REPRODUCTIVE ECOLOGY OF THE GOLDEN MOUSE (*OCHROTOMYS NUTTALLI*) AND THE WHITE-FOOTED MOUSE (*PEROMYSCUS LEUCOPUS*)

by

NATHAN LEE PRATT

(Under the Direction of Gary W. Barrett)

ABSTRACT

Patterns of seasonal reproduction for golden mice (*Ochrotomys nuttalli*) and white-footed mice (*Peromyscus leucopus*) are nearly identical, revealing a trend for summer breeding in northern populations and winter breeding in southern populations. It appears that there exists a geographic transition point around 35° north latitude, where mean annual temperature decreases below 15.6°C (60°F), and where reproductive strategy changes for both species. Despite their similarities, *O. nuttalli* tend to be more social than *P. leucopus*, frequently nesting with conspecifics. Laboratory breeding of golden mice was conducted to evaluate the ability of golden mice bred in captivity to survive and reproduce in natural deciduous forest habitat and to compare survivorship and reproduction in mice released in autumn and spring. Laboratory-breeding was expected to reduce fecundity and survivorship for golden mice reared in captivity and released into a natural riparian forest habitat compared to a native population of golden mice.

INDEX WORDS: breeding season, geographic isothermal transition point, laboratory breeding, *Ochrotomys nuttalli*, *Peromyscus leucopus*, Temperate Deciduous Forest Biome.

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NATHAN LEE PRATT

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NATHAN LEE PRATT

Major Professor:	Gary W. Barrett
Committee:	Alan Covich Steven Castleberry

Electronic Version Approved:

Maureen Grasso
Dean of the Graduate School
The University of Georgia
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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

White-footed mice (*Peromyscus leucopus*) are considered habitat generalists that occur ubiquitously throughout the northeastern and southeastern United States, as well as the Midwest; as far north as southern Canada and as far south as Mexico (Lackey et al. 1985). *Peromyscus leucopus* inhabit the edges or interiors of deciduous forests (Lackey et al. 1985). White-footed mice have been found to sustain higher population densities at edges of small deciduous forest patches, possibly as a result of increased vegetative cover, reduced population density of competitors, and increased food resources (Adler and Wilson 1987; Anderson et al. 2003; Kamler and Pennock 2004; Yahner 1992). There is some disagreement as to the habitat quality of forest edges with regard to *P. leucopus* abundance. Some research indicates that heightened predation risk at forest edges causes edge habitat to be of lower quality; however, *P. leucopus* was still found to exist at higher densities at forest edges (Wolf and Batzli 2002, 2004).

Golden mice (*Ochrotomys nuttalli*) are sparsely distributed across the southeastern United States from central-Florida to northwestern Virginia and from the Atlantic coast west to eastern Texas and Oklahoma, and throughout southeastern Missouri to southern Illinois and most of Kentucky (Feldhamer and Linzey 2008; Linzey and Packard 1977). This semi-arboreal species is considered a habitat specialist, preferentially inhabiting forest-edge habitat where vegetative cover is densest and food resources are most abundant (Barrett 2008; Christopher and Barrett 2006; Dueser and Hallett 1980; Dueser and Shugart 1978, 1979; Wagner et al. 2000; Wolff and Barrett 2008). *Ochrotomys nuttalli* constructs a wide variety of nest types with the globular and communal nests being most common (Luhring and Barrett 2008). Although forest edges provide *O. nuttalli* with increased food and nesting resources, this habitat also exposes individuals to greater risk of predation, primarily from snakes (Blouin-Demers and Weatherhead 2001; Wolf and Batzli 2002, 2004).

Ochrotomys nuttalli and *P. leucopus* share many key life history traits, including season of reproduction, body size, home range size, and food and habitat preference (Christopher and Barrett 2006, 2007; Goodpaster and Hoffmeister 1954; Knuth and Barrett 1984; Lackey et al. 1985; Linzey and Packard 1977). However, *O. nuttalli* tend be more social than *P. leucopus*, frequently nesting with several non-related conspecifics (Barrett 2008; Linzey and Packard 1977; Luhring and Barrett 2008; Springer et al. 1981). *Peromyscus leucopus* (and *Peromyscus* spp. in general) are reported to be more aggressive toward unrelated conspecifics and other small mammal species than the more docile and social *O. nuttalli* (Bradstreet 2006; Christopher and Barrett 2007). However, there is some evidence for complex social structure in *P. leucopus* from double captures of conspecifics in Sherman live traps (Christopher and Barrett 2007; Feldhamer et al. 2008).

Numerous studies have evaluated the direct and indirect effects of seasonality on reproductive ecology of small mammals (Deitloff et al. 2010; Elias et al. 2004; Heideman et al. 1999; Lackey 1973, 1978; Long 1973; Vandergrift et al. 2008; Wang et al. 2009). Most comparisons concentrate on differences regarding population abundance (Clotfelter et al. 2007; Deitloff et al. 2010; Manjerovic et al. 2009; Wang et al. 2009), parasitism and predation (Vandergrift et al. 2008), or sex ratios and litter sizes (Lackey 1973, 1978; Long 1973). Although Smith and McGinnis (1968) and Millar et al. (1979) reported small, insignificant differences in litter size of *P. leucopus* with latitude, no significant latitudinal trends have been reported within species. Latitudinal variation in patterns of reproduction has been shown for small mammal species (Lackey 1973; Long 1973); however, few studies have elucidated the geographic and climatic relationship to season of reproduction within small mammal species at the landscape and biome levels of organization.

Latitudinal variation focusing on season of reproduction for small mammals has not been explicitly studied with regard to a geographic mean annual temperature (MAT) transition point in reproductive strategy within a species (i.e., switching from a summer to winter breeding season within the same species). In general, we find that northern populations of *P. leucopus* and *O. nuttalli* tend to reproduce primarily in the warmer summer months (Lackey et al. 1985; Rose 2008), whereas southern populations of these two small mammal species tend to be reproductively inactive during summer months, with breeding occurring mainly during colder winter months (Lackey et al. 1985; Rose 2008). We hypothesize that there exists a mechanistic isothermal transition point, where mean annual temperature is 15.6°C (60°F), between reproductive strategies for these two small mammal species across the Eastern Deciduous Forest Biome.

Peromyscus leucopus have been studied in a variety of field experiments, including the release of laboratory-bred mice into the natural environment. Survivorship and reproductive capacity of laboratory-bred *P. leucopus* when released into the natural environment declined significantly in these studies (Jimenez et al. 1994; Schwartz and Mills 2005). Laboratory-bred *O. nuttalli* have not been studied with regard to their ability to survive following release into a natural environment. It is possible that inbreeding occurs in natural populations of *O. nuttalli*, as closely related individuals are frequently found in natural nests (Goodpaster and Hoffmeister 1954; Springer et al. 1981), as well as captured together in Sherman live traps (Christopher and

Barrett 2007; Luhring and Barrett 2008). However, some research indicates that for social species of mammals, inbreeding may not be deleterious to survivorship or reproductive capacity (Keane et al. 1996). This theory suggests that *O. nuttalli* may be better able to survive and reproduce in natural environment following captive inbreeding than *P. leucopus*. Thus, if highly social mammals possess a resistance to inbreeding, *O. nuttalli* may be impacted less severely by laboratory-breeding than *P. leucopus* (Kalinowski et al. 1999; Keane 1990; Keane et al. 1996). We hypothesize that laboratory-bred *O. nuttalli* released into a natural forest habitat will have a higher rate of survivorship than laboratory-bred *P. leucopus*.

There is some evidence that survivorship of laboratory-bred animals released into a natural environment may decline due to inbreeding, as well as behavioral adjustment to the captive environment (Leberg and Firmin 2008; White et al. 2005). Population abundance and reproduction for *O. nuttalli* in the northeastern Georgia is season (Rose 2008). Predation risk from black rat snakes (*Elaphe obsoleta*) and corn snakes (*Elaphe guttata*) increases during the warmer spring months (Blouin-Demers and Weatherhead 2001; Blouin-Demers et al. 2000). Thus, we hypothesize that laboratory-bred *O. nuttalli* released into a natural riparian forest habitat during spring will have decreased survival and reproduction compared to mice released during autumn.

This thesis is composed of four chapters. The second chapter addresses patterns of reproduction in northern and southern populations of *O. nuttalli* and *P. leucopus* in the Eastern Deciduous Forest Biome. This chapter will be submitted to the Journal of Mammalogy to be considered for publication. The third chapter addresses the survival and reproduction of laboratory-bred *O. nuttalli* compared with a native population of *O. nuttalli* in a riparian deciduous forest habitat. This chapter will be revised and submitted to the journal Conservation Biology authored by N.L. Pratt, T.L. Barrett and G.W. Barrett.

CHAPTER 2

PATTERNS OF REPRODUCTION IN NORTHERN AND SOUTHERN POPULATIONS OF GOLDEN MICE (*OCHROTOMYS NUTTALLI*) AND WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*) IN THE TEMPERATE DECIDUOUS FOREST BIOME

INTRODUCTION

Golden mice (*Ochrotomys nuttalli*) are a small, semi-arboreal, Cricetid rodent distributed from lower Florida to eastern Texas and as far north as West Virginia and southern Illinois (Feldhamer and Linzey 2008; Linzey and Packard 1977). *Ochrotomys nuttalli* is considered a habitat specialist which prefers areas of dense vegetation that provide food resources, nesting sites, and refuge from predators (Barrett 2008; Christopher and Barrett 2006; Dueser and Hallett 1980; Dueser and Shugart 1978, 1979; Wagner et al. 2000; Wolff and Barrett 2008). Because there is abundant information describing the use of edge habitat by golden mice, *O. nuttalli* has been described as an edge-habitat species (Seagle 1985; Wolff and Barrett 2008). Edge habitat includes riparian stream sides (Miller et al. 2004), edge of drainage ways (Andrews 1963), and edge of power-line right-of-way corridors (Linzey 1968). As with our investigation, dense understory vegetation typically characterizes edge habitats which are frequently preferred by golden mice (Morzillo et al. 2003).

White-footed mice (*Peromyscus leucopus*) occur throughout the northeastern and southeastern United States, as well as the Midwest and as far south as Mexico (Lackey et al. 1985). *Peromyscus leucopus* is considered a habitat generalist that also preferentially uses forest edge habitats (Adler and Wilson 1987; Kalmer and Pennock 2004; Lackey et al. 1985).

The objective of this study was to compare the seasonal patterns of reproduction of *O. nuttalli* and *P. leucopus* based on a climatic, Eastern Deciduous Forest Biome perspective, using female pregnancies and juvenile births to determine differences in patterns of reproduction between northern and southern populations of *O. nuttalli* and *P. leucopus*. We hypothesize that there exists a geographic, latitudinal mean annual isothermal transition point at which seasonal reproductive strategy shifts for northern and southern populations of *O. nuttalli* and *P. leucopus*.

Peromyscus leucopus is remarkably similar to *O. nuttalli* in body mass, nest-site preference, feeding behavior, bioenergetics, home range size, periods of activity, and natural history (Christopher and Barrett 2006; Goodpaster and Hoffmeister 1954; Knuth and Barrett 1984; Lackey et al. 1985; Linzey 1968; Linzey and Packard 1977; Pruett et al. 2002). In spite of these similarities and comparable life histories, *O. nuttalli* and *P. leucopus* often coexist within the same habitat, which suggests that community dynamics are structured not by interference or exploitation competition (Barrett and Feldhamer, 2008; Callaway, 2007; Christopher and Barrett 2006; Kikvidze and Callaway 2009; Stachowicz 2001). Evidence of positive interactions include interspecific double captures (n=14) of *O. nuttalli* and *P. leucopus* during live trapping (Christopher and Barrett 2007), and both species sharing the same nest (Barrett 2008). Additionally, an experimental extirpation of *P. leucopus* from a riparian deciduous forest habitat did not result in increased or decreased population density for *O. nuttalli*, indicating that resource competition may not be the primary driving force behind the community dynamic in these two species (Christopher and Barrett 2006). Sympatric habitat occupation with other *Peromyscus* species (e.g., cotton mice [*P. gossypinus*]) further indicates that community dynamics for *O. nuttalli* with other small mammal species may not be governed mainly by competition (Bradstreet 2006).

