiterrae*, the cloudland deer mouse (Table 2.1), beginning with an investigation of the ecological differentiation of the species fifty years ago (Klein 1960). Although these taxa are very similar, there is no evidence of interbreeding in the laboratory or in nature (Dice 1933). The population ecologies and feeding habits of the two species are extremely similar (Wolff 1985a; Wolff et al. 1985), but some research has suggested that the two species exhibit differences in microhabitat use, nest use, and winter survivorship. One study showed that *Peromyscus leucopus* is active earlier in the night and when the weather is comparably warmer, more humid, and more overcast (Drickamer and Capone 1977). Another study suggested that *Peromyscus maniculatus* exhibits more pronounced behavioral and physiological changes in response to winter, including larger nests, increased food hoarding behavior, and a greater use of torpor (Pierce and Vogt 1993). Both species

prefer arboreal nests when in allopatry, but *P. leucopus* seemed to move to ground nests when sympatric with *P. maniculatus* (Dooley and Dueser 1996). Finally, coexistence of these two species has been partially attributed to interspecific differences in winter acclimatization paired with fluctuating environmental conditions, which allow *P. leucopus* to increase in relative abundance during summers and warm years and *P. maniculatus* to increase in relative abundance during winters and cold years (Long 1996; Wolff 1996). Despite a great deal of research on the ecology and morphology of these species, mechanisms behind their coexistence remain largely unknown. This could be because morphology and ecology are not the primary niche axes along which these two coexisting species differentiate themselves, and should thus lead us to examine other niche axes.

The ecological and evolutionary implications of repeatable individual differences in behavior are being increasingly examined. These are termed temperaments (Réale et al. 2007), behavioral syndromes (Sih et al. 2004a), or personalities (Dingemanse et al. 2003). For the purpose of this chapter, I will use the term personality to refer to any behavior that is repeatable over time and across contexts. Personalities can strongly influence community ecology, population dynamics (e.g., dispersal), and landscape ecology (Réale et al. 2007). Given a community with a wide variety of personality types, individuals of each personality type may be adapted to different environmental conditions (Minderman et al. 2009). If certain personalities achieve higher fitness in particular environments, then fluctuations in environmental conditions might cause balancing selection (Boon et al. 2007) within a species, which can allow different personality types within a population to persist, or these fluctuations

might mediate competition between species that differ in personality. If *P. leucopus* and *P. maniculatus* differ in mean personality, with one species being better at certain tasks in certain environments, this could facilitate their coexistence, and in changing environments, could lead to the range changes and shifts in species abundance (Sih et al. 2004b) that have already been documented in the Great Lakes region (Myers et al. 2005; Myers et al. 2009).

The purpose of this study was to examine intraspecific and interspecific variation in behavior and personality in *Peromyscus leucopus noveboracensis* and *Peromyscus maniculatus gracilis* in the northern lower peninsula of Michigan where the two species have historically coexisted in sympatry (Myers et al. 2009). The field site where these data were collected has historically supported high population densities of both *P. maniculatus* and *P. leucopus* and has experienced climatic warming over the last 30-40 years (Assel and Robertson 1995; Austin and Colman 2007; Field et al. 2007; Magnuson et al. 2000; Myers et al. 2005; Myers et al. 2009). *Peromyscus maniculatus* has a more northerly range and prefers colder temperatures than *P. leucopus* (Drickamer and Capone 1977; Myers et al. 2009). Recent research revealing a link between energy metabolism and animal personality uncovered that, in colder environments, deer mice that are more active and have the capacity to raise their maximal metabolic rates are expected to have higher fitness (Sears et al. 2009). Careau et al. (2009) also found that mice benefit from high activity (termed exploration in his study), in unproductive environments. These findings contrast with the competing hypothesis that deer mice reduce energetic costs in colder temperatures by limiting activity (Stebbins 1971). Because basal metabolic rates are correlated with maximal metabolic rates (Rezende et

al. 2004), and because *P. maniculatus* has a higher basal metabolic rate than *P. leucopus* (Deavers and Hudson 1981; Sieg et al. 2009; White and Seymour 2003), I predict that *P. maniculatus* will have higher mean activity levels than *P. leucopus* and that activity level will be correlated across contexts within an individual to form a personality. Examination of the differences in personality between *P. leucopus* and *P. maniculatus* could provide further insight into both their stable coexistence in historically sympatric areas and the recent shifts in abundance where the species have become newly sympatric.

MATERIALS AND METHODS

Study site and population

This study was conducted on a 14.4 hectare grid in the Pigeon River State Forest in the northern lower peninsula of Michigan (45.3°N, 84.4°W). Individual mice were monitored by livetrapping from May to August 2008 (11,603 trap nights). Sherman live traps (7.62 x 8.89 x 22.86 cm and 5.08 x 12.70 x 16.51 cm) were placed at 20-m intervals throughout the grid and baited with rolled oats. Traps were set at dusk and checked between 0000 h and 0300 h, 4 to 6 nights per week. At first capture, I ear-tagged each mouse and recorded sex and several additional variables. Weight was measured with a Pesola scale to the nearest 0.5 g. Age was recorded based on pelage where juveniles were grey, subadults were grey and brown, and adults were brown (Schug et al. 1991). For males, reproductive status was recorded as testes abdominal or testes scrotal. For females, reproductive status was recorded as nipples small, nipples enlarged but not lactating, lactating, or pregnant. Finally, I recorded putative species based on ear size and general appearance and behavior. *P. leucopus* were generally

more excitable when handled and had smaller ears and a “roman” nose. Saliva samples were collected from each mouse upon first capture for later species typing by salivary amylase electrophoresis (Aquadro and Patton 1980). During subsequent captures, I recorded ear tag numbers, weight, sex, reproductive status, and putative species.

Open field behavioral trials

Open field behavioral trials were performed in a portable arena that was placed 0.5 km from the trapping grid to control for home range effects on aggression (Oyegbile and Marler 2006). The portable arena was a 70 cm x 50 cm x 40 cm painted wooden box with a plexiglass lid and two holding areas made from 7.62 cm PVC pipes placed on opposite sides of the arena. I performed three different types of trials on the mice: basic, scent, and dyadic aggression trials (hereafter referred to as dyadic trials). Basic and scent trials were conducted on 40 *P. maniculatus* individuals and 18 *P. leucopus* individuals, with between one and three repetitions per mouse. This ratio of *P. maniculatus* to *P. leucopus* was representative of their relative frequency in the area at the time of the study. I also performed dyadic trials on 17 *P. maniculatus* individuals and 12 *P. leucopus* individuals, with between one and three repetitions per mouse. On a given night, an individual mouse was either subjected to all three trial types, to only the basic and scent trials, or to only the dyadic trial, with at least five minutes between trials. The order of trials for an individual mouse on a given night was always basic, scent, then dyadic. Individuals were subjected to each trial type between one and three times with at least two weeks between repetitions of a particular type of trial to avoid habituation. All trials were recorded on a Sony DCR-SR45 Hard-Drive Handicam under

red light. All methods were approved by the Michigan State University All University Committee on Animal Use and Care (AUF# 03/08-034-00).

For the basic trial, a toilet paper roll was taped in each corner of the bottom of the arena to provide a hiding place for the mouse. A single mouse was then placed in one of the holding areas for five minutes to acclimatize. At the end of five minutes, the door between the holding area and the rest of the arena was opened, giving the mouse the option to leave the holding area and enter the arena. The mouse was allotted three minutes to enter the arena. If at the end of three minutes, the mouse still had not left the holding area, it was placed into the center of the arena. Once in the arena, the mouse was recorded continuously for five minutes.

For the scent trial, a paper plate (Walgreens 6" Paper Plates) containing bedding (filling from a mattress) sprayed with three sprays of bobcat urine (Bobcat Pee™) was placed in one corner of the arena. The opposite corner of the arena contained a plate with "forest" scented bedding (three sprays of Scent Killer® Autumn Formula®). Toilet paper rolls were taped to the corners of the other two quadrants to provide hiding places. The mouse was placed into the center of the arena following a five minute acclimation period in the holding area and was then recorded continuously for five minutes.

The dyadic trials were conducted between mice of the same sex, age, and reproductive status, but differed with respect to whether mice were paired inter- or intraspecifically. Mice were tagged but were not conspicuously marked for these trials. For this reason, the toilet paper rolls were removed from the arena so that the mice could not move out of sight. To avoid sibling dyads, mice were paired with individuals

that were trapped farthest from their trap location. Each mouse was initially placed in a separate holding area for five minutes of acclimation. The mice were then placed simultaneously into the arena directly in front of each holding area and given 10 minutes to interact. I never needed to separate the mice because there was never an instance where aggression threatened to harm a mouse. The mice were recorded continuously for 10 minutes.

Data extraction

Behavioral variables were extracted from the video files using JWatcher + Video 1.0 (Blumstein et al. 2006). All videos were watched and recorded continuously in their entirety. The basic trial was watched a total of three times to extract all variables. During the first viewing of the basic trial, I extracted the latency to leave the holding area in seconds, the number of times the mouse looked out of the holding area, the number of rears, the number of jumps, and the proportions of time climbing on the walls, in contact with a toilet paper roll, in the holding area after the initial exit, running, sitting, and sniffing. These behaviors were all mutually exclusive. During the second viewing, I extracted the number of quadrant changes per minute, as a proxy for speed. During the third viewing, I extracted the proportion of time the mouse spent in the center of the arena and along the edge of the arena, which were mutually exclusive.

Each scent trial was watched twice. During the first viewing, I extracted the proportions of time in the quadrant containing the bobcat urine but not actively sniffing the bobcat urine or on the bobcat plate, visibly sniffing the bobcat urine, on the bobcat plate but not visibly sniffing, in the empty quadrants, in the quadrant containing the forest scent but not actively sniffing the forest scent or on the plate, visibly sniffing the

forest scent, on the forest plate but not visibly sniffing, and in contact with a toilet paper roll. All behaviors were mutually exclusive. During the second viewing, I extracted the proportions of time running, sitting, and climbing on the walls. These three behaviors were mutually exclusive.

For each dyadic trial, I watched each video twice and extracted the following variables for each mouse separately: the proportions of time cuddling, ignoring the opponent, on its back under the opponent, on top of the opponent, wrestling, and the number of anogenital sniffs, the number of chases, the number of jumps away from the opponent, the number of approaches toward the opponent, the number of retreats from the opponent, and the number of rears in response to the opponent. All behaviors were mutually exclusive.

Statistical analyses

I used generalized linear models with either a quasibinomial link (to account for non-integer weights in proportion data) or a Poisson link (for count data) to determine the effect of species on each behavior for all three trial types, and of opponent species on each behavior for *P. maniculatus* and *P. leucopus* separately in dyadic trials.

Variables from the basic trial, the scent trial, and the dyadic trial were then loaded into three separate principal component analyses using correlation matrices to reduce dimensionality of the data and uncover behavioral axes. Before loading, I attempted to normalize the variables by log transformation, arc-sin transformation, cube-root or 1/8 root transformations. While normality was not always achieved, all variables became near-normal. Principal component scores (referred to as PC# with the trial type in subscript; e.g., PC1_{basic}) for each of the three trial types were standardized by

subtracting the mean and dividing by the standard deviation and then analyzed using linear models and linear mixed effects models (nlme package in R). Principal component axes that were interpreted as activity and arboreality axes (see results) were tested using Pearson's correlations to determine whether mouse behavior was consistent across contexts (*i.e.*, types of open field trials), thus appropriately termed 'personalities' (Dingemanse et al. 2003). The significance of individual identity was assessed for each PC score by comparing the mixed effect model (nlme package in R) that included individual identity as a random effect and the best combination of fixed effects (e.g., species, sex, age, trial number) to the linear model with the same fixed effects, but without the individual identity random effect using a likelihood ratio test (Bolker et al. 2009; Pinheiro and Bates 2000). All statistical analyses were performed in R version 2.9.2 (R Development Core Team 2009). Values are presented as means \pm one standard error unless otherwise noted. Parameters from linear models are reported as b_x for factors, where the subscripted term (x) indicates the factor level associated with the parameter. For example $b_{leucopus}$ is the parameter representing the effect of the mouse being a *P. leucopus* as compared to a *P. maniculatus*. Z-scores are presented for generalized linear models with a Poisson link, while t-scores are presented for generalized linear models with a quasibinomial link. The magnitudes of effect sizes are based on raw behavioral data with statistics from linear models in parentheses.

One mouse (a *P. leucopus*) was unusually inactive in both the basic trial and the scent trial. It remained perfectly still before, during, and after the trials, but otherwise seemed healthy and then ran away when released. Based on my observations of many open field trials, this behavior was not within the range of typical *Peromyscus*

responses. As a result, data from the basic and scent trials for this single mouse were excluded from subsequent analyses. My general conclusions were not affected by the inclusion or exclusion of these two observations.

RESULTS

During the basic trials, on average, mice of both species left the holding area after 60.6 ± 9.7 s and spent the largest proportions of time running and sniffing ($30.7 \pm 1.1\%$ and $27.8 \pm 1.1\%$ respectively) on the edge ($60.2 \pm 1.9\%$) of the arena, sitting only $14.9 \pm 1.9\%$ of the time, and climbing only $11.1 \pm 1.6\%$ of the time. In contrast, during the scent trials, mice spent the most time in the empty quadrants and sitting ($47.5 \pm 3.3\%$ and $67.2 \pm 3.0\%$ respectively), while they spent relatively little time running, climbing, or exploring the scents.

During the ten minutes that the dyadic trials lasted, on average, both species retreated from the opponent 4.0 ± 0.9 times and approached the opponent 4.6 ± 0.9 times. Both species spent most of their time ignoring the opponent ($72.2 \pm 5.4\%$) and very little time in contact with the other mouse, but *P. maniculatus* jumped away from the opponent only 0.41 ± 0.23 times, while *P. leucopus* jumped away from the opponent 4.8 ± 2.1 times ($b_{maniculatus} \pm SE = -2.4 \pm 0.40$, $t = -6.1$, $p < 0.001$).

Interspecific differences in behavior

For the basic trial, the first two principal components (PCs) had eigenvalues greater than one and explained 47.0 % of the variance (Table 2.2). The number of quadrant changes, proportion of time running, and number of rears loaded heavily and negatively into PC1_{basic}, while the proportion of time sitting loaded heavily and

positively. PC1_{basic} was interpreted as an activity axis in which mice with lower scores were more active. Linear models using only the first trial for each mouse revealed that *P. maniculatus* had significantly lower PC1_{basic} scores than *P. leucopus* ($F = 6.0$, d.f. = 1, 55, $P = 0.02$, Fig. 2.1). In other words, *P. maniculatus* was more active as reflected by more quadrant changes, running more, and rearing more, while *P. leucopus* sat more. The statistics reported for the following species differences come from generalized linear models while the effect sizes are based on actual differences in raw data. Raw behavioral variables supported this finding by revealing that *P. leucopus* left the holding area to explore the arena 38% later than *P. maniculatus* ($b_{maniculatus} \pm SE = -0.33 \pm 0.001$, $z = -296.4$, d.f. = 56, $P < 0.0001$). *Peromyscus maniculatus* also spent 23% more time running during the basic trial ($b_{maniculatus} \pm SE = 0.29 \pm 0.11$, $t = 2.55$, d.f. = 56, $P = 0.01$), 60% more time running during the scent trial ($b_{maniculatus} \pm SE = 0.56 \pm 0.23$, $t = 2.43$, d.f. = 56, $P = 0.02$), and reared 1.3 times as much during the basic trial ($b_{maniculatus} \pm SE = 0.27 \pm 0.06$, $z = 4.78$, d.f. = 56, $P < 0.0001$) when compared to *P. leucopus*.

Proportion of time climbing and on the edge of the arena loaded heavily and negatively into PC2_{basic}, while proportion of time in the center of the arena and in the holding area loaded heavily and positively (Table 2.2). PC2_{basic} was interpreted as a location of activity axis in which mice with lower scores climbed more and spent more time on the edge, while those with higher scores stayed either in the center of the arena

or in the holding area. There were no significant differences between species in this principal component axis ($F = 0.1$, d.f. = 1, 55, $P = 0.7$).

For the scent trial, the first two components had eigenvalues greater than one and explained 46.6 % of the total variance (Table 2.2). Proportion of time running loaded heavily and negatively into $PC1_{\text{scent}}$, while proportion of time in the empty quadrants and proportion of time sitting loaded heavily and positively. $PC1_{\text{scent}}$ was interpreted as an activity axis in which mice with higher scores were less active. The proportion of time climbing loaded heavily and positively into $PC2_{\text{scent}}$, while proportion of time sniffing the forest scent and the bobcat scent, proportion of time sitting, and proportions of time on the forest plate and bobcat plate loaded heavily and negatively. $PC2_{\text{scent}}$ was interpreted as a location of activity axis in which mice with higher scores climbed up the walls and those with lower scores stayed on the ground. There were no significant differences between species in either $PC1_{\text{scent}}$ ($F = 0.9$, d.f. = 1, 55, $P = 0.3$, Fig. 2.1) or $PC2_{\text{scent}}$ ($F_1 = 0.1$, d.f. = 1, 55, $P = 0.7$).

For the dyadic trial, the first two principal components had eigenvalues greater than one and explained 45.5 % of the total variance (Table 2.2). The number of jumps away from the opponent, the proportion of time ignoring the opponent, the number of retreats, and the number of rears in response to the opponent loaded heavily and negatively into $PC1_{\text{dyadic}}$, while the proportion of time cuddling loaded heavily and positively. $PC1_{\text{dyadic}}$ was interpreted as a sociality axis in which mice with higher PC scores had contact with the opponent more often and mice with lower scores avoided

the opponent. During the dyadic trial, *P. maniculatus* had significantly higher PC1_{dyadic} scores than *P. leucopus* ($F = 8.9$, d.f. = 1, 27, $P = 0.006$, Fig. 2.2). In other words, *P. maniculatus* cuddled with the opponent more, while *P. leucopus* jumped away from the opponent, ignored the opponent, retreated from the opponent, and reared in response to the opponent. The statistics reported for the following species differences come from generalized linear models while the effect sizes are based on actual differences in raw data. *P. maniculatus* wrestled 5.5 times as often ($b_{\text{maniculatus}} = 1.82 \pm 0.74$, $t = 2.5$, d.f. = 28, $P = 0.02$), sniffed the opponent's anogenital region 3.9 times as often ($b_{\text{maniculatus}} = 1.35 \pm 0.35$, $z = 3.95$, d.f. = 28, $P < 0.0001$), and chased the opponent 3.8 times as often as *P. leucopus* ($b_{\text{maniculatus}} = 1.31 \pm 0.55$, $z = 2.40$, d.f. = 28, $P = 0.02$). *Peromyscus leucopus* jumped away from the opponent 11.6 times as often as *P. maniculatus* ($b_{\text{maniculatus}} = -2.44 \pm 0.40$, $t = -6.11$, d.f. = 28, $P < 0.0001$).