Although *P. leucopus* is considered a habitat generalist, population abundance and reproductive success are also greater in forest-edge habitats than in forest interiors (Adler and Wilson 1987; Anderson et al. 2003; Dueser and Hallett 1980; Feldhamer and Morzillo 2008; Kamler and Pennock 2004; Lackey et al. 1985; Odum, 1949; Wilder and Meikle, 2005; Yahner 1992). As an edge-habitat specialist, *O. nuttalli* is predicted to be the superior competitor in its preferred habitat; however, *O. nuttalli* is typically less populous than *P. leucopus* in the same edge habitat (Christopher and Barrett 2006, 2007; Dueser and Hallett 1980; Feldhamer and Maycroft 1992; Rose 2008). Christopher and Barrett (2006) found that removal of *P. leucopus* did not significantly increase population abundance of *O. nuttalli*, further indicating a lack of interference competition between these two species. Because of niche overlap, we hypothesize that seasonal patterns of reproduction might best help to explain the coexistence of these two small mammal species at the local, regional, and geographic ranges.

Southern populations of *O. nuttalli* and *P. leucopus* both experience increased predation risk during the late spring and early summer months when rat snakes (*Elaphe obsoleta*) and corn snakes (*Elaphe guttata*) are most active (Blouin-Demers and Weatherhead, 2001; Blouin-Demers et al. 2000). *Peromyscus leucopus* exhibits a trend for seasonal reproduction that is similar to that of *O. nuttalli* (Lackey et al. 1985; Linzey and Packard 1977).

Previous studies concerning strategies of reproduction in *P. leucopus* and *O. nuttalli* have focused primarily on sex ratios, population densities, and latitudinal variation in litter size (Clotfelter et al. 2007; Deitloff et al. 2010; Linzey and Packard 1977; Marcello et al. 2008; McCarley 1958; Reilly et al. 2006; Vandegrift et al. 2008; Wang et al. 2009; Wolff and Durr 1986; Young and Nelson 2000). Long (1973) performed a study similar to our investigation by comparing relative abundance of juvenile *P. leucopus* near the northern edge of its range in northern Wisconsin to populations of *P. leucopus* located farther south in central Illinois; however, he did not consider eastern populations of *P. leucopus* and did not attempt to determine a latitudinal gradient at which northern and southern reproductive strategies change.

Peromyscus leucopus breeding season.–Although continuous reproduction has been observed for *P. leucopus* throughout its southern geographic range (Carlson et al. 1989; Golley 1966; Lackey et al. 1985), *P. leucopus* are most reproductively active from late fall to early spring in the southeastern United States (Lackey 1978; Lackey et al. 1985; Scarlett 2004). Summer breeding in southern populations appears to be limited by parasitism, increased snake predation, changes in the abiotic environment (photoperiod and temperature), or food availability (Blouin-Demers and Weatherhead 2001; Marcello et al. 2008; Reilly et al. 2006; Vandegrift et al. 2008; Wang et al. 2009; Young and Nelson 2000). In contrast, northern populations of *P. leucopus* tend to breed mainly from late March to early November (Burt 1940; Cornish and Bradshaw 1978; Heideman et al. 1999; Lackey et al. 1985; Long 1973; Wolff and Durr 1986). Peaks in reproductive activity occur in spring and late summer for northern populations of *P. leucopus* (Table 2.1).

Ochrotomys nuttalli breeding season.–Peak reproductive activity for southern populations of *O. nuttalli* occurs during late autumn through early spring (Christopher and Barrett 2006; Layne 1960; Linzey and Packard 1977; McCarley 1958; Pearson 1953; Rose 2008). Patterns of reproduction for northern populations of *O. nuttalli* are less well known; however, peak population densities typically occur during late spring until early fall (Rose 2008; Rose and Walke 1988). Rose (2008) hypothesized that southern populations of *O. nuttalli* attain highest densities in winter/spring, whereas northern populations attain highest densities in summer/autumn. An objective of this investigation was to test this hypothesis. Previous investigations tend to support differences in breeding season for *O. nuttalli* based on a geographic temperature gradient. For example, Goodpaster and Hoffmeister (1954) observed pregnant female *O. nuttalli* from March until early October in northeastern Kentucky. Barbour (1951) also describes an adult female *O. nuttalli* with three young captured in August in Harlan County, Kentucky. Similar reproductive activity was observed in Tennessee, but with increased reproductive activity in late spring and early autumn (Linzey 1968; Linzey and Packard 1977). The most likely cause for differences in breeding and reproductive season in northern and southern populations of *O. nuttalli* is the mean annual temperature (MAT) gradient (Linzey and Packard 1977). The mean annual temperature gradient between 35°N to 37°N latitude, where MAT is 15.6°C (60°F), represents an isothermal transition point, concerning a change in reproductive strategy for *O. nuttalli* (Table 2.2).

Peromyscus leucopus sustains greater population abundance than *O. nuttalli* in most habitats (Christopher and Barrett 2006, 2007; Dueser and Hallett 1980; Rose 2008). We hypothesize that the peak breeding season for *P. leucopus* is longer in duration, including greater number of juvenile offspring beginning in the early spring and lasting until autumn in the north (north of 35°N, where mean annual temperature decreases below 15.6°C), whereas southern populations of *P. leucopus* exhibit peak patterns of reproduction mainly during winter months. Thus, southern populations of *P. leucopus* exhibit a shorter winter breeding season than the spring and fall breeding season of northern populations of *P. leucopus*.

We hypothesize that there exists a mean annual temperature geographic isotherm at which both *O. nuttalli* and *P. leucopus* switch reproductive strategies (i.e., change from a northern late spring/summer peak reproduction to a southern late fall/winter reproductive zenith). Specifically, we predict that the 60°F (15.6°C) mean annual temperature geographic isotherm represents the transition point for northern and southern reproductive strategies of both *P. leucopus* and *O. nuttalli*. The extended breeding season of *P. leucopus* compared to *O. nuttalli* may also partially explain greater population abundance for *P. leucopus* throughout its geographic range.

MATERIALS AND METHODS

Study Area.–This study was conducted at the HorseShoe Bend (HSB) Experimental site located in Clarke County, Georgia (33°57’ N, 83°23’ W). HSB is a 15-hectare peninsula created by a meander of the North Oconee River covered primarily by deciduous forest (Christopher and Barrett 2006; Klee et al. 2004). Forest habitat is composed of bottomland forest, dominated by River Birch (*Betula nigra*) and Sweetgum (*Liquidambar styraciflua*), and upland forest dominated by white oak (*Quercus alba*) and American Beech (*Fagus grandifolia*). Water oak (*Quercus nigra*), Chinese privet (*Ligustrum sinense*), greenbrier (*Smilax*) and Amur and Japanese Honeysuckle (*Lonicera maackii* and *L. japonica*, respectively) are prevalent in lowland and upland forest habitats.

Research design.–Eight experimental plots, each 0.14-hectare, were established in November 2007. Plots were evenly divided between the upland and bottomland forest. Each plot was located along a gravel road or old field approximately 3 meters into the forest-edge habitat. Each plot consists of eight nest box (Lewellen and Vessey 1999) and eight Sherman live trap (H.B. Sherman Traps, Inc. Tallahassee, Florida) stations (N = 64 stations total), arranged in a linear pattern 10 ± 2 meters apart along the edge of the forest (Fig. 2.1). This design was established to maximize the amount of edge habitat sampled and where small mammals are most abundant (Barrett 2008; Feldhamer and Morzillo 2008; Wolf and Batzli 2002; Yahner 1992). Nest boxes were located within dense *Ligustrum sinense*, *Lonicera maackii* and *Lonicera* *japonica* and attached to trees with bungee cords approximately 1.5 meters above ground. Within each plot, in alternating fashion, four of the eight nest boxes were filled with non-absorbent cotton, and four left empty to serve as nest cavities for caching food resources. Within 2-3 weeks small mammals moved cotton into all nest boxes. Sherman live traps (7.6 cm x 7.6 cm x 25.4 cm) were located in the same habitat with each trap placed on an L-shaped wooden platform approximately 1.5 meters above ground (Christopher and Barrett 2006).

Sampling procedure.–Live trapping was conducted from 1 November 2007 to 30 October 2009. Nest boxes were generally checked on alternating weeks at 0800 h, but checked weekly from 7 March to 9 May 2009 to estimate population abundance following the peak breeding season. Sherman live trapping was conducted on a biweekly basis throughout the study (1 November 2007 to 30 October 2009). Live traps were baited with sunflower seed and non-absorbent cotton was provided as bedding when overnight low temperatures were below 10°C (50°F). Live trapping was conducted twice weekly from 1 June 2009 to 31 July 2009.

Captured mice were identified to species, ear tagged for field identification, weighed to the nearest g, and released at the site of capture. Reproductive condition (females: open or closed vaginal orifice, pregnant or lactating; males: scrotal or abdominal testes) was recorded for each *O. nuttalli* and *P. leucopus* captured. Newly captured individuals of both species weighing less than 10g and having abdominal testes (males) or a closed vaginal orifice (females), were considered juveniles. Juveniles observed as attached pinkies were not subsequently recounted as juveniles upon recapture to more accurately estimate the exact number of reproduced individuals. Animals were handled in accordance with the guidelines approved by the American Society of Mammalogists (ASM Animal Care and Use Committee, 1998; Gannon et al. 2007) and approved by the University of Georgia Animal Care and Use Committee (AUP #2007-10220).

Statistics.–Reproduction for *O. nuttalli* was compared with reproduction for *P. leucopus* using a single factor analysis of variance (ANOVA). Reproductive rates for *O. nuttalli* and *P. leucopus* were calculated monthly during each breeding season by dividing the total number of juveniles produced by the total number of adult (body mass ≥ 12g) females in the population. Linear regression analysis was performed to compare prevalence of *Elaphe obsoleta* and *Elaphe guttata* with reproduction for both species of small mammals.

Literature Review.–In order to provide an accurate and unbiased assessment of the intraspecific geographic breeding patterns of *O. nuttalli* and *P. leucopus* we searched the following databases: *Academic Search Complete, Ecology Abstracts, JSTOR, Science Direct,* and *Web of Science*. We used only publications that recorded juveniles or pregnancies. Studies that only addressed reproductive condition of *O. nuttalli* and *P. leucopus* (i.e., males scrotal or abdominal testes and females open or closed vaginal orifice) were excluded.

RESULTS

Seasonal Differences in Reproduction.–The reproductive seasons for *O. nuttalli* and *P. leucopus* varied only slightly across the two-year period of observation. *Peromyscus leucopus* began breeding in early November and ceased breeding by early May of the following year. The breeding season for *O. nuttalli* extended from early January until the end of April. No reproductive activity was observed for either species during summer and early autumn, June through the end of October (Fig. 2.2). The reproductive season for *P. leucopus* not only began before that of *O. nuttalli* in each of the two years, but also extended at least one month beyond that of *O. nuttalli* (Fig. 2.2).

Annual peak reproductive output for *P. leucopus* during each breeding seasons occurred in March 2008 and January 2009. Throughout the two-year study, *P. leucopus* was highly productive with 140 juveniles recorded (Fig. 2.2). Conversely, *O. nuttalli* produced only 23 juveniles. The months of peak reproduction for *O. nuttalli* were coincident with those for *P. leucopus*, occurring in March 2008 and January 2009. However, reproduction for *O. nuttalli* was significantly less than for *P. leucopus* (p = 0.01). March 2008 was the most productive month for both *O. nuttalli* and *P. leucopus* (Fig. 2.2). However, *O. nuttalli* produced only 7 individuals in this month; whereas, *P. leucopus* produced 32 individuals. Clearly, reproductive output for *P. leucopus* was much greater than that for *O. nuttalli* at HorseShoe Bend during the 2007-2008 and 2008-2009 breeding seasons.

Reproductive Rate.–Reproductive rate for *P. leucopus* during the 2007-2008 breeding season (1.36 juveniles per adult female) was slightly lower than during the 2008-2009 breeding season (1.69 juveniles per adult female). Decreased reproductive rates were observed for *O. nuttalli* compared to *P. leucopus* in both the 2007-2008 breeding season (1.14 juveniles per adult female) and during the 2008-2009 breeding season (0.26 juveniles per adult female). Over the course of the two-year study, *P. leucopus* (1.56 juveniles per adult female) had a higher reproductive rate than *O. nuttalli* (0.61 juveniles per adult female).