The number of rears in response to the opponent, the proportion of time cuddling, the number of retreats, the proportion of time wrestling, and the proportion of time on the back under the opponent loaded heavily and negatively into PC2_{dyadic}, while the proportion of time ignoring the opponent loaded heavily and positively and the number of approaches and proportion of time on top of the mouse loaded moderately and positively (Table 2.2). PC2_{dyadic} was interpreted as an aggression axis, with mice with lower scores being more submissive and mice with higher scores being more aggressive. There were no significant differences between species in PC2_{dyadic} ($F = 0.5$, d.f. = 1, 27, $P = 0.5$, Fig. 2.2).

Intraspecific variation and individual repeatability

When assessing the significance of individual identity in a model describing PC1_{basic} (*i.e.*, the activity axis), the addition of mouse identity as a random effect significantly improved the fit of the model to the data ($\chi^2 = 14.3$, d.f. = 1, $P < 0.001$). Mouse identity accounted for 52% of the variance in the PC1_{basic} data not accounted for by species, sex, the interaction of species and sex, age, and trial number. Noting that in this case, more negative activity scores represented higher activity levels, this model indicated that *P. maniculatus* was more active than *P. leucopus* ($b_{\text{maniculatus}} = -1.47 \pm 0.42$, $t = -3.5$, d.f. = 53, $P = 0.001$), males were more active than females ($b_{\text{male}} = -1.03 \pm 0.45$, $t = -2.3$, d.f. = 53, $P = 0.025$), *P. leucopus* males were more active than conspecific females, but there was little difference between *P. maniculatus* males and females ($b_{\text{maniculatus}*\text{male}} = 1.49 \pm 0.51$, $t = 2.9$, d.f. = 53, $P = 0.005$), juveniles and sub-adults were not significantly different from adults ($b_{\text{juvenile}} = -0.38 \pm 0.31$, $t = -1.2$, d.f. = 53, $P = 0.23$, $b_{\text{subadult}} = -0.39 \pm 0.23$, $t = -1.8$, d.f. = 53, $P = 0.09$), and mice became less active with increasing trial repetitions ($b = 0.66 \pm 0.11$, $t = 5.9$, d.f. = 53, $P < 0.001$).

The addition of mouse identity as a random effect did not improve the fit of the best models to describe PC2_{basic} ($\chi^2 = 0.8$, d.f. = 1, $P = 0.4$), PC1_{scent} ($\chi^2 = 2.3$, d.f. = 1, $P = 0.13$), PC2_{scent} ($\chi^2 = 0.3$, d.f. = 1, $P = 0.6$), PC1_{dyadic} ($\chi^2 = 0.1$, d.f. = 1, $P = 0.7$) or PC2_{dyadic} ($\chi^2 < 0.001$, d.f. = 1, $P = 0.9$).

All linear models using principal component scores and all further analyses were done using only the first trials (*i.e.*, the first basic, scent, and dyadic trials) performed on each mouse to avoid confounding habituation.

Correlation of behavioral axes across contexts to form personalities

By definition, a personality refers to individual behavioral differences that are repeatable across time and situations (Réale et al. 2007). PC1_{basic} and PC1_{scent} were both interpreted as activity axes and were positively correlated (Pearson's $r = 0.55$, $P < 0.0001$, Fig. 2.1). PC2_{basic} and PC2_{scent} were both interpreted as location axes, but several behavioral variables loaded in opposite directions on these two axes (e.g., proportion of time climbing loaded negatively into PC2_{basic} and positively into PC2_{scent}, see Table 2.2). PC2_{basic} and PC2_{scent} were found to be negatively correlated with marginal significance (Pearson's $r = -0.24$, $P = 0.07$), meaning that mice that climbed more in the basic trial also climbed more in the scent trial.

No difference in dyadic behavior between interspecific and intraspecific dyads

Using linear models to test for the effects of intraspecific versus interspecific dyads on PC1_{dyadic} and PC2_{dyadic}, I found no difference in behavior for *P. maniculatus* or *P. leucopus*; the focal mouse behaved the same towards heterospecifics as toward conspecifics. For *P. maniculatus*, there was no effect of the opponent species on PC1_{dyadic} ($F = 0.2$, d.f. = 1, 8, $P = 0.7$) or PC2_{dyadic} ($F = 2.0$, d.f. = 1, 8, $P = 0.2$). There was also no effect of opponent species for *P. leucopus* on PC1_{dyadic} ($F = 0.09$, d.f. = 1, 5, $P = 0.8$) or PC2_{dyadic} ($F = 0.8$, d.f. = 1, 5, $P = 0.4$).

Despite the similarities I found when examining principal component scores, when looking at the raw behavioral data extracted from the dyadic trials for each species separately using generalized linear models, I found that both species approached heterospecific opponents more often than they approached conspecifics and both retreated from *P. maniculatus* opponents more often than from *P. leucopus* opponents. As was noted previously, effect sizes are based on raw means while statistics from supporting generalized linear models are given in parentheses for each behavior. Specifically, *Peromyscus maniculatus* approached heterospecifics 1.8 times as often as conspecifics ($b_{\text{conspecifics}} = -0.6 \pm 0.20$, $z = -3.0$, $d.f = 18$, $P = 0.003$) and retreated from conspecifics 12.5 times as often as from heterospecifics ($b_{\text{conspecifics}} = 2.53 \pm 1.01$, $z = 2.5$, $d.f = 18$, $P = 0.01$). *Peromyscus leucopus* approached heterospecifics 3.3 times as often as conspecifics ($b_{\text{heterospecifics}} = 1.20 \pm 0.61$, $z = 2.0$, $d.f = 6$, $P = 0.05$) and retreated from heterospecifics 13.6 times as often as from conspecifics ($b_{\text{heterospecifics}} = 2.61 \pm 1.01$, $z = 2.5$, $d.f = 6$, $P = 0.01$). *Peromyscus maniculatus* was also on top of heterospecifics 16.7 times as often as on top of conspecifics ($b_{\text{conspecifics}} = -2.85 \pm 0.99$, $z = -2.9$, $d.f = 18$, $P = 0.01$). The other eight behaviors showed no effect of opponent species.

DISCUSSION

For two species to coexist, they must be sufficiently different to allow niche differentiation (Gause 1934; Hardin 1960; MacArthur and Levins 1967). Most studies that examine coexistence look to morphology or ecology for evidence of niche differentiation. In particular, there is a great deal of research revealing that *Peromyscus maniculatus* and *P. leucopus* are extremely similar ecologically and morphologically (Table 2.1). My results, indicating mean differences in personality between these two

species, complement this existing body of literature (Table 2.1) to provide a more comprehensive understanding of the potential mechanism behind their coexistence.

Activity

My findings from both the principal component axes and analysis of raw behavioral data revealed that *P. maniculatus* is more active than *P. leucopus*. *Peromyscus maniculatus* and *P. leucopus* occupy different geographic ranges, with *P. maniculatus* extending farther north, into colder temperatures, than *P. leucopus*. This preference for more northern habitats has also been observed in microhabitat studies, where *P. maniculatus* was found to prefer colder microhabitats than *P. leucopus* (Drickamer and Capone 1977). In a recent study of deer mice, individuals spent less time active as temperatures decreased, with the duration of each activity bout decreasing, but the number of bouts staying the same (Sears et al. 2009). Furthermore, mice with higher maximal metabolic rates were better able to support activity in colder temperatures (Sears et al. 2009). It is possible that the higher activity levels exhibited by *P. maniculatus* allow it to generate more heat by exercise thermogenesis, thus making this species better able to avoid excessive heat loss (Makinen et al. 1996) and to thrive in colder temperatures than *P. leucopus*.

My findings are in contrast to those from a recent study, which found a negative correlation between basal metabolic rate and exploration in muroid rodent species (Careau et al. 2009). The authors used percent time spent in locomotion as a proxy for activity level, and equated activity level in the open field with exploration. In their meta-analysis, *P. maniculatus* was in locomotion 46.5 % of the time and had an average BMR of 36.9 mL O₂ per hour. On this basis, they described *P. maniculatus* as a

superficial explorer with a low BMR. *Peromyscus leucopus* was in locomotion 54.6 % of the time and had an average BMR of 33.2 mL O₂ per hour and was described as a thorough explorer with a low BMR. These findings are in contrast to my findings that *P. maniculatus* is more active (43.2% of time in motion) than *P. leucopus* (38.4% of time in motion). A possible explanation for this discrepancy is that the data for *P. maniculatus* in the Careau et al. (2009) study were averaged between the two subspecies *P. m. bairdii* (prairie deer mouse) and *P. m. blandus* (Chihuahua deer mouse), both of which differ in morphology, behavior, and habitat preference from *P. m. gracilis*, the mouse I studied (Baker 1983; Barry 1976; King 1968).

Furthermore, my estimates of personality for *P. leucopus* might not be representative of the species (or subspecies) as a whole. In particular, most of my study mice were likely recent dispersers. I began trapping on 7 May 2008, but did not trap any *P. leucopus* until 5 June 2008. Trappability (sum of all individuals' number of captures minus the first and last divided by the sum of all individuals' number of potential captures minus the first and last—Lusk and Millar 1989) on my study site was 81.8%, so it is unlikely that these animals were resident on the grid but remained undetected during this time period. Dispersing individuals in other species have been previously shown to differ in personality from philopatric individuals, being bolder, more aggressive, faster explorers that are less social (Clobert et al. 2009; Cote and Clobert 2007; Dingemanse et al. 2003; Duckworth and Badyaev 2007; Duckworth and Kruuk 2009). As a result, some of the differences between these two species that I have documented might be due to the increased proportion of dispersing individuals in my *P. leucopus* sample.

Contact with opponent mouse

Peromyscus maniculatus had more contact with opponents than *P. leucopus* and was thus more sociable (Cote et al. 2010). This is consistent with the reported superiority of the former with respect to adaptation to cold temperatures, as small mammals often use communal nesting as a way to conserve energy in the winter (Merritt and Zegers 2002; West and Dublin 1984). In the wild, *P. maniculatus* and *P. leucopus* have both been found to engage in communal nesting (Millar and Derrickson 1992; Wolff 1994), often doing so as population densities increase (Wolff 1994). To understand the greater amount of contact *P. maniculatus* had with opponents when compared to *P. leucopus*, I might look to their native ranges and note that *P. maniculatus gracilis* has a range that extends farther north than *P. leucopus*, while the range of *P. leucopus noveboracensis* extends much farther south into warmer climates, possibly making the need for communal nesting as an energy conservation strategy less important.

Arboreality

The second principal component axes from the basic and scent trials represented location of activity axes and indicated that animals that climbed more in the basic trial also climbed more in the scent trial. These results should be examined with caution, however, due to the lack of individual repeatability. Differences among mice in the amount of climbing behavior could reflect differences in arboreality or differences in escape behavior. Inter- and intraspecific variation in climbing behavior has been previously demonstrated in the genus *Peromyscus* (Lemen 1980), thus emphasizing the

need for future behavioral trials that examine climbing behavior so as to differentiate between these two possibilities.

Dyadic trials

When looking at PC scores from the dyadic trials for each species separately, I found no differences in any of the PC scores based on whether the opponent was a conspecific or a heterospecific. These findings are in agreement with past research that found no difference in inter- versus intraspecific aggression for home ranges (Wolff 1985b). Wolff (1985b) determined that home range size is density dependent, and is based on the population density of both species rather than just one.

When looking at the raw behavioral data extracted from the dyadic trials, however, I found that both species approached heterospecific opponents more often than they approached conspecifics, possibly suggesting aggression towards heterospecifics. However, both species retreated from *P. maniculatus* opponents more often than from *P. leucopus* opponents, suggesting that *P. maniculatus* wins these encounters more often than *P. leucopus*. These results suggest that there might be differences in aggression between the two species that I failed to uncover through my principal component analyses. This could be due to the fact that some of the behaviors that loaded heavily into the principle component axes did not differ between heterospecifics and conspecifics, whereas the behaviors that I found to differ between conspecifics and heterospecifics were less important to overall variation in dyadic behavior. Future research should further examine dyadic behavior to better understand the complexities of intraspecific and interspecific interactions between these two similar species.

Differences in activity level might permit coexistence in a changing environment

The field site where these data were collected has historically supported high population densities of both *P. maniculatus* and *P. leucopus*, and has experienced climatic warming over the last 30-40 years (Assel and Robertson 1995; Austin and Colman 2007; Field et al. 2007; Magnuson et al. 2000; Myers et al. 2005; Myers et al. 2009). It is possible that differences in activity level in these species may mediate their coexistence in this location. If each species is better adapted to either colder or warmer temperatures by being more or less active, population abundances should shift as the environment changes from warmer to colder and vice versa. During warmer years, *P. leucopus* might increase in relative abundance, while *P. maniculatus*, which is more active and thus will experience higher fitness in cooler temperatures (Sears et al. 2009), might thrive in cooler years. These predictions are consistent with recent changes in relative abundances associated with climate change (Myers et al. 2005; Myers et al. 2009).

In the northern lower peninsula of Michigan, where this study was conducted, the percentage of *P. leucopus* among small forest mammal captures has increased from 38.3% (1883 to 1980) to 77.7% (1981 to 2006—Myers et al. 2009). Over the same time frame, representation of *P. maniculatus* has decreased from 28% of small mammal captures (1883 to 1980) to only 5.9% (1981 to 2006—Myers et al. 2009). These shifts in abundance are part of a large-scale range shift that involves several other small mammals in the Great Lakes region (Myers et al. 2009). Previously documented associations between higher activity level, colder temperatures and fitness (Sears et al.

2009), suggest that the more active *P. maniculatus* is not as able as the less active *P. leucopus* to exploit the warming temperatures produced by climate change in this area.

Using the relationships extrapolated from this research, I can begin to predict how individual populations of *Peromyscus* will respond to climate change. For *P. maniculatus*, populations of mice in which individuals are especially active, and thus are well adapted to cold temperatures (Sears et al. 2009), may be the most vulnerable to climatic warming. Less active populations of *P. leucopus*, which are thus less adapted to cold temperatures, should do well at expanding their ranges as temperatures increase and may out-compete more active *P. maniculatus* populations.

Table 2.1: Ecological and morphological differences between *Peromyscus leucopus* and *Peromyscus maniculatus*. In cases where the subspecies and/or location are not noted, it is assumed that this information was not available and that the characteristics are representative of each species as a whole.

Trait	<i>P. leucopus</i>	<i>P. maniculatus</i>	Subspecies	Location	Reference
Age at first reproduction	70 days	77 days	<i>P. leucopus</i> and <i>P. maniculatus</i>	Unknown	Duncan et al. 2007
Basal Metabolic Rate	33.2 mL O ₂ per hour	36.9 mL O ₂ per hour	<i>P. leucopus</i> and <i>P. maniculatus</i>	Unknown	via Careau et al. 2009 White and Seymour 2003 via Careau et al. 2009
Food	35.2 mL O ₂ per hour Arthropods, fruit, nuts, green vegetation, fungi Seeds, fruits, nuts, plants, bark, buds, insects, eggs Non-arboreal	39.2 mL O ₂ per hour Arthropods, fruit, nuts, green vegetation, fungi Seeds, fruits, nuts, plants, bark, buds, insects, eggs Arboreal	<i>P. leucopus</i> and <i>P. maniculatus</i> <i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i>	Unknown Southwestern Virginia	Deavers and Hudson 1981; Sieg et al. 2009 Wolff et al. 1985
Nest Use			<i>P. l. noveboracensis</i> and <i>P. m. gracilis</i>	Ann Arbor, MI and Elmira, MI	Cogshall 1928
Microhabitat	Vertical microhabitat segregation was not sufficient to reduce niche overlap Warmer temperatures, higher humidity, under overcast skies, and with light rain.	Vertical microhabitat segregation was not sufficient to reduce niche overlap Lower temperatures, lower humidity, under clear skies, with no rain.	<i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i> <i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i>	Southwestern Virginia Southwestern Virginia	Dooley and Dueser 1996 Graves et al. 1988
			<i>P. l. noveboracensis</i> and <i>P. m. gracilis</i>	New England deciduous forest	Drickamer and Capone 1977

Habitat	Deciduous forest	Deciduous and coniferous forests	<i>P. leucopus</i> and <i>P. maniculatus</i>	Maine	Garman et al. 1994
Home Range	590 m ²	590 m ²	<i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i>	Southwestern Virginia	Wolff 1985b
Litter Size	3.6+-0.89	3.47+-0.80	<i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i>	Southwestern Virginia	Wolff 1994
Morphology	Indistinguishable	Indistinguishable	<i>P. l. noveboracensis</i> and <i>P. m. gracilis</i>	Central New York	Lindquist et al. 2003
Temporal Activity	Early portion of the night	Late in the night, early morning	<i>P. l. noveboracensis</i> and <i>P. m. gracilis</i>	New England deciduous forest	Drickamer 1987
	Early portion of the night	Activity peaks throughout the night	<i>P. l. noveboracensis</i> and <i>P. m. nubiterrae</i>	Central Appalachians	Bruseo and Barry 1995
Winter Acclimatization	Smaller nests, 15-20% of mice use torpor, hoard less food, eat more food	Larger nests, 40% of mice use torpor, hoard more food, eat less food	<i>P. l. noveboracensis</i> and <i>P. m. gracilis</i>	New York	Pierce and Vogt 1993

Table 2.2: Loadings from the principal component analysis using the correlation matrix of behavioral variables from basic, scent, and dyadic trials for both *Peromyscus maniculatus* and *Peromyscus leucopus*. Zeros are used for variables with very small loadings (close to zero). Behaviors refer to the proportion of time spent doing each behavior or in each area of the arena, unless noted otherwise. Behaviors that were measured as count data are indicated by a # sign.

Behaviors: basic trial	PC1	PC2	Scent trial	PC1	PC2	Dyadic trial	PC1	PC2
Latency to leave holding	0.272	0	In bobcat quadrant	-0.175	-0.188	Cuddling	0.374	-0.353
# lookouts from holding	0	0	Sniffing bobcat scent	-0.177	-0.309	Ignoring opponent	-0.404	0.395
# quadrant changes/min	-0.443	0	On bobcat plate	-0.290	-0.386	On back under opponent	0.191	-0.307
In center of arena	0	0.565	In empty quadrants	0.488	-0.104	On top of opponent	0	0.142
On edge of arena	0	-0.562	In forest quadrant	-0.141	0	Wrestling	0.291	-0.328
Climbing	-0.183	-0.372	Sniffing forest scent	-0.213	-0.423	# anogenital sniffs	0.19	-0.118
Contact with paper roll	0	0	On forest plate	-0.275	-0.311	# chases	0.196	0
In holding after exit	0	0.324	Contact with paper roll	-0.138	0	# jumps from opponent	-0.485	-0.291
Running	-0.428	0.137	Running	-0.423	0	# approach to opponent	0	0.273
Sitting	0.481	0	Sitting	0.440	-0.397	# retreats	-0.373	-0.333
Sniffing	-0.180	0.110	Climbing	-0.289	0.522	# rears toward opponent	-0.343	-0.453
# rears	-0.421	0						
# jumps	-0.253	-0.282						
Variance explained	26.5%	20.5%		28.9%	17.6%		23.6%	21.9%
Cumulative variance explained	26.5%	47.0%		28.9%	46.6%		23.6%	45.5%

Figure 2.1: Principal component scores from the basic trial and the scent trial PCA on *Peromyscus maniculatus* and *Peromyscus leucopus* (displaying first trial scores only). $PC1_{\text{basic}}$ and $PC1_{\text{scent}}$ are both interpreted as activity axes. Boxplot lines represent the minimum, maximum, quartiles, and median, from the outside in. An asterisk indicates a significant difference between species. The diagonal line represents the regression line of $PC1_{\text{basic}}$ on $PC1_{\text{scent}}$ ($F = 23.4$, d.f. = 1, 55, $P < 0.0001$).