Snake Capture and Small Mammal Reproduction.–We frequently captured black rat snakes (*Elaphe obsoleta*) and corn snakes (*Elaphe guttata*) within nest boxes and around natural *O. nuttalli* nests. Snake capture reached its zenith (9 snakes captured) in April 2009, and then declined throughout the remainder of the summer. Prevalence of snakes tended to increase as reproductive output for *O. nuttalli* and *P. leucopus* decreased (Fig. 2.3). However, snake prevalence was not significantly correlated with reproductive output for either *O. nuttalli* ($R^2 < 0.001$; $p = 0.95$) or *P. leucopus* ($R^2 = 0.12$; $p = 0.50$).

Comparison of Breeding Season of O. nuttalli and P. leucopus at the biome scale.–An extensive review of literature describing the breeding habits of *O. nuttalli* and *P. leucopus* indicates that the breeding season varies similarly for both species across the Eastern Temperate Deciduous Biome (Fig. 2.4). Throughout the northern portion of their respective ranges (i.e., north of 35°N latitude, where mean annual temperature decreases below 15.6°C [60°F]), both *O. nuttalli* and *P. leucopus* exhibit a summer breeding season, extending from late spring through early autumn (Fig. 2.4). In contrast, the peak breeding season for southern populations of *O. nuttalli* and *P. leucopus* occurs during winter south of 35°N, where mean annual temperature is greater than 15.6°C (60°F) (Fig. 2.4).

DISCUSSION

This study examined intraspecific differences in patterns of reproduction across a latitudinal gradient between two similar species of small mammals, *O. nuttalli* and *P. leucopus*, which occur relatively ubiquitously across the Eastern Temperate Deciduous Forest Biome. Although previous studies have elucidated differences in the number of offspring produced, population densities and sex ratios across a latitudinal gradient, there is a paucity of information contrasting the differences in reproductive season or an attempt to determine if a geographic reproductive isothermal transition point exists based on mean annual temperature regarding reproductive strategy for either *O. nuttalli* or *P. leucopus* (Lackey 1978; Linzey and Packard 1977; Long 1978; Marcello et al. 2008; McCarley 1958; Reilly et al. 2006; Smith and McGinnis 1968; Vandegrift et al. 2008; Wang et al. 2009; Wolff and Durr 1986; Young and Nelson 2000).

Seasonal reproductive activity for *O. nuttalli* and *P. leucopus* tends to be nearly identical throughout the sympatric portion of their ranges; however, a few exceptions do exist. For example, throughout southeastern Texas, *P. leucopus* has been observed to reproduce year-round, whereas *O. nuttalli* is reproductively active exclusively in the winter months (Judd et al. 1978; McCarley 1958). Additionally, *O. nuttalli* is reproductively active for almost nine months in central Florida (from September through May), which is outside the range of *P. leucopus* (Lackey et al. 1985; Layne 1960). In Louisiana, both *O. nuttalli* and *P. leucopus* have been reported to be reproductively active throughout the year (Lowery 1974).

We observed that the summer breeding season, beginning in late spring and ending in early autumn, for populations of *O. nuttalli* and *P. leucopus* occurs when mean annual temperatures are lower than 15.6°C (60°F) (Fig. 2.4). Lack of winter breeding of *O. nuttalli* and *P. leucopus* in northern populations (i.e., populations of *O. nuttalli* and *P. leucopus* north of the 15.6°C MAT isotherm) is attributed to colder temperatures (Lackey 1973; Lackey 1978; Lackey et al. 1985; Linzey and Linzey 1967; Linzey and Packard 1977; Wang et al. 2009). For southern populations (i.e., populations of *O. nuttalli* and *P. leucopus* south of the 15.6°C isotherm), moderate to high food resource availability, especially *Quercus* acorn food mast (Christopher and Barrett 2006; Wolff 1996) along with milder temperatures, facilitates a winter breeding season extending from late autumn to early spring (Lackey et al. 1985; Linzey and Packard 1977; Rose 2008). We suggest that differences in risk of predation, particularly from snakes (Blouin-Demers et al. 2000; Sexton and Hunt 1980), botfly parasitism (Jennison et al. 2006), and food availability (Wolff 1996) are significant determinants of intraspecific variation in breeding season for *O. nuttalli* and *P. leucopus* (Rose 2008; Vandergrift et al. 2008; Wang et al. 2009; Wolff 1996).

Declines in reproductive activity during midsummer for northern populations of *P. leucopus* have been linked to increased population size, an increased number of pre-reproductive females, increased parasitism and increased predation (Lackey et al. 1985; Vandergrift et al. 2008; Wang et al. 2009). Abiotic factors (decreases in temperature and photoperiod) contribute to the cessation of reproductive activity in both male and female *P. leucopus* during winter months (Carlson et al. 1989; Lackey et al. 1985; Terman 1993; Wang et al. 2009; Wolff and Durr 1986; Young and Nelson 2000).

Increased breeding activity in early spring through early autumn in northern populations of *P. leucopus* is due to hospitable environmental conditions, such as increased food availability and decreased rates of parasitism (Vandergrift et al. 2008; Wang et al. 2009). Vandergrift et al. (2008) found that increased parasitism from intestinal helminths reduced fecundity in populations of *P. leucopus* during mid-summer in northern populations. This finding helps to explain the trend for northern populations of *P. leucopus* to exhibit decreased reproductive activity during the warmest summer months. Interestingly, habitat quality (measured by food availability) did not significantly impact demographic variables such as density or reproduction. Conversely, Wang et al. (2009) linked long-term fluctuations in population density for *P. leucopus* to acorn mast, which often best represents food availability and influences population dynamics for many small mammal species (Elias et al. 2004). The immediacy of parasitism is more clearly illustrated in the short-term; whereas the effects of limited food availability tend to cause long-term density-dependent fluctuations in population density for *O. nuttalli* and *P. leucopus* (Elias et al. 2004; Saitoh et al. 1999; Wang et al. 2009; Wolff 1996).

Southern populations of *O. nuttalli* and *P. leucopus* reproduce almost exclusively in the winter (Fig. 2.4). We feel that the best explanation for this reproductive behavior is reduced risk of predation for edge-dwelling species during winter. Common predators for *O. nuttalli* and *P. leucopus* in northeastern Georgia include black rat snakes (*Elaphe obsoleta*), corn snakes (*Elaphe guttata*), various hawk species (especially the red tailed-hawk [*Buteo jamaicensis*]) and feral cats (*Felis cattus*) (Lowery 1974). Because snake predation is eliminated during the cold winter months due to snake hibernation (Blouin-Demers et al. 2000; Sexton and Hunt 1980), increased population densities for *O. nuttalli* and *P. leucopus* coincide with the periods of hibernation of *E. obsoleta* and *E. guttata* in the southeastern United States (Blouin-Demers et al. 2000; Rose 2008). During the warmer summer months, population densities for *O. nuttalli* and *P. leucopus* tend to decline for southern populations (Christopher and Barrett 2006; Golley 1966; Judd et al. 1978; Layne 1960; McCarley 1958; Rose 2008). The effects of predation are exacerbated for *O. nuttalli* and *P. leucopus*, because they preferentially occupy edge habitat where risk of predation is greatest (Wolf and Batzli 2002, 2004).

Population density of *O. nuttalli* is generally much lower than population density for *P. leucopus* in similar habitat locations (Christopher and Barrett 2006; Christopher and Barrett 2007; Dueser and Hallett 1980; Rose 2008). Trends in reproductive season vary consistently interspecifically across the latitudinal gradient, in spite of disparities in population density and productivity between *O. nuttalli* and *P. leucopus*. For example, we found that the rate of reproduction for *O. nuttalli* was considerably lower than *P. leucopus* at the HorseShoe Bend Experimental Site. This difference was attributed to decreased productivity for *O. nuttalli* during a slightly shorter winter breeding season. This difference perhaps helps to explain the disparity in population density between these two small mammal species at the landscape or regional scale. Unless survival rates for *O. nuttalli* offspring are significantly greater than those of *P. leucopus*, abundance of *O. nuttalli* will remain low compared with *P. leucopus*. We recognize that some reproduction in *O. nuttalli* may not be accurately reflected because these mice tend to mate and give birth to young in a variety of nest structures and habitat cavities (Barrett 2008; Luhring and Barrett 2008).

The geographic mean annual temperature transition point for *O. nuttalli* and *P. leucopus* to change from summer to winter reproductive strategy appears to occur near the isotherm where mean annual temperature is 15.6°C (60°F). North of this isotherm, where the mean annual temperature is less than 15.6°C, both *O. nuttalli* and *P. leucopus* shift to a summer breeding season, and where peak reproduction occurs in late spring and early autumn. Conversely, south of this isotherm, where the mean annual temperature is greater than 15.6°C, *O. nuttalli* and *P. leucopus* have evolved a winter breeding season, extending from late autumn through early spring.

Figure 2.1 – HorseShoe Bend Experimental Site. White dots represent location of live traps and nest boxes within experimental grids. Image courtesy GoogleEarth ®

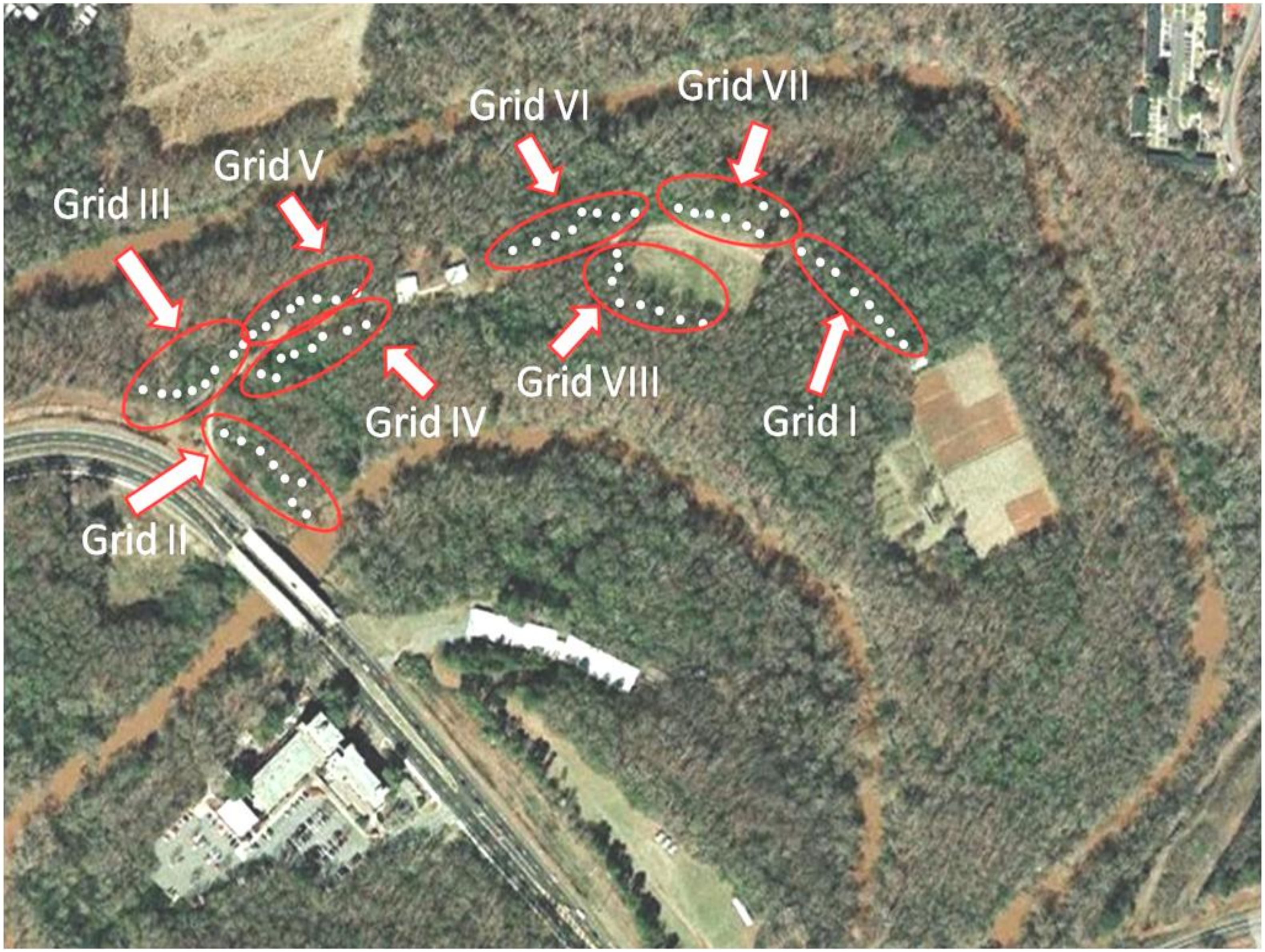

Grid VI
Grid VII
Grid V
Grid III
Grid VIII
Grid I
Grid IV
Grid II

Figure 2.2 – Diagram depicting reproductive activity for *O. nuttalli* and *P. leucopus*. Pinkies and juveniles are counted only once.