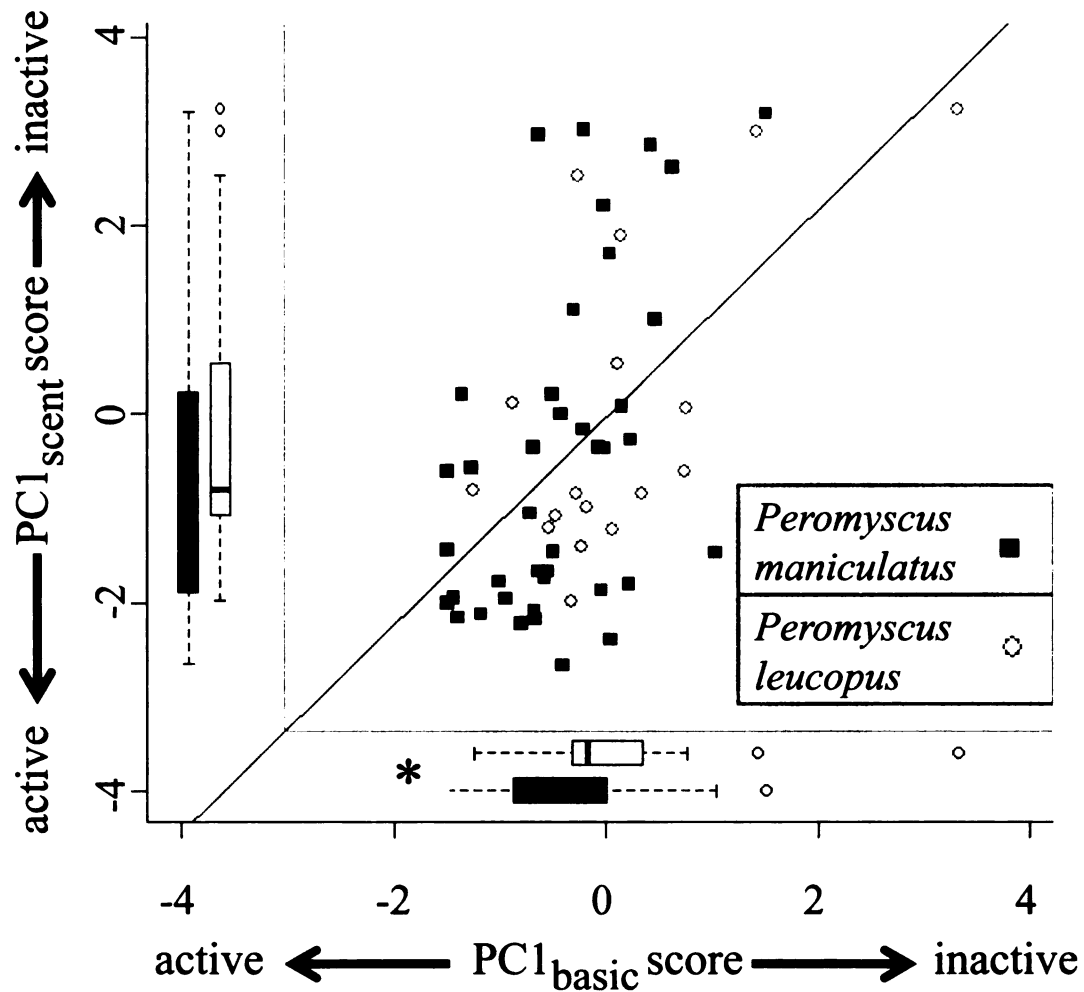
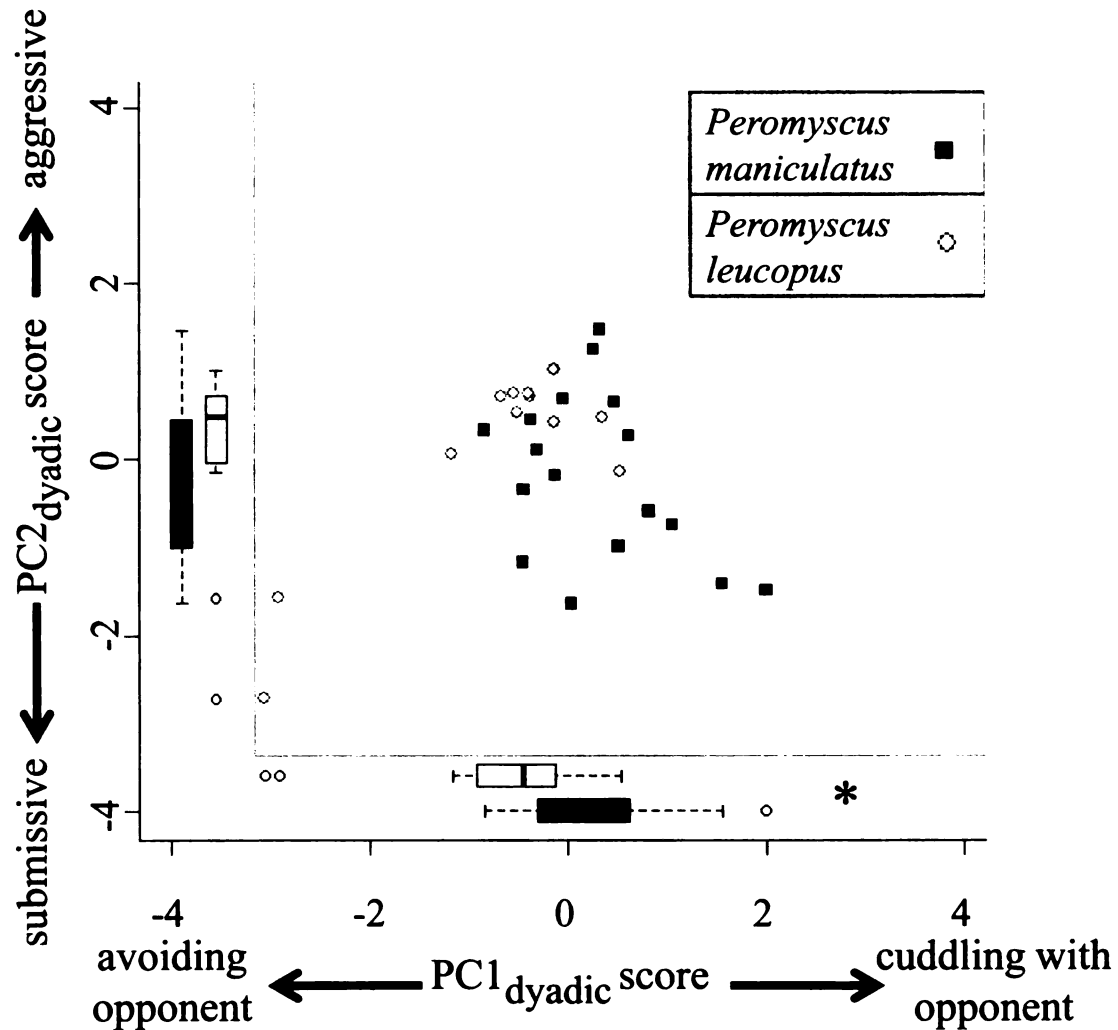


Figure 2.2: Principal component scores from the dyadic trial PCA on *Peromyscus maniculatus* and *Peromyscus leucopus* (displaying first trial scores only). PC1_{dyadic} is interpreted as a sociality axis while PC2_{dyadic} is interpreted as an aggression axis. Boxplot lines represent the minimum, maximum, quartiles, and median, from the outside in. An asterisk indicates a significant difference between species.



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CHAPTER THREE

Personality is associated with dispersal in *Peromyscus*

INTRODUCTION

In order for an animal to colonize a new habitat prior to the onset of spring breeding, it must have successfully over-wintered and must be a suitable candidate for dispersal. In general, the decision to disperse is affected by multiple factors, including external factors like inbreeding risk and competition, and internal phenotypic factors like physiology, morphology, life history, and behavior (Clobert et al. 2009). With respect to behavior, a new area of research has developed that focuses on repeatable individual differences in behavior, referred to as temperaments (Réale et al. 2007), behavioral syndromes (Sih et al. 2004), and/or personalities (Dingemanse et al. 2003).

Individual variation in personality has been linked to dispersal in several vertebrate species and may lend insight into the question of what personality phenotypes are most likely to colonize de-populated habitats. For instance, among mosquitofish (*Gambusia affinis*), asocial individuals were more likely to disperse than social individuals (Cote et al. 2010). In the common lizard (*Lacerta vivipara*), the interaction of sociality and population density at the natal site predicted dispersal behavior (Cote and Clobert 2007). Among great tits (*Parus major*), immigrant birds were faster explorers than those that were born on the study site (Dingemanse et al. 2003). In bluebirds, biased dispersal of highly aggressive western bluebirds (*Sialia mexicana*) facilitated their range expansion and the displacement of less aggressive mountain bluebirds (*Sialia currucoides* —Duckworth and Badyaev 2007). Finally, in

Trinidad killifish (*Rivulus hartii*), bold individuals dispersed farther than shy individuals (Fraser et al. 2001). I chose to examine this link between personality and dispersal in deer mice of the genus *Peromyscus*.

The abundances of white-footed mice, *Peromyscus leucopus*, and deer mice, *P. maniculatus*, fluctuate and are driven by weather and food resources, with peaks in the late summer and crashes in the winter followed by population growth from early spring through late summer (Falls et al. 2007; Kalcounis-Rueppell et al. 2002; Lewellen and Vessey 1998; Merritt et al. 2001). Overwinter mortality can result in depopulated habitat fragments that are then re-colonized in the spring (Krohne et al. 1984). For a mouse to re-colonize a depopulated habitat early in the spring, before spring breeding, it must have successfully over-wintered and then be able to disperse from its current habitat to the new habitat.

Much is already known about dispersal in the ecologically and morphologically similar species, *P. leucopus* and *P. maniculatus* (Cogshall 1928; Drickamer 1987; Drickamer and Capone 1977; Lindquist et al. 2003; Pierce and Vogt 1993; Wolff 1985; Wolff et al. 1985). Two types of dispersers have been identified, colonists and non-colonists. Colonists are adult mice that disperse into habitat that has experienced extreme winter mortality early in the spring, while non-colonizing dispersers disperse into an already populated area (Krohne et al. 1984). Mice that do not disperse are termed residents. Previous studies of *Peromyscus* have shown that mice disperse more often during times of increasing population density and most often in the spring and fall rather than in winter (Fairbairn 1978; Krohne et al. 1984; Nadeau et al. 1981). Among dispersers, males disperse more often and farther than females (Jacquot and Vessey

1995; Krohne et al. 1984). On the contrary, if one considers only colonist dispersers, adult females disperse slightly more often than adult males (Jacquot and Vessey 1995; Krohne et al. 1984). While juveniles cannot be early colonists (sensu Krohne et al. 1984), they do disperse, potentially as a means to avoid inbreeding and/or to reduce reproductive or resource competition with parents and same-sexed offspring (Wolff 1992).

Recent research on interspecific and intraspecific variation in animal personality in *P. leucopus noveboracensis* and *P. maniculatus gracilis* in Michigan has revealed behavioral axes representative of activity level, sociality, and aggression (Chapter 2). In 2008, I live-trapped *P. leucopus* and *P. maniculatus gracilis* in the Pigeon River State Forest, Michigan. My 14.4-hectare grid supported one resident mouse in early May 2008, leaving a large area to be re-colonized. In the fall of 2008, the grid supported 40 residents. The purpose of this study was to use basic descriptive data (*i.e.* age, sex, and species) and behavioral axes to understand how the behavioral phenotypes of dispersers change as the season progresses. The extremely low spring abundance allowed me to examine which personality types were best able to colonize suitable habitat early in the season compared with those that arrived in the area later in the breeding season. I used small sample corrected Akaike's Information Criteria (AIC_C) to determine which of three *a priori* linear models best described arrival date on the grid: 1) a basic model containing descriptor variables like age and sex 2) a model containing three behavioral axes, or 3) a model combining basic and behavioral variables.

MATERIALS AND METHODS

Study site and population

This study was conducted on a 14.4-hectare grid in the Pigeon River State Forest in the northern lower peninsula of Michigan (45.3°N, 84.4°W). Individual mice were monitored by livetrapping from May to August 2008 (11,603 trap nights). Sherman live traps (7.62 x 8.89 x 22.86 cm and 5.08 x 12.70 x 16.51 cm) were placed at 20-m intervals throughout the grid and baited with rolled oats. Traps were set at dusk and checked between 0000 h and 0300 h, 4 to 6 nights per week. Details on trapping data collection can be found in Chapter 2. Briefly, at first capture, I ear-tagged each mouse and recorded weight (measured with a Pesola scale to the nearest 0.5 g), sex, age (based on pelage: grey = juvenile, grey and brown = subadult, brown = adult —Schug et al. 1991), reproductive status (males: testes abdominal or testes scrotal; females: nipples small, nipples enlarged but not lactating, lactating, or pregnant), and putative species (based on ear size and general appearance and behavior). Saliva samples were collected from each mouse upon first capture for later species typing by salivary amylase electrophoresis (Aquadro and Patton 1980). During subsequent captures, I recorded ear tag numbers, weight, sex, reproductive status, and putative species.

Extraction of behavioral axes

Details on the open-field trials can be found in Chapter 2. Briefly, open-field behavioral trials were performed in a portable arena that was placed 0.5 km from the trapping grid to control for home range effects on aggression (Oyegbile and Marler 2006). I performed three different types of trials on the mice: basic, scent, and dyadic trials. During the basic trial, each mouse was video-recorded for five minutes in the

arena containing a toilet paper roll taped to each corner of the bottom of the arena.

During the scent trial, each mouse was recorded for five minutes in the arena containing two toilet paper rolls, a paper plate with Bobcat Pee™ scented bedding, and a paper plate with “forest” scented bedding (Scent Killer® Autumn Formula®). For the dyadic trial, two mice of the same sex, age, and reproductive status, but the same or different species, were recorded together in an empty arena for 10 minutes. All methods were approved by the Michigan State University All University Committee on Animal Use and Care (AUF# 03/08-034-00).

Behavioral variables were extracted from the video files using JWatcher + Video 1.0 (Blumstein et al. 2006) and analyzed using principal component analysis to uncover the behavioral axes that captured most of the variation in these behaviors (activity, sociality, aggression, Table 3.1). By definition, a personality refers to individual behavioral differences that are repeatable across time and situations (Réale et al. 2007). The activity axes in the basic and scent trials were positively correlated, thus forming a personality (Chapter 2). Sociality and aggression were extracted only from the dyadic trial, and were thus only measured in a single context, with most mice being tested only once, thus making it difficult to assess the repeatability of these traits across time and context and making it impossible to determine if these are actual personalities.

From the mice that had scores for all three trial types, I subset out mice that dispersed onto my grid (those that were first trapped as adults or as subadults greater than 15 grams, n=13). All analyses on dispersers used only these mice. Analyses on all mice included dispersers as well as any mice for which I could not determine dispersal status (mice that were first trapped as juveniles or subadults less than 15 grams, n=16).

I calculated trappability for all mice as the sum of all individuals' number of captures (minus the first and last) divided by the sum of all individuals' number of potential captures (minus the first and last) (Lusk and Millar 1989). Trappability was calculated at 81.8% in 2008, indicating that the first time I trapped each mouse was likely close to its arrival date on the grid.

Statistical analyses

To uncover factors affecting the timing of arrival on my grid, I used linear models to assess the significance of species, sex, age, activity, sociality, and aggression on arrival date of dispersers. The effects of these variables as predictors of arrival date were assessed by comparing three *a priori* models using AIC_C: 1) a basic model that included species, sex and age, 2) a behavioral model that included activity, sociality, and aggression, and 3) a full model that included all of the basic and behavioral variables. Behavioral metrics (e.g., activity, sociality, aggression) were based on appropriate PC scores from the first open-field trial for each mouse only (see Chapter 2 for details). Principal component scores for activity were multiplied by -1 so that higher scores represented higher activity levels.

After finding that all three variables in the behavioral model had significant effects on arrival date, I tested whether habituation and plasticity had any effect on activity, sociality, and aggression. Habituation refers to a directional change in behavior as mice become accustomed to the behavioral trials. To examine the effect of habituation on activity, I included trial number as a fixed effect in statistical models of mouse behavior. If trial number showed a significant effect, it would indicate that the mice became habituated to the open-field trials. For the purpose of this paper, I define

plasticity as a directional change in behavior over the course of the season. To examine the role of plasticity in changes in activity, sociality, and aggression in dispersers, I included trial date as a fixed effect in the statistical models described below. If trial date showed a significant effect on any of three behavioral axes, it would indicate that the mice showed directional plasticity in that behavior over the course of the season. I used Pearson's correlations to determine if arrival date was correlated with trial date, and if trial date was correlated with trial number. All dates used were based on the Julian calendar.

For activity, I created a mixed effects linear model (nlme package in R) with activity as the response variable and arrival date, trial number, and trial date as fixed effects. I used mouse ID as a random effect to test for individual repeatability. Because arrival date is only relevant for dispersers, and is thus equivalent to emergence date for mice born on the grid, I then created a mixed effect linear model using only trial number and trial date as fixed effects and mouse identity as a random effect. The activity models examined 57 mice and a total of 93 trials.

For sociality and aggression, only 7 mice out of 29 had more than one trial (and only 1 mouse had 3 trials). For this reason, I used only the first trial for each mouse and created linear models with the behavioral axis (sociality or aggression) as the response variable and arrival date and trial date as fixed effects. Again, because arrival date is only relevant for dispersers, I then created linear models using only trial date as a fixed effect. The sociality and aggression models examined 29 mice. All statistical analyses were performed in R version 2.9.2 (R Development Core Team 2009).