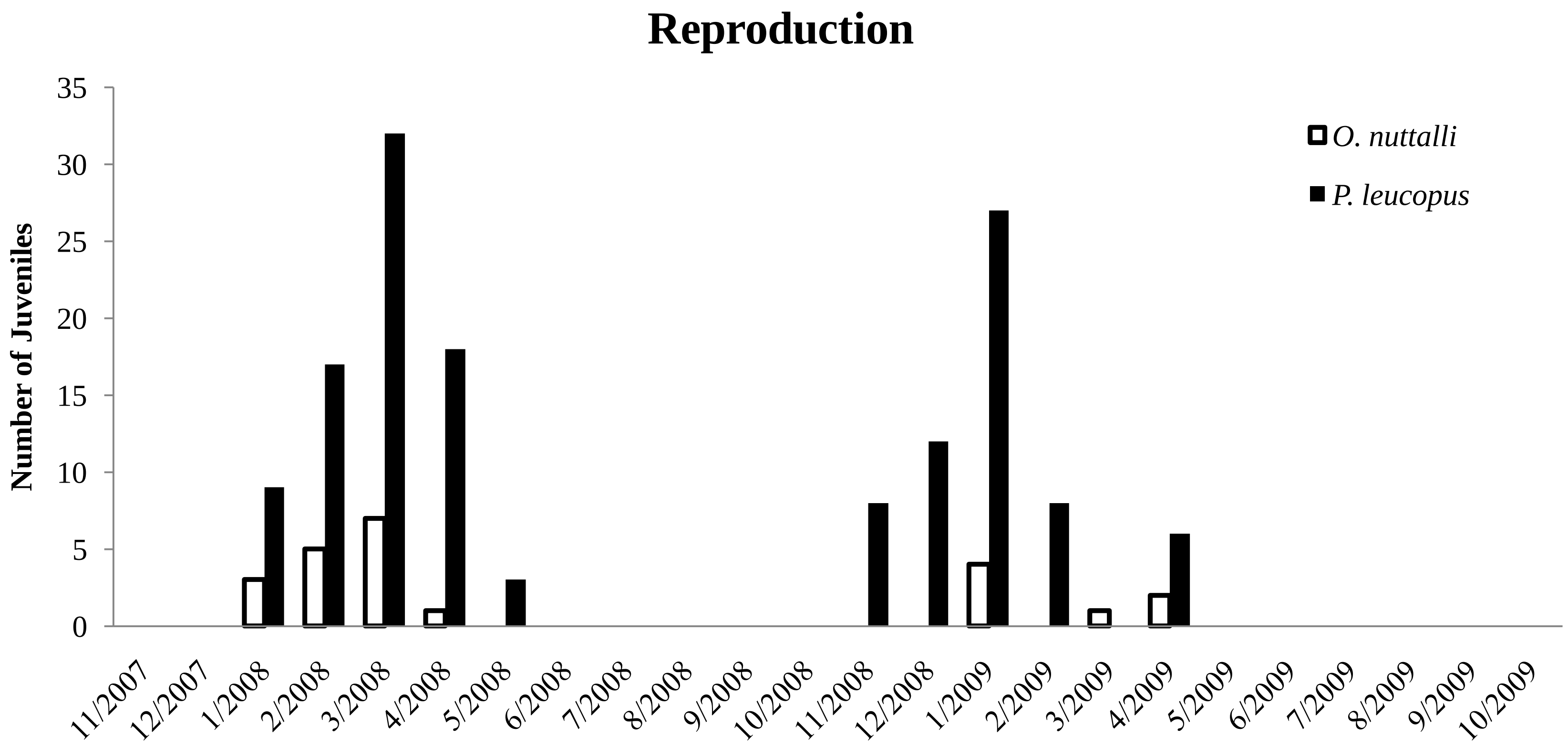

Reproduction
Number of Juveniles
35
30
25
20
15
10
5
0
O. nuttalli
P. leucopus
11/2007
12/2007
1/2008
2/2008
3/2008
4/2008
5/2008
6/2008
7/2008
8/2008
9/2008
10/2008
11/2008
12/2008
1/2009
2/2009
3/2009
4/2009
5/2009
6/2009
7/2009
8/2009
9/2009
10/2009

Figure 2.3 – Snake (*Elaphe obsoleta* and *Elaphe guttata*) capture and small mammal reproduction at HorseShoe Bend. Decrease in reproductive activity occurred with increased number of snakes captured.

Snake Capture and Mouse Reproduction

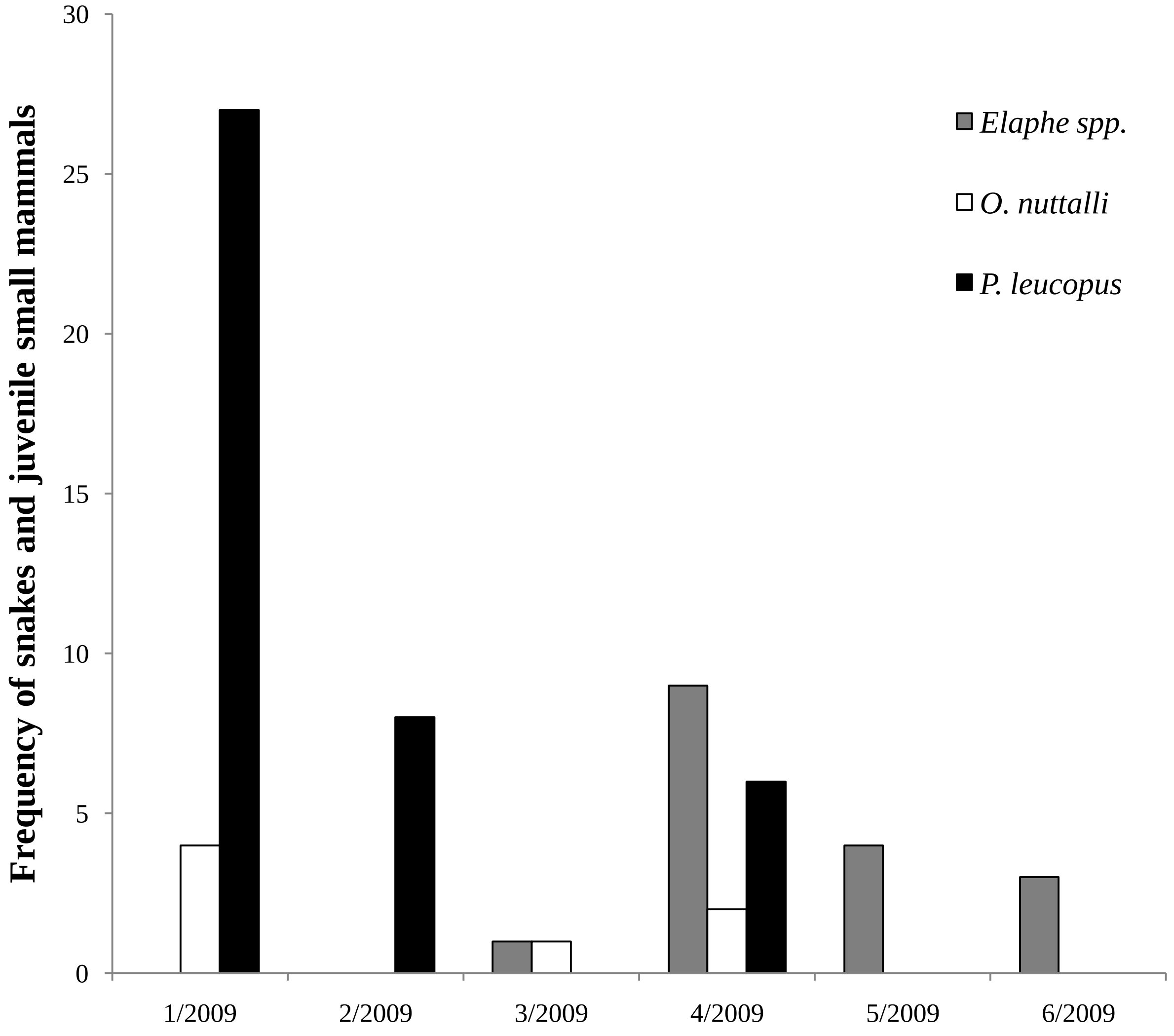


Figure 2.4 – Breeding season for *O. nuttalli* (squares) and *P. leucopus* (circles). “S” denotes peak breeding in summer; “W” denotes peak breeding in winter. Highlighted line denotes the northerly shift to mean annual temperature greater than 15.6°C. Numbers and letters correspond to reference legends available in Tables 2.1 and 2.2. Map courtesy USGS.

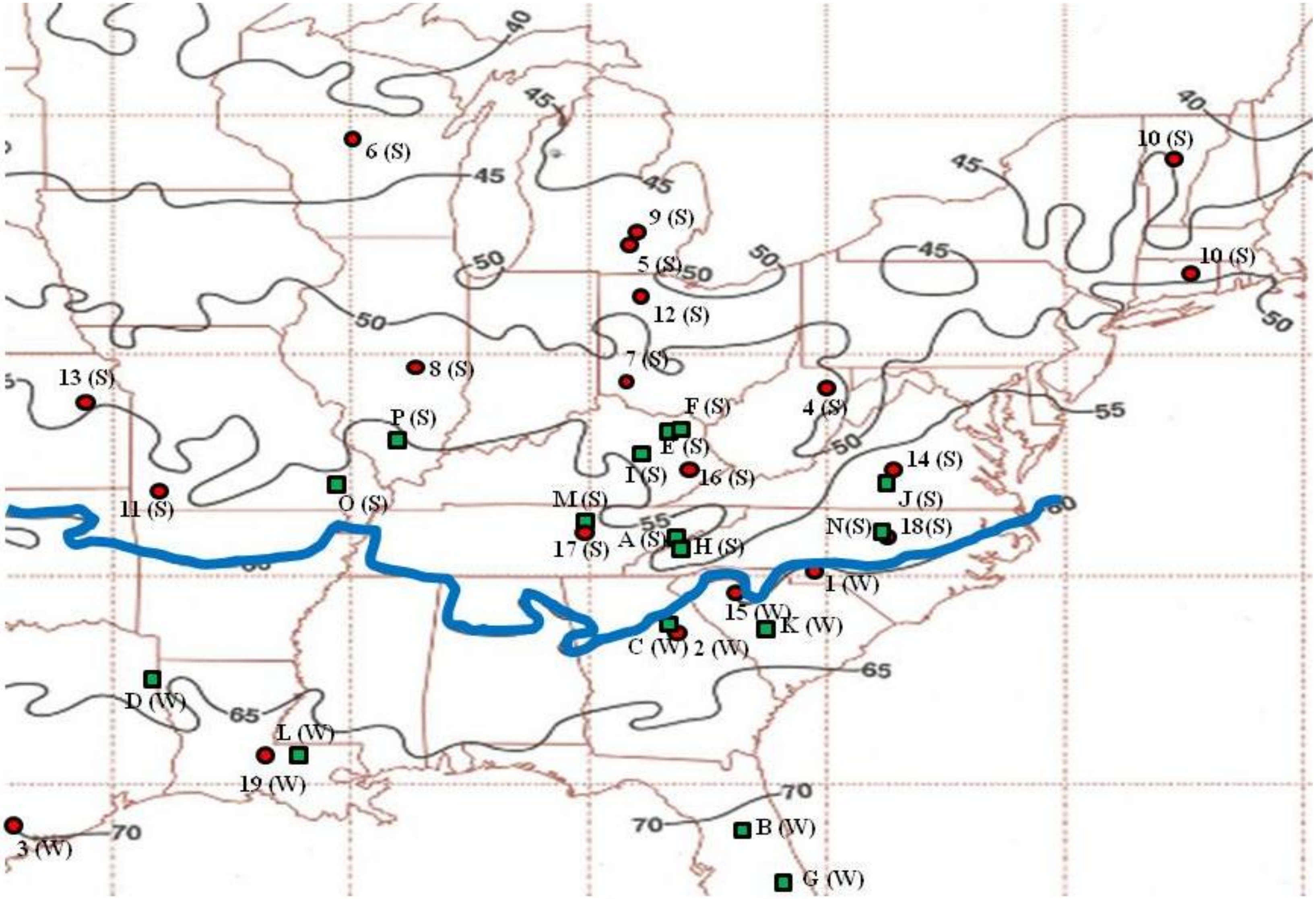

40
45
6 (S)
45
45
40
10 (S)
45
9 (S)
5 (S)
50
50
50
45
10 (S)
12 (S)
50
50
13 (S)
8 (S)
7 (S)
4 (S)
55
F (S)
P (S)
E (S)
50
14 (S)
I (S)
16 (S)
11 (S)
O (S)
M (S)
J (S)
60
55
N(S)
18(S)
17 (S)
A (S)
H (S)
60
1 (W)
15 (W)
K (W)
C (W)
2 (W)
65
D (W)
65
L (W)
19 (W)
70
70
B (W)
3 (W)
70
G (W)

Table 1 – *Peromyscus leucopus* reproduction studies.

Location	**Breeding Season**	**Reference**	**Legend**
Southern North Carolina	Winter	Scarlett 2004	1
Northeastern Georgia	Winter	HSB 2008-2009	2
Southeastern Texas	Winter	Judd et al. 1978	3
Northern West Virginia	Summer	Cornish and Bradshaw 1978	4
Southern Michigan	Summer	Burt 1940	5
Central Wisconsin	Summer	Long 1973	6
Southern Ohio	Summer	Wilder and Meikle 2006	7
Central Illinois	Summer	Batzli 1977	8
Southern Michigan	Summer	Lackey 1973	9
Northern Vermont	Summer	Miller and Getz 1977	10
Northeastern Connecticut	Summer	Miller and Getz 1977	10
Southwestern Missouri	Summer	Brown 1964	11
Northwestern Ohio	Summer	Rintamaa et al. 1976	12
Northeastern Kansas	Summer	Svedsen 1964	13
Virginia	Summer	Bailey 1946	14
South Carolina	Winter	Golley 1966	15
Northeastern Kentucky	Summer	Barbour and Davis 1974	16
Cumberland Mts TN	Summer	Howell and Conaway 1952	17
Raleigh, NC	Summer	Brimley 1923	18
Central Louisiana	Winter	Lowery 1974	19

Table 2 – *Ochrotomys nuttalli* reproduction studies.

Location	**Peak Breeding**	**Reference**	**Legend**
Eastern Tennessee	Summer	Linzey and Linzey 1967	A
Northern Florida	Winter	Layne 1960	B
Northeastern Georgia	Winter	Fig. 2.2	C
Eastern Texas	Winter	McCarley 1958	D
Northern Kentucky	Summer	Goodpaster and Hoffmeister 1954	E
Northern Kentucky	Summer	Welter and Sollberger 1939	F
Eastern Florida	Winter	Ivey 1949	G
Eastern Tennessee	Summer	Odum 1949	H
Eastern Kentucky	Summer	Wallace 1969	I
Virginia	Summer	Bailey 1946 and Hamilton 1943	J
South Carolina	Winter	Golley 1966	K
Louisiana	Winter	Lowery 1974	L
Cumberland Mts., Tennessee	Summer	Howell and Conaway 1952	M
Northern North Carolina	Summer	Brimley 1923 and 1945	N
Southeastern Missouri	Summer	Easterla 1968	O
Southern Illinois	Summer	Feldhamer 2010 – unpublished data	P

CHAPTER 3

COMPARISON OF LABORATORY-BRED WITH NATIVE POPULATION OF GOLDEN MICE (*OCHROTOMYS NUTTALLI*) IN A RIPARIAN FOREST HABITAT

INTRODUCTION

Laboratory breeding of small mammals is frequently used in field and laboratory research, as well as conservation efforts for threatened and endangered species (Amstislavsky et al. 2008; Jimenez et al. 1994; Schwartz and Mills 2005). Inbreeding commonly occurs associated with laboratory breeding investigations as a result of small initial population sizes, which can lead to decreased reproductive success and survivorship of laboratory-bred organisms (Jimenez et al. 1994; Leberg and Firmin 2008; Van Collie et al. 2008). Inbreeding is generally thought to result in at least moderately deleterious effects on animal populations (Lacy 1997; Moss et al. 2007; Schwartz and Mills 2005). However, there have been several studies to indicate that in certain populations (e.g., Kalinowski et al. 1999; Keane et al. 1996; Visscher et al. 2001) the effects of laboratory-inbreeding are non-deleterious or only marginally deleterious.

The objective of this study is to investigate the effects of laboratory breeding on survivorship and reproduction compared with a natural population of *O. nuttalli*. We hypothesize that a second or third generation, laboratory-bred population of *O. nuttalli* will have lower long-term survivorship and decreased reproduction compared to a native population of the same species. This difference in survivorship and reproduction of laboratory-bred mice will be in response to their benign environment.

Although the negative effects of inbreeding on species of small mammals that develop in captivity have been demonstrated (Jimenez et al. 1994, Schwartz and Mills 2005), the effects of a benign laboratory environment compared to a natural habitat on survival for a population have not been thoroughly assessed. Even the most elaborate semi-natural enclosures (Barrett 1968, 1988) cannot accurately simulate the conditions in natural habitat of an organism. For example, laboratory-bred organisms receive adequate food and water, as well as refuge from any natural predators and most parasites (Jimenez et al. 1994; Schwartz and Mills 2005). If organisms adjust to these conditions, the transition into a natural environment may result in a higher mortality rate than that of a natural population (White et al. 2005). The more broadly distributed and less abundant food resources, coupled with the presence of predators and parasites in the natural habitat, may result in greater stress of laboratory-reared individuals compared to a natural population.

Golden mouse (*Ochrotomys nuttalli*) is a small, semi-arboreal, Cricetid rodent distributed from lower Florida to eastern Texas and as far north as West Virginia and southern Illinois (Feldhamer and Linzey 2008; Linzey and Packard 1977). *Ochrotomys nuttalli* is considered a habitat specialist which prefers areas of dense vegetation that provide food resources, nesting sites, and refuge from predators (Barrett 2008; Christopher and Barrett 2006; Dueser and Hallett 1980; Dueser and Shugart 1978, 1979; McCarley 1958; Wagner et al. 2000; Wolff and Barrett 2008). Communal nesting occurs regularly, especially among closely related *O. nuttalli* during the winter breeding season (Barrett 2008; Luhring and Barrett 2008; Stueck et al. 1977). Communal nests can contain as many as 6-8 individual *O. nuttalli* (Barbour 1942; Jewell et al. 1991; Springer et al. 1981; Stueck et al. 1977). Other similar small-mammal species nest in groups only when mating or when juveniles are present in the nest (Barrett 2008; Christopher and Barrett 2006; Rose 2008; Rose and Walke 1988).

Northern populations of *O. nuttalli* tend to reach peak abundance between June and August, following the breeding season (Goodpaster and Hoffmeister 1954; Linzey and Linzey 1967; Rose 2008). However, peak population density for southern populations of *O. nuttalli* tends to occur between December and February (Ivey 1949; McCarley 1958; Rose 2008). Thus, season-of-release will likely impact not only survival of laboratory-bred *O. nuttalli*, but also reproductive success. Natural populations of *O. nuttalli* in the southeastern United States experience decreases in population density by mid-May due largely to increased predation. Black rat snakes (*Elaphe obsoleta*) and corn snakes (*Elaphe guttata guttata*) emerge in early spring and feed primarily on small mammals such as *O. nuttalli* (Blouin-Demers and Weatherhead 2001; Blouin-Demers et al. 2000). This trend in snake predation is perhaps related to the winter breeding season observed for southern populations of *O. nuttalli* (Golley 1966; Layne 1960; Linzey and Packard 1977) and will likely impact survivorship and reproduction for laboratory-bred mice, when introduced into the natural environment.

White-footed mouse (*Peromyscus leucopus*) occurs sympatrically with *O. nuttalli* in the southeastern and midwestern United States (Lackey et al. 1985; Linzey and Packard 1977). *Ochrotomys nuttalli* and *P. leucopus* are both semi-arboreal small mammals and have similar body mass, diets, home range sizes, life histories, and periods of activity; however, *P. leucopus* is considered less social than *O. nuttalli* (Barrett 2008; Christopher and Barrett 2006; Lackey et al. 1985). However, Christopher and Barrett (2007) and Feldhamer et al. (2008) observed a relatively high number of intraspecific double captures of *P. leucopus* during winter, which may indicate a more complex social structure for this species than previously reported.

A previous study involving the release of laboratory inbred compared to non-inbred *P. leucopus* indicates that inbreeding leads to decreased survivorship in *P. leucopus* (Jimenez et al. 1994). A similar study involving deer mice (*Peromyscus maniculatus*) showed that the negative effects of inbreeding were mitigated when successive generations were allowed to breed with unrelated conspecifics (Schwartz and Mills 2005). As a highly social species which commonly nests in communal nests with closely related conspecifics, *O. nuttalli* would likely benefit from a genetic resistance to inbreeding (Keane et al. 1996).

Because inbreeding has been reported to reduce fitness and fecundity (Jimenez et al. 1994; Schwartz and Mills 2005), we predict that laboratory-bred mice will reproduce at a lower rate than native *O. nuttalli* under natural field conditions. There is a dearth of data to verify the background rate of inbreeding in native populations of *O. nuttalli*; however, given the close social interactions between related conspecifics, we predict a higher rate of inbreeding than other similar species such as *P. leucopus* (Barrett 2008; Christopher and Barrett 2006; Lackey et al. 1985).

Population dynamic parameters, such as density, sex ratio, and survivorship, will be quantified to compare released laboratory-bred *O. nuttalli* with a native population under identical natural field conditions. Season-of-release may also impact survivorship for laboratory-bred *O. nuttalli*, as natural trends in population cycles will influence both laboratory-bred and native *O. nuttalli* (Rose 2008). We hypothesize that laboratory-bred *O. nuttalli* released in early spring, near the end of the winter breeding season, will have higher rates of mortality and produce fewer offspring than laboratory-bred *O. nuttalli* released in late autumn, near the beginning of the winter breeding season. We predict that the native population of *O. nuttalli* will have increased survivorship and reproduction compared with the laboratory-bred population of *O. nuttalli* released into the same natural riparian forest habitat.

MATERIALS AND METHODS

Study Area.–This study was conducted at the HorseShoe Bend (HSB) Experimental site located in Clarke County, Georgia (33°57’ N, 83°23’ W). HSB is a 15-hectare peninsula created by a meander of the North Oconee River covered primarily by deciduous forest (Christopher and Barrett 2006; Klee et al. 2004). Forest habitat is composed of bottomland forest, dominated by River Birch (*Betula nigra*) and Sweetgum (*Liquidambar styraciflua*), and upland forest dominated by white oak (*Quercus alba*) and American Beech (*Fagus grandifolia*). Water oak (*Quercus nigra*), Chinese privet (*Ligustrum sinense*), greenbrier (*Smilax*) and Amur and Japanese Honeysuckle (*Lonicera maackii* and *L. japonica*, respectively) are prevalent in lowland and upland forest habitats.

Experimental design.–Eight experimental plots, each 0.14 hectare, were established in November 2007. Plots were evenly divided between upland and bottomland forest habitat. Each plot was located along a gravel road or old field habitat approximately 3 meters into the forest edge habitat (Fig. 3.1). Each plot consists of eight stations (n = 64 stations total). Each station consists of one nest box and one Sherman live trap (7.6 cm x 7.6 cm x 25.4 cm), arranged in a linear pattern 10 ± 2 meters apart along the edge of the forest. This design was established to maximize the amount of edge habitat sampled where *O. nuttalli,* an edge species, are most abundant (Barrett 2008; Linzey and Packard 1977). Nest boxes and traps were located within dense *L. sinense, L. maackii* and *L. japonica*. Nest boxes were attached to trees with bungee cords approximately 1.5 meters above ground (Lewellen and Vessey 1999). Within each plot, in alternating fashion, four of the eight nest boxes were filled with non-absorbent cotton, and four left empty to serve as nest cavities for caching food resources. Sherman live traps (H.B. Sherman Traps, Inc. Tallahassee, Florida) were placed on an L-shaped wooden platform approximately 1.5 meters above ground (Christopher and Barrett 2006).