RESULTS

Model selection

The basic *a priori* model revealed that age and sex were significant predictors of arrival date, while species showed no effect, with adults arriving 24.6 ± 8.9 days before subadults and males arriving 21.1 ± 9.2 days before females (Table 3.2). The full model revealed that activity, sociality, aggression, and species were significant predictors of arrival date, with age and sex not being significant (Table 3.2). Model selection of these three models using AIC_C revealed that the behavioral model was overwhelmingly the best at predicting arrival date and will be referred to as the best model (Table 3.3). The best model revealed that activity, sociality, and aggression were all significant predictors of arrival date. Specifically, mice that arrived on the grid earlier in the season were more active, more social, and less aggressive than mice that arrived later in the season (Table 3.2 and see Table 3.1, Figure 3.1).

Do early dispersers differ in personality because of individual variation, plasticity, or habituation?

Arrival date was significantly correlated with the date on which the behavioral trials were performed (Pearson's $r = 0.79$, $P < 0.0001$). As expected, the date on which the trial was performed was also correlated with the trial number (Pearson's $r = 0.28$, $P = 0.007$). Mixed effect linear models designed to estimate the effect of plasticity and habituation on these three behavioral axes showed different results for each behavioral axis (activity, sociality, and aggression). For the activity axis, repeatability in activity within an individual was demonstrated by mouse ID accounting for 55.8% of the variation not accounted for by arrival date, trial date, or trial number. The addition of

this random effect significantly improved the fit of the model to the data ($\chi^2 = 15.9$, d.f. = 1, $P < 0.001$). Only trial date had a marginally significant effect on activity level (trial date: $b = -0.04 \pm 0.02$, d.f. = 34, $t = -1.8$, $P = 0.08$, arrival date: $b = 0.02 \pm 0.02$, d.f. = 55, $t = 1.1$, $P = 0.28$, trial number: $b = -0.09 \pm 0.34$, d.f. = 34, $t = -0.28$, $P = 0.78$), revealing that mice became less active as the season progressed. When arrival date was removed from this model, trial date ($b = -0.02 \pm 0.006$, d.f. = 34, $t = -2.5$, $P = 0.02$) and trial number became significant ($b = -0.44$, SE = 0.12, d.f. = 34, $t = -3.5$, $P = 0.002$) predictors of activity level.

For the sociality axis, neither arrival date nor trial date had a significant effect on sociality (arrival: $b = 0.0005 \pm 0.02$, $t = 0.28$, $P = 0.98$, Julian: $b = -0.03 \pm 0.02$, $t = -1.1$, $P = 0.28$ model statistics: $F = 2.0$, d.f. = 2, 26, $P = 0.15$). When arrival date was removed, trial date became a significant predictor of sociality ($F = 4.2$, d.f. = 1, 27, $P = 0.05$), demonstrating that mice became less social as the season progressed.

For the aggression axis, neither arrival date nor trial date had a significant effect on aggression (arrival: $b = -0.000 \pm 0.02$, $t = -0.001$, $P = 1.0$, Julian: $b = 0.01 \pm 0.02$, $t = 0.47$, $P = 0.6$, model statistics: $F = 0.4$, d.f. = 2, 26, $P = 0.7$). When arrival date was removed, trial date still had no effect ($F = 0.8$, d.f. = 1, 27, $P = 0.4$), demonstrating that mice show no trend in aggression over the season.

DISCUSSION

Most studies that examine dispersal examine either basic descriptor variables like age and sex (Jacquot and Vessey 1995; Krohne et al. 1984) or personality variables (Cote et al. 2010; Duckworth and Badyaev 2007) as predictors of dispersal. My study examined both basic descriptor variables and personality variables, and revealed that

personality describes disperser phenotypes better than basic descriptor variables. Early dispersers on my trapping grid were active, social, and submissive mice, while later-season dispersers were less active, less social, and more aggressive. While the basic model was marginally significant and indicated that early dispersers were likely adult males, the full model containing basic descriptor and personality variables revealed that the personality variables were the best predictors of arrival date (Table 3.2). Prior studies of dispersal in *Peromyscus* focused solely on basic descriptor variables (Jacquot and Vessey 1995; Krohne et al. 1984), finding that males dispersed farther and more often than females but early dispersers into an empty habitat were more likely adult females. However, they did not examine the mechanism behind these dispersal phenotypes. My study illustrates that personality may be mediating the relationship between basic variables like age and sex and dispersal behavior.

While species was not a significant predictor of arrival date in the basic model, when behavioral axes were added to the model, it became significant, revealing that *P. maniculatus* arrived 12.4 days later than *P. leucopus* (Table 3.2). This shift from being non-significant in the basic model to becoming significant in the full model suggests that the species effect was counteracted by an opposite effect of some personality metric that differed between the two species. Specifically, more active mice arrived earlier than less active mice and *P. maniculatus* were more active than *P. leucopus*. However, after controlling for the effects of activity on arrival date, *P. maniculatus* were found to arrive on the grid later than *P. leucopus*.

Activity

Previous work on muroid rodents suggests that in unproductive environments, like northern Michigan in late winter and early spring, animals with high exploration, or activity level, are better able to find scarce resources (Careau et al. 2009). The trends I uncovered in the activity personality axis among dispersers, which is repeatable across time and across contexts, may be explained by the relationship between activity level and the ability to find resources. Thus, early in the spring, when the forest is less productive than later in the summer, mice should be more active and thus more likely to disperse in order to find food (and hence more exploratory, according to the definition in Careau et al. 2009). As the season progresses and forest productivity increases, mice should reduce their activity levels because the abundance of resources makes them easier to find. How then is activity level linked to later-season dispersal?

After discovering from my best model that early dispersers were more active than later dispersers, I proceeded to test whether plasticity had any effect on personality in all of the mice I tested. My models revealed that activity was indeed a plastic behavioral axis, with all mice showing a trend to become less active as the season progressed and as trial number increased. This is expected, as activity is beneficial in the unproductive environment of early spring but not as beneficial when the forest is at high productivity (Careau et al. 2009).

Sociality

Previous studies have demonstrated that asocial animals are more likely to disperse, thus moving away from conspecifics (Cote et al. 2010). However, my results revealed that early dispersers were more social than late dispersers. This trend could be

due to a link between personality and over-winter survival, rather than dispersal. Because cuddling is used in cold tolerance (Andrews and Belknap 1993a, 1993b; Merritt and Zegers 2002), early in the spring when temperatures are colder, over-wintered mice should be more social than later in the summer when temperatures are warmer. Sociality played an important role in my best model, with the largest effect on arrival date, and was thus likely an important trait in early dispersers. This suggests that early dispersers may have over-wintered successfully as a result of using cuddling as a method of cold tolerance.

As with activity, it is straightforward to link sociality to early dispersal because mice that disperse early must have over-wintered successfully, and would thus have benefitted from communal nesting (Andrews and Belknap 1993a, 1993b; Merritt and Zegers 2002). The link between late-season dispersal and low sociality is less clear, as late-season dispersers are dispersing into higher population densities. Thus, I conclude that the sociality trends may be due to plasticity among all mice. Sociality was found to be a plastic behavioral axis, with mice becoming less social as the season progressed, most likely in response to rising temperatures and a lower need for communal nesting as a method of cold tolerance.

Aggression

Because mice are less aggressive at low population densities (Wolff 1985), most likely as a way to conserve energy when aggression is not necessary, early dispersers dispersing into almost empty habitat can be submissive individuals, while late-season dispersers should be aggressive individuals. However, aggression was not plastic, showing no distinct trends among all mice as the season progressed. This is likely

because the greatest population density on my trapping grid was 1.52 mice per hectare, never reaching the density necessary to affect aggression (greater than 25 mice per hectare—Wolff 1985). This finding suggests that aggression plays a key role in differentiating early dispersers from late-season dispersers. Hence, while the general trend among mice was to reduce activity level and sociality as the season progressed, mice that were active, social, and submissive were likely to be early dispersers while mice that were less active, less social, and aggressive were likely to be later dispersers. Early dispersers are more likely to be less aggressive than late-season dispersers because early dispersers disperse into lower population densities than late-season dispersers, and thus do not need to devote energy to aggression (Wolff 1985b).

Conclusion

This study illustrates the utility of personality as a predictor of dispersal and overwintering and emphasizes the need to examine more than one personality axis. If I had studied only activity or sociality, my results would have been hard to tease apart and might have suggested that, because all mice exhibit plasticity in these traits, neither behavioral axis is sufficient to describe disperser phenotypes. However, when I used the three behavioral axes together, I discovered that early dispersers are the most active, most social, and least aggressive dispersers, with later-season dispersers becoming less active, less social, and more aggressive. I know that these differences are distinct from the plasticity seen in activity and sociality because of the different temporal trends in aggression in dispersers versus the general population. Future studies of personality should examine more than one behavioral axis, with multiple measures of each axis per individual, for both the population under study (e.g. dispersers) and all animals in the

population to ensure that what appears as individual variation in personality is not only due to plasticity.

Table 3.1: Behavioral axes in *Peromyscus leucopus* and *Peromyscus maniculatus* uncovered during open-field trials.