Laboratory breeding.–Laboratory breeding of *O. nuttalli* began at HorseShoe Bend Ecological Research Site in January 2008, with one adult male and two adult females captured at HorseShoe Bend. Laboratory mice were fed a diet of blueberries, slices of apple, and sunflower seeds 2 to 3 times each week. Fresh water was maintained ad libitum. We did not employ a specific breeding protocol; rather, mice were permitted to interact freely within microcosm (120 cm x 73 cm x 45 cm) tanks. Each microcosm tank was created to simulate the natural environment encountered by *O. nuttalli* in a southeastern deciduous forest edge habitat. Floors of the containers were lined with a layer of rocks and covered by field soil. Limbs from *Quercus alba* and *Q. nigra* trees were placed inside each container, which provided nesting sites for laboratory mice (Fig. 3.2). Non-absorbent cotton was placed in each microcosm as nesting material. Breeding produced over 70 *O. nuttalli* during an 18-month period following establishment of the original captive-breeding colony. Three microcosm tanks were required to house the mice. The building housing the laboratory-breeding microcosms was kept at a constant 21°C (70°F).

Release of laboratory-bred mice.–Sixteen adult pairs of laboratory-bred *O. nuttalli* were ear-tagged and released into the riparian forest habitat at 0900 h on 8 March 2009 (n = 32 total mice released). Two pairs of mice were released into each of the eight experimental plots (Fig. 3.1). The research design was repeated on 2 November 2009, when sixteen adult pairs of laboratory-bred *O. nuttalli* were released into each plot to compare differences in survival and reproductive success between autumn and spring. All mice released into the riparian forest habitat were first or second generation laboratory-bred. With only one exception, each pair shared a microcosm tank prior to release. Each pair was released into an unoccupied nest box located at least 40 ± 8 m from the nearest released pair. Nest boxes were filled with non-absorbent cotton for nesting material and 100g of *Q. alba* acorns were added initially to ensure adequate food resources for acclimation following release.

Sampling procedure.–Spring and summer animal capture was conducted from 8 March to 31 July 2009. Nest boxes were checked weekly at 0800 h from 8 March to 16 May 2009 to closely evaluate survivorship and reproductive success of newly released captive-bred *O. nuttalli*, and to compare these parameters with the native population of *O. nuttalli* inhabiting the same edge habitat then checked on alternating weeks from 30 May to 31 July 2009. The fall-winter study was conducted from 2 November 2009 to 10 April 2010. Nest boxes were checked weekly at 0800 h from 26 September to 10 April 2010, because low temperatures prevented live-trapping in January and February 2010. Nest boxes and live traps were filled with non-absorbent cotton, which was removed from all live traps and nest boxes on 13 June 2009, due to increasing temperatures. Cotton was replaced in nest boxes on 26 September 2009 before the beginning of the winter breeding season. Live traps were checked weekly from 1 March to 1 July 2009.

Traps were set at 1700h, baited with sunflower seed and non-absorbent cotton was provided for bedding when temperatures decreased below 16°C and checked the following day at 0730 hours. Captured mice were identified to species, ear tagged for field identification, weighed to the nearest gram. Reproductive condition (females: open or closed vaginal orifice, pregnant or lactating; males: scrotal or abdominal testes) was recorded for each *O. nuttalli* captured. Maternity was determined for all juveniles, by observing lactating females captured with juveniles, to determine whether a juvenile was produced from the native or laboratory-bred population of *O. nuttalli*. Animals were handled in accordance with the guidelines approved by the American Society of Mammalogists (ASM Animal Care and use Committee, 1998; Gannon et al. 2007) and approved by the University of Georgia Animal Care and Use Committee (AUP #2007-10220).

Statistics.–Weekly population estimates of both laboratory-bred and native *O. nuttalli* were determined using the Minimum Number Known Alive (MNKA) method (Krebs 1996). Survivorship estimates for each seasonal release of laboratory-bred *O. nuttalli* were calculated by dividing MNKA by total number of laboratory-bred *O. nuttalli* released. Survivorship estimates for native *O. nuttalli* in spring were calculated by dividing MNKA by the number of adult mice in the population on 7 March 2010, the date of laboratory-bred release. Two survivorship estimates were evaluated for native *O. nuttalli* in the autumn release. The first was calculated in a manner identical to the estimate for native *O. nuttalli* survivorship during the spring release. Because of the low population size of native *O. nuttalli* at the date-of-release, a second estimate was calculated by dividing MNKA at the end of the 15-week experiment by the total number of native *O. nuttalli* captured during the course of the experiment.

Mean monthly population sizes were calculated by averaging the weekly population estimates from MNKA estimates. Monthly population estimates for laboratory-bred and native *O. nuttalli* were compared via linear regression with mean monthly temperature for Athens-Clarke County, GA recorded by the Southeastern Regional Climate Center (SERCC).

Reproduction was evaluated by counting the number of juveniles produced by laboratory-bred and native *O. nuttalli*. Maternity was determined by observing pinkies attached to a lactating female *O. nuttalli*. Juveniles produced by native *O. nuttalli* were counted as part of the population of native *O. nuttalli* after being ear-tagged. Juveniles produced by laboratory-bred *O.*

nuttalli were not counted as part of either the laboratory-bred population or native population of *O. nuttalli*, to ensure proper evaluation of survivorship of laboratory-bred *O. nuttalli*. Reproductive rates were calculated by dividing the number of juveniles observed by the estimated number of adult females (body mass ≥ 15g) in the population. Total reproductive rate was determined by summing the number of juveniles produced during the experiment and dividing this by the total of adult females in the population throughout the experiment. A single factor analysis of variance (ANOVA) was conducted to compare total reproduction in laboratory-bred and native *O. nuttalli* during the course of both seasonal releases.

Male-to-female sex ratios were computed by dividing the estimated number of male by female *O. nuttalli* in the laboratory-bred and native populations. These were compared against each other weekly throughout the 15-week experiment using an ANOVA to determine whether laboratory-breeding would affect sex ratio. Sex ratios were also compared against an expected male-to-female sex ratio of 1 using a chi-squared analysis to evaluate whether weekly sex-ratios were significantly different from the expected ratio.

Mean monthly population sizes were estimated by averaging MNKA each week throughout the month. Correlation coefficients were determined between snake capture and mean monthly population density for laboratory-bred and native *O. nuttalli*.

RESULTS

Population size.–Laboratory-bred and native *O. nuttalli* maintained higher population densities during the winter release at the beginning of breeding season (Figs. 3.3, 3.4). In each study, native *O. nuttalli* had a smaller initial population size than the released laboratory-bred *O. nuttalli*; however, survivorship over a 15-week period was higher for native *O. nuttalli* following autumn or spring release.

Population densities for native and laboratory-bred *O. nuttalli* reached their zenith in mid-March during the release in spring 2009. Population densities declined throughout the spring and dropped precipitously by early summer (Fig 3.3). Almost half of the laboratory-bred *O. nuttalli* never were recaptured following the initial release, after five (5) weeks the population size was reduced to only 10 individuals; whereas, the native population of *O. nuttalli* maintained a population size of 17 individuals for 9 weeks into the study. By week 10, only two (2) laboratory-bred individuals were still surviving in the population; whereas, native *O. nuttalli* had a population size of 14 individuals (Fig. 3.3). This spring-release comparative study was concluded on 18 July 2009. One laboratory-bred individual was captured on 18 July 2009, after which no laboratory-bred individuals were captured (Fig. 3.3).

The largest decline in population size for the laboratory-bred *O. nuttalli* for the winter-release experiment occurred during the second week after release. Of the 32 individuals released into the nest boxes, ten (10) individuals were not recaptured after the first week of the study. Of these 10 mice, four (4) were never recaptured. After this initial decline, the laboratory-bred population size did not decline below 16 individuals until after the fourteenth week following release (Fig. 3.4). By the fifteenth week of the study, the population size was estimated to be 15 individuals (Fig. 3.5). The native population of *O. nuttalli* was initially smaller than during the spring release; however, population size increased steadily through January and February, reaching a maximum of 34 individuals on 7 February 2010 (14 weeks after the initial release). In the course of 2 weeks from 20 December 2009 to 3 January 2010, twelve (12) individuals were added to the population due to reproductive activity in native *O. nuttalli* (Fig. 3.4).

Survivorship.–Declines in population size for native and laboratory-bred *O. nuttalli* were relatively severe during the fifteen week period following the 7 March 2009 release. Of the 22 native *O. nuttalli* in the population at the beginning of this study, only four (4) individuals survived throughout the course of the 15-week study (~18 percent survival). However, the laboratory-bred population consisted of a lone female *O. nuttalli* by week 13 following release (~3.1 percent survival). Native *O. nuttalli* survived at a much higher rate than laboratory-bred mice following spring release.

About 47 percent of the laboratory-bred *O. nuttalli* released on 2 November 2009 survived over fifteen weeks. Three of the four *O. nuttalli* recorded in the native population on the date of release (2 November 2010) survived throughout the 15-week experiment. This provides an estimated 75 percent survivorship. However, for all native *O. nuttalli* captured during the course of the 15-week experiment, ~45 percent survivorship was estimated; although, higher mortality rate for young-of-the-year may have caused this survival rate to be slightly lower than for adult *O. nuttalli*.

Reproduction.–Reproductive activity was minimal for native *O. nuttalli* and non-existent for laboratory-bred *O. nuttalli* during the first release in spring. Laboratory-bred *O. nuttalli* did not reproduce during the course of the experiment. Native *O. nuttalli* produced only one (1) juvenile in March 2009, two (2) in April 2009 and none in May, June or July 2009 (Fig. 3.6). Monthly reproductive rate for laboratory-bred females during the spring release was 0; whereas the reproductive rate for native females was 0.095 juveniles per female for March and 0.22 juveniles per female for April. May is recognized as the end of the breeding season for *O. nuttalli* in the Southeastern United States (Golley 1966; Layne 1960; Linzey and Packard 1977; Rose 2008), thus we did not expect reproductive activity for either native or laboratory-bred mice during June or July.

Increased reproductive activity, however, was observed for both native and laboratory-bred *O. nuttalli* during the release in late autumn. Peak reproduction for laboratory-bred *O. nuttalli* occurred during January with a total of thirteen (13) juveniles. Peak reproductive activity for native *O. nuttalli* occurred during December with twelve (12) juveniles produced. The first juvenile recorded for the native population of *O. nuttalli* occurred in November 2009, whereas reproduction for laboratory-bred *O. nuttalli* did not begin until December 2009 (Fig 3.7). Native *O. nuttalli* produced a total of 21 juveniles from November 2009 through March 2010. No reproductive activity was observed for native *O. nuttalli* during March 2010. During the same time period, laboratory-bred *O. nuttalli* produced 20 juveniles. Reproduction began in December 2009 and concluded in March 2010; although no reproductive activity was observed during February for laboratory-bred *O. nuttalli* (Figs. 3.7, 3.8).

Monthly reproductive rate was highly variable for both laboratory-bred and native *O. nuttalli*. Laboratory-bred *O. nuttalli* produced young at a rate of 0.44 juveniles per female in December, 1.59 juveniles per female in January and 0.56 juveniles per female in March. Native *O. nuttalli* reproduced at a rate of 0.45 juveniles per female in November, 2.09 juveniles per female in December, 0.45 juveniles per female in January, and 0.062 juveniles per female in February. Total reproductive rate for native *O. nuttalli* was 1.24 juveniles per adult female; whereas, laboratory-bred *O. nuttalli* reproduced at a rate of 1.33 juveniles per adult female. Reproduction was not statistically different for native and laboratory-bred *O. nuttalli* ($p = 0.8$)

Total reproductive output throughout the experiment for *O. nuttalli* was 44 juveniles. Of the total reproductive activity, native *O. nuttalli* females accounted for 24 juveniles (~54 percent of total juveniles); whereas, laboratory-bred *O. nuttalli* females produced 20 juveniles (~46 percent of total juveniles).

Temperature and Population size.–Decline in average monthly population size for the native population of *O. nuttalli* was significantly inversely related to an increase in average monthly temperature ($R^2 = 0.995$; $p < 0.05$). A similar relationship was found to exist for laboratory-bred *O. nuttalli*; however, this relationship was not found to be statistically significant ($R^2 = 0.800$; $p = 0.1$). The laboratory-bred population of *O. nuttalli* released during autumn declined through the colder winter months, producing no significant relationship with temperature ($R^2 = 0.0804$; $p = 0.64$). Population abundance of native *O. nuttalli* tended to increase with decreasing temperature; however, the relationship was not significant ($R^2 = 0.393$; $p = 0.25$).