Axis of:	Lower PC score	Higher PC score
Activity	Less active	More active
Sociality	Less social	More social
Aggression	Less aggressive	More aggressive

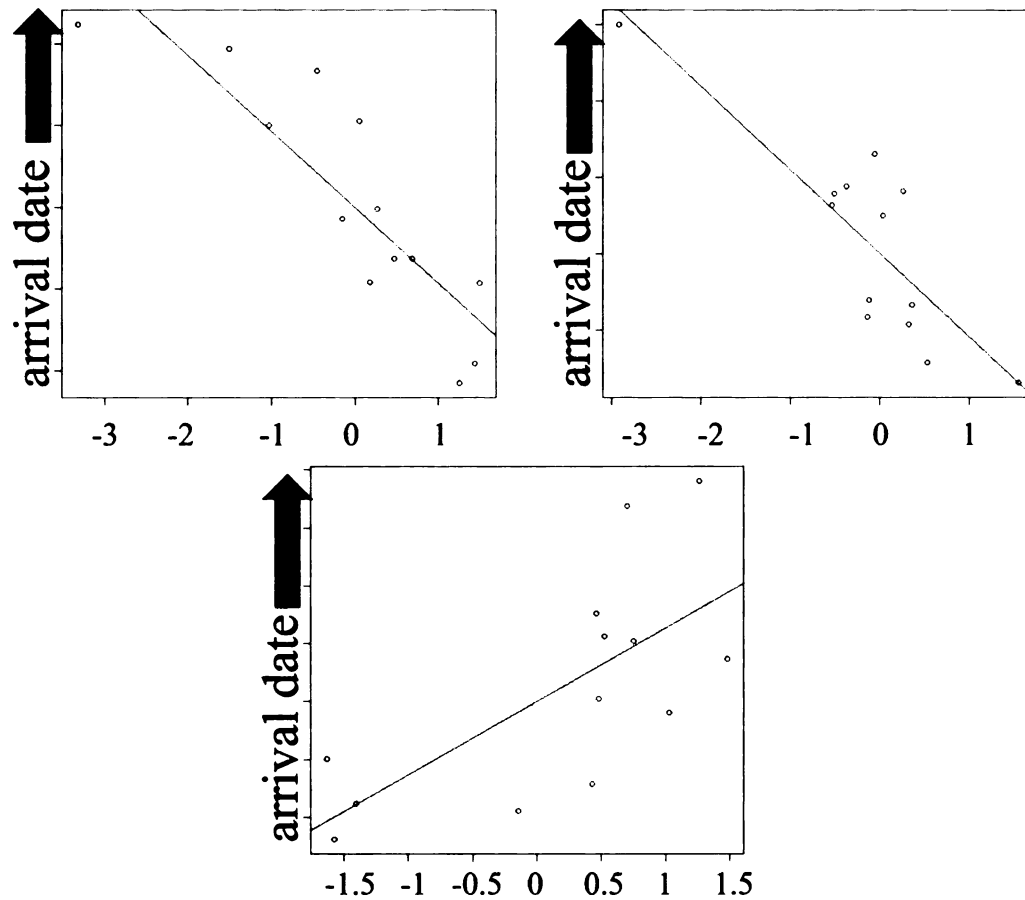
Table 3.2: Candidate models to describe arrival date in *Peromyscus leucopus* and *Peromyscus maniculatus*. Slopes (b), standard errors (SE), t-values and p-values are presented for each predictor variable, while F-statistics, degrees of freedom, and p-values are presented for each model.

Model	Fixed effect	b ± SE	t	p-value	F-statistic	df	p-value
Basic	intercept: adult, female, <i>leucopus</i>	206.5 ± 8.2	25.2	<0.0001	3.1	3,9	0.08
	age _{subadult}	24.6 ± 8.9	2.8	0.02			
	sex _{male}	-21.1 ± 9.2	-2.3	0.05			
	species _{maniculatus}	-1.7 ± 7.6	7.6	0.82			
Full	intercept: adult, female, <i>leucopus</i>	191.6 ± 4.0	47.4	<0.0001	16.9	6,6	0.002
	age _{subadult}	-3.6 ± 6.6	-0.5	0.6			
	sex _{male}	8.7 ± 6.3	1.4	0.2			
	species _{maniculatus}	14.4 ± 3.9	3.7	0.01			
	Activity	-12.8 ± 2.5	-5.2	0.002			
	Sociality	-15.9 ± 2.4	-6.7	0.0005			
	Aggression	8.9 ± 2.1	4.2	0.006			
	Intercept	203.3 ± 2.4	86.4	<0.0001			
Personality (best model)	Activity	-9.3 ± 1.9	-5.0	0.0007	13.0	3,9	0.001
	Sociality	-11.0 ± 2.5	-4.5	0.0002			
	Aggression	6.3 ± 2.4	2.7	0.02			
	Intercept	203.3 ± 2.4	86.4	<0.0001			

Table 3.3: Candidate models to describe arrival date in *Peromyscus leucopus* and *Peromyscus maniculatus*, Akaike's Information Criteria (AIC_C) results for effects of basic and personality variables on arrival date. Number of parameters (model complexity) is represented by K_i. Models were evaluated based on differences among AIC_C scores (Δ_i) and AIC_C lights (w_i). Model rank is based on differences among AIC_C scores.

Model	K _i	Log-likelihood	AIC _C	Δ_i	w_i	Rank
Personality: activity + sociality + aggression	3	-43.4	105.4	0	0.998	1
Basic: age + sex + species	3	-49.6	117.8	12.4	.002	2
Full: age + sex + species + activity + sociality + aggression	6	-35.5	123.0	17.6	<0.0001	3

Figure 3.1: Partial residual plots created using the best model from AIC_C selection describing activity, sociality, and aggression of dispersing *Peromyscus leucopus* and *Peromyscus maniculatus* in relation to their arrival date on the grid.



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CHAPTER FOUR

General conclusion: Personality in *Peromyscus*

The goal of many ecological studies is to achieve a better understanding of the mechanisms mediating classic ecological phenomena such as the coexistence of similar species and the drivers of dispersal. Deer mice of the genus *Peromyscus* are widespread across North America (King 1968), are relatively easy to live-trap, and thus are a prime model system in which to address these questions. Although ecological research has traditionally regarded individual variation as statistical noise, a new area of research utilizes these individual differences to make inferences about ecological processes by examining the implications of repeatable individual differences in behavior (Réale et al. 2007; Sih et al. 2004). These are termed temperaments (Réale et al. 2007), behavioral syndromes (Sih et al. 2004), or personalities (Dingemanse et al. 2003). Because *Peromyscus* have been so well studied, much is already known about their ecology and morphology. For this reason, I chose to examine personality in two species of sympatric *Peromyscus* in an attempt to uncover behavioral axes that might serve as axes of niche differentiation and better describe dispersal phenotypes in these mice.

In Chapter 2, I examined inter- and intraspecific variation in personality using open field behavioral trials in two species of deer mice in the northern Lower Peninsula of Michigan, *Peromyscus leucopus noveboracensis*, the white-footed mouse, and *P. maniculatus gracilis*, the woodland deer mouse. I uncovered four behavioral axes that describe activity, sociality, location, and aggression in these species. I found that *P. maniculatus* was more active than *P. leucopus*. As activity is related to cold tolerance (Sears et al. 2009), this finding is consistent with the difference in geographical range

between the two species, with *P. maniculatus* extending farther north, into colder temperatures, than *P. leucopus*. It is possible that the higher activity levels exhibited by *P. maniculatus* allow it to generate more heat by exercise thermogenesis, thus making this species better able to avoid excessive heat loss (Makinen et al. 1996) and to thrive in colder temperatures than *P. leucopus*.

Peromyscus maniculatus also had more contact with the opponent in dyadic trials than *P. leucopus* and was thus more sociable (Cote et al. 2010). This is consistent with the reported superiority of the former with respect to adaptation to cold temperatures, as small mammals often use communal nesting as a way to conserve energy in the winter (Merritt and Zegers 2002; West and Dublin 1984).

When looking at sociality and aggression for each species separately, I found no differences based on whether the opponent was a conspecific or a heterospecific. These findings are in agreement with past research that found no difference in inter- versus intraspecific aggression for home ranges (Wolff 1985). Wolff (1985) determined that home range size is density dependent, and is based on the population density of both species rather than just one. However, raw behavioral variables did reveal differences in approach and retreat behaviors that should be further examined.

In Chapter 3, I used three of these personality axes to examine the personalities of mice that dispersed onto my trapping grid early in the season compared to those that dispersed onto my trapping grid later in the season. I found that early dispersers on my trapping grid were active, social, and submissive mice, with later-season dispersers becoming less active, less social, and more aggressive. I also found that activity and sociality showed a plastic trend in response to trial date among all mice while

aggression showed no such trend, thus highlighting the importance of aggression in describing dispersal phenotypes in *Peromyscus*.

In conclusion, *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* may coexist along behavioral axes of activity level and sociality. As winters fluctuate from year to year, the relative abundances of these two species should also fluctuate. *Peromyscus maniculatus*, which is more active and more social, should increase in abundance in colder years, when higher activity levels will allow procurement of resources in an unproductive environment (Careau et al. 2009) and cuddling will be used as a means of cold tolerance (Andrews and Belknap 1993a, 1993b; Merritt and Zegers 2002). In colder years, *P. leucopus* should decrease in abundance because it is less active and less social, and is thus less able to procure resources and stay warm in cold years. Then in warmer years, *P. leucopus* should increase in abundance while *P. maniculatus* should either stay the same or decrease in abundance. Furthermore, the behavioral axes I uncovered are useful to describe individual variation in disperser phenotypes, with early season dispersers being more active, more social, and less aggressive than late-season dispersers. While individual behavioral variation plays a large role in describing disperser phenotypes, two of these axes were also shown to be plastic, with all mice in general becoming less active and less social as the season progressed.

This thesis highlights the value of including personality variables in ecological field studies. I have made a contribution to the already vast body of literature that examines coexistence in *Peromyscus leucopus* and *P. maniculatus* and have used the personality axes that I uncovered in the first study to better understand which

individuals are likely to disperse. Because of the wide variance in personality phenotypes, studies that include personality will give a detailed understanding of many phenomena central to the study of ecology.

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