Sex Ratios.–Sex ratios for laboratory-bred *O. nuttalli* did not differ significantly from either an expected even sex ratio ($\chi^2 = 0.98$; df = 1; $p > 0.25$) or the sex ratio of the native population of *O. nuttalli* at during the experiment ($p = 0.5$). Sex ratio for laboratory-bred *O. nuttalli* released in autumn did not differ significantly from either an expected even sex ratio ($\chi^2 = 1.00$; df = 1; $p > 0.25$) or from the sex-ratio of the native population of *O. nuttalli* ($p = 0.1$).

Population Abundance and Snake Capture.–We frequently captured black rat snakes (*Elaphe obsoleta*) and corn snakes (*Elaphe guttata*) within nest boxes and around natural *O. nuttalli* nests. Snake capture reached its zenith in April 2009, and then declined throughout the remainder of the summer (Fig. 3.9). Prevalence of snakes tended to increase as population abundance for laboratory-bred and native *O. nuttalli* decreased; however, snake capture was not significantly correlated to mean monthly population size for either laboratory-bred ($R^2 = 0.18$; $p = 0.5$) or native ($R^2 = -0.61$; $p = 0.2$) *O. nuttalli*.

DISCUSSION

Season-of-release is a major determinant of survivorship as well as reproductive capacity for laboratory-bred *O. nuttalli*. Seasonal Climatic trends for *O. nuttalli* in the southeastern United States likely drive most of the differences seen in survivorship and reproduction for laboratory-bred *O. nuttalli*. However, the effects of predation, parasitism and sparse food resources (especially *Q. alba* and *Q. nigra* acorns) appear to be more pronounced in both native and laboratory-bred mice during early spring.

Laboratory-bred *O. nuttalli* are capable of surviving in a natural riparian deciduous forest habitat after being released in late fall-early winter. Laboratory-bred *O. nuttalli* released in November, for example, were capable of not only surviving throughout the winter, but also reproducing. On several occasions (N = 16), native males and females paired with laboratory-bred *O. nuttalli*. In at least three instances, native male *O. nuttalli* sired offspring with laboratory-bred female mice. This indicates inferior ability to compete for mates for laboratory-bred males; however, male laboratory-bred *O. nuttalli* were found nesting with native female *O. nuttalli* that were either pregnant or nursing juveniles on several occasions (N = 4).

Reproductive capacity of laboratory-bred *O. nuttalli* in a natural environment has not previously been tested; however, this experiment indicates that laboratory-bred *O. nuttalli* are capable of reproducing at a rate similar to native mice. Laboratory-breeding has not significantly affected the ability of male and female *O. nuttalli* to find mates and produce offspring. Reproductive rate for laboratory-bred female *O. nuttalli* (1.33 juveniles per adult female) was not significantly different from the reproductive rate for native *O. nuttalli* (1.24 juveniles per adult female). Generally, laboratory-bred *O. nuttalli* males and females paired with native mice, rather than nesting and mating with laboratory-bred conspecifics. Keane (1990) found that *P. leucopus* tend to avoid inbreeding through behavioral traits such as dispersal.

This indicates that kin-recognition plays a role in dispersal and inbreeding avoidance in *O. nuttalli* similar to *P. leucopus* (Bollinger et al. 1993; Keane 1990; Pusey and Wolf 1996; Wolff et al. 1988); however, dispersal was not quantified for laboratory-bred or native mice in this study. Additionally, it is relatively common to find closely related *O. nuttalli*, particularly young-of-the-year inhabiting the same nest (Barrett 2008; Christopher and Barrett 2007; Linzey and Packard 1977; Luhring and Barrett 2008; Rose 2008). Keane and colleagues (1996) also indicated that inbreeding depression was not observed in a social carnivore despite a lack of inbreeding avoidance behavior; therefore, it may be possible for highly social species of mammals to mate with closely related conspecifics without highly deleterious effects. The level of inbreeding for the laboratory-bred *O. nuttalli* was not quantified in this study; thus, direct conclusions about the effects of inbreeding on *O. nuttalli* are not available.

A linear relationship exists between temperature and population abundance in *O. nuttalli* during spring. However, mean monthly temperatures did not correlate closely with population size following the autumn release. We attributed declines in population abundance and reproduction for native and laboratory-bred *O. nuttalli* following the spring release to increased predation and parasitism (Blouin-Demers and Weatherhead 2001; Blouin-Demers et al. 2000; Jennison et al. 2006; Vandergrift et al. 2008). Edge habitat specialist species such as *O. nuttalli* encounter greater predation than species that more frequently inhabit forest core (Lidicker Jr. 1999; Weatherhead and Blouin-Demers 2003; Weatherhead et al. 2010). Increased snake predation indicates that season-of-release is an important factor in survivorship for laboratory-bred *O. nuttalli*. One possibility is that additional time living in the wild prior to the appearance of predators acclimated the laboratory-bred population to removal from the benign surroundings of the laboratory microcosms.

Jimenez et al. (1994) conducted a similar study to evaluate the effects of laboratory-inbreeding on survival of *P. leucopus* in a deciduous forest in Illinois. Recapture success was much lower (~0.16) for laboratory-bred *P. leucopus* released from late spring to early autumn in the previous study than for laboratory-bred *O. nuttalli* (~0.70) in both releases during the course of the present experiment. In addition, survivorship for laboratory-bred *P. leucopus* was estimated to be considerably lower over a 10-week period than for *O. nuttalli* released in late autumn. Techniques used to measure population abundance were less conservative than MNKA and are difficult to compare; however, a 10-week survival rate of over 50 percent was observed in *O. nuttalli* released during autumn 2009 (Fig. 3.5). Nevertheless, trapping procedures and number of individuals released differed significantly between the two studies, making direct comparison of the effects of laboratory-breeding on *O. nuttalli* and *P. leucopus* difficult (Jimenez et al. 1994).

Schwartz and Mills (2005) followed up the study by Jimenez et al. (1994) by evaluating survival of non-inbred, inbred and out-crossed *P. leucopus* into an enclosed old-field habitat. Schwartz and Mills (2005) indicated that the deleterious effects of inbreeding can be offset by breeding inbred mice with unrelated conspecifics. The 6-week survival rate for laboratory-bred *P. leucopus* in the Schwartz and Mills (2005) study was ~0.93, which is considerably higher than the survival rate observed for *O. nuttalli* in our study. However, the laboratory-bred *P. leucopus* were released into an enclosed environment, absent any natural predators or other small-mammal competitors. The 6-week survival rate for *O. nuttalli* in a natural forest habitat during the autumn release experiment was ~0.60; however, a higher mortality rate is expected for this experiment as laboratory-bred mice were released into a natural riparian forest habitat.

Laboratory-bred mice faced competitive pressure from conspecifics, as well as other small mammal species such as *P. leucopus*, Eastern gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*) and Southern flying squirrels (*Glaucomys volans*). Additionally, predation risk from red-tailed hawks (*Buteo jamaicensis*), great horned owls (*Bubo virginianus*), and barred owls (*Strix varia*) observed in or near our riparian habitat likely contributed to a lower overall survival rate; although, no evidence of predation by these species was recorded in our study.

Reproductive capacity for *O. nuttalli* in a natural riparian forest habitat is not significantly impaired by laboratory-inbreeding (Fig. 3.8). Season-of-release impacted both survival and reproductive capacity more than laboratory-breeding for *O. nuttalli* and is considered important when releasing mice or stocking enclosures (Barrett 1968, 1985) for experimental investigations. Predation and parasitism pressures, as well as competition from other small mammal species, were more severe for laboratory-bred mice that were adjusted to living in a benign laboratory environment; whereas, native *O. nuttalli* were better able to compete in the natural habitat.

Figure 3.1 – HorseShoe Bend Experimental Site. White dots represent location of traps within experimental grids. Image courtesy GoogleEarth ®

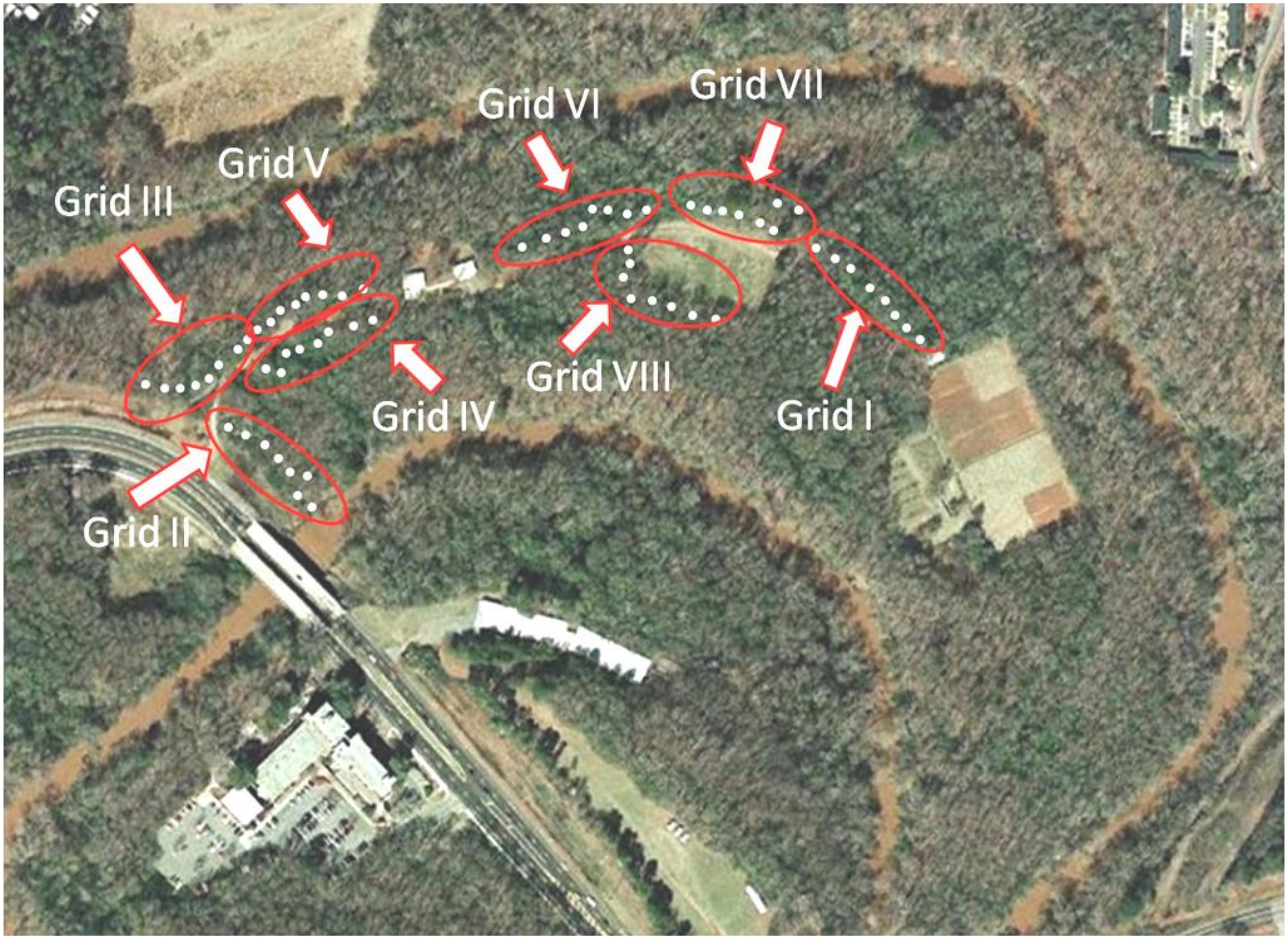

Grid VI
Grid VII
Grid V
Grid III
Grid VIII
Grid I
Grid IV
Grid II

Figure 3.2 – Laboratory-breeding microcosm at HorseShoe Bend. Image courtesy Luis Rodas.

Figure 3.3 – Minimum number known alive following spring release (8 March 2009) of laboratory-bred compared with the native *O. nuttalli* population. No laboratory-bred *O. nuttalli* were captured after 30 July 2009.

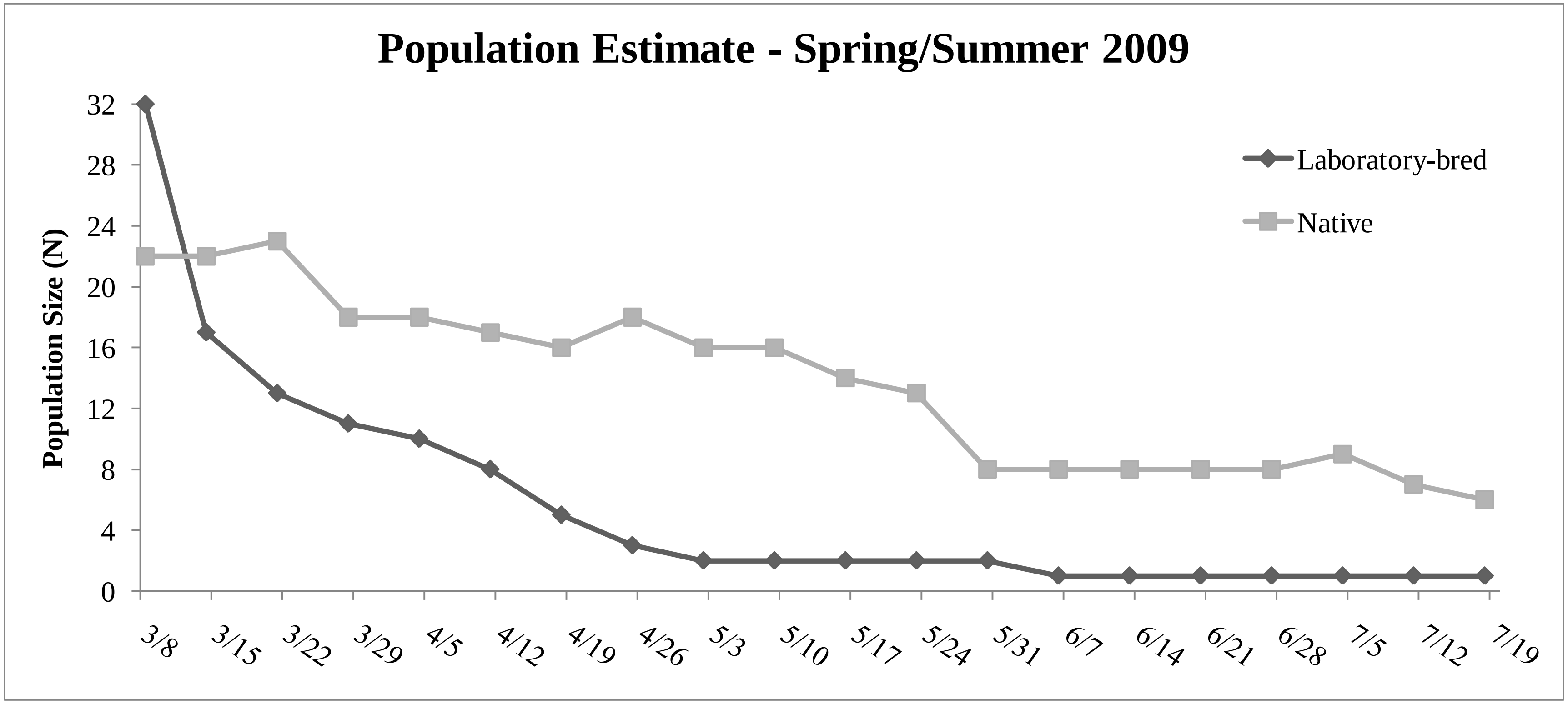

Population Estimate - Spring/Summer 2009
Population Size (N)
32
28
24
20
16
12
8
4
0
3/8
3/15
3/22
3/29
4/5
4/12
4/19
4/26
5/3
5/10
5/17
5/24
5/31
6/7
6/14
6/21
6/28
7/5
7/12
7/19
Laboratory-bred
Native

Figure 3.4 – Minimum number known alive during autumn release (2 November 2009) of laboratory-bred *O. nuttalli* compared with the native *O. nuttalli* population. Native *O. nuttalli* population was initially small; however, reproductive success increased throughout the winter breeding season.

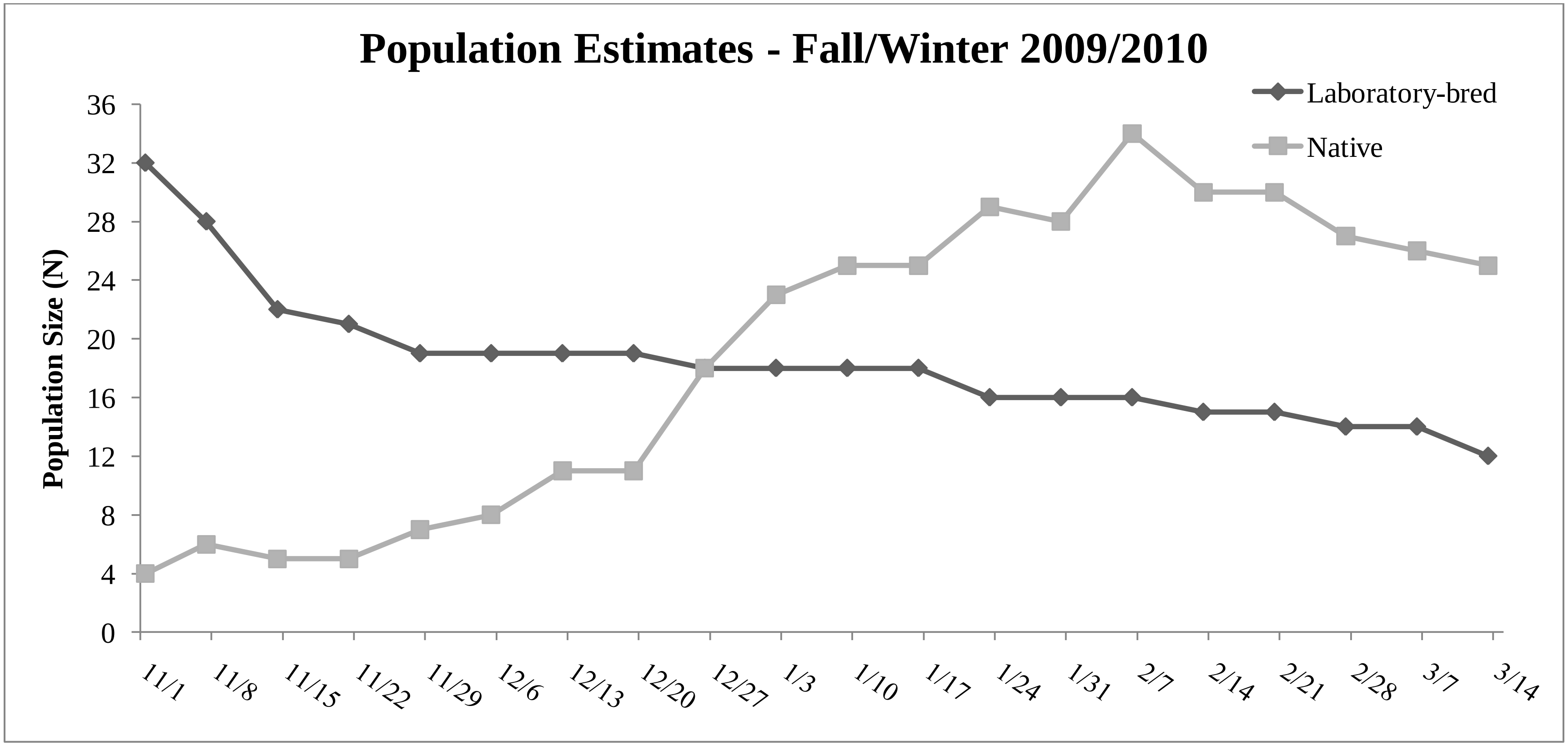

Population Estimates - Fall/Winter 2009/2010
Laboratory-bred
Native
Population Size (N)
36
32
28
24
20
16
12
8
4
0
11/1
11/8
11/15
11/22
11/29
12/6
12/13
12/20
12/27
1/3
1/10
1/17
1/24
1/31
2/7
2/14
2/21
2/28
3/7
3/14

Figure 3.5 – Comparison of minimum number known alive of *O. nuttalli* released during spring 2009 and autumn 2009.

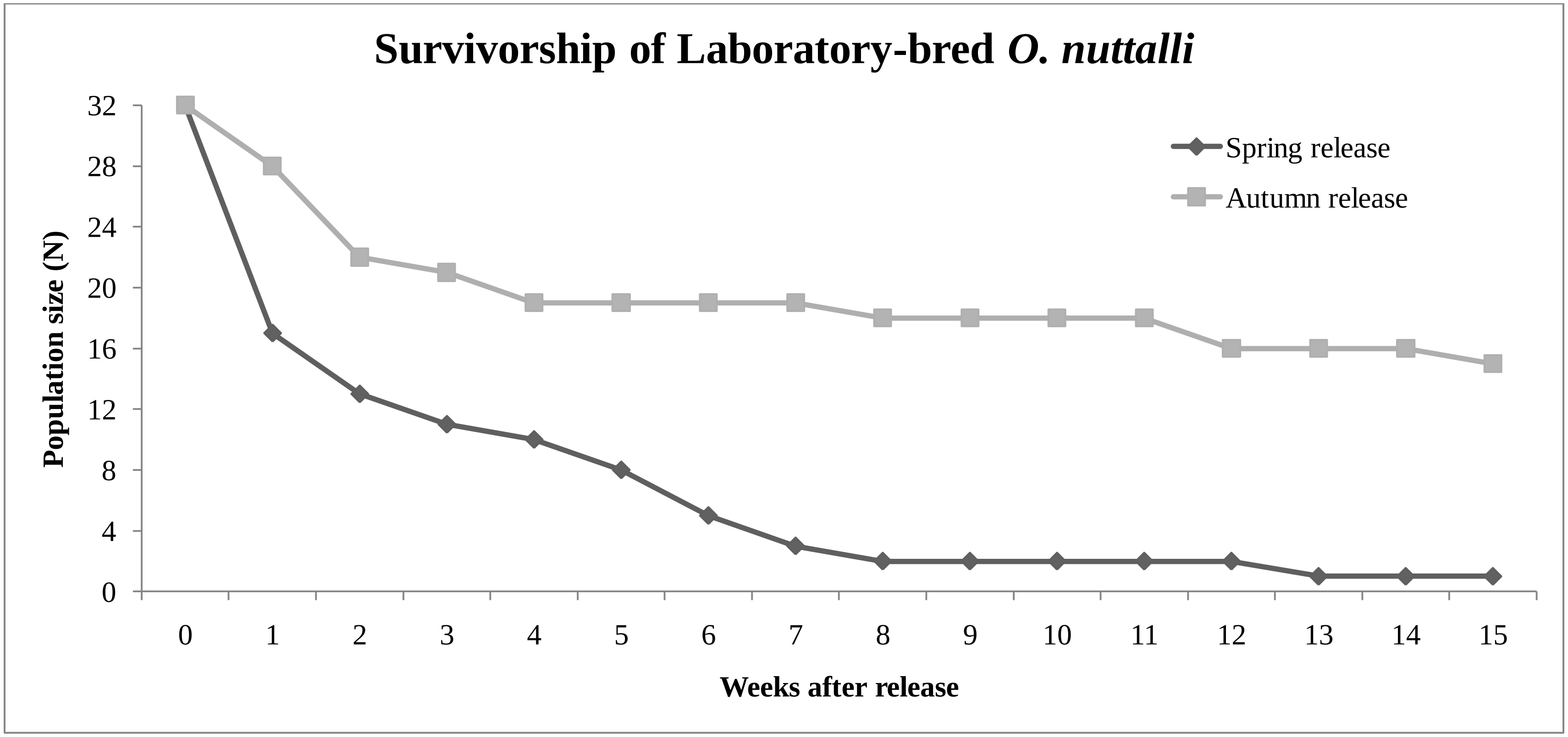

Survivorship of Laboratory-bred *O. nuttalli*
Spring release
Autumn release
Population size (N)
32
28
24
20
16
12
8
4
0
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Weeks after release

Figure 3.6 – Reproductive activity during spring release (March 2009) of laboratory-bred *O. nuttalli*. No reproductive activity observed after April for native *O. nuttalli*. No reproductive activity observed for laboratory-bred *O. nuttalli*.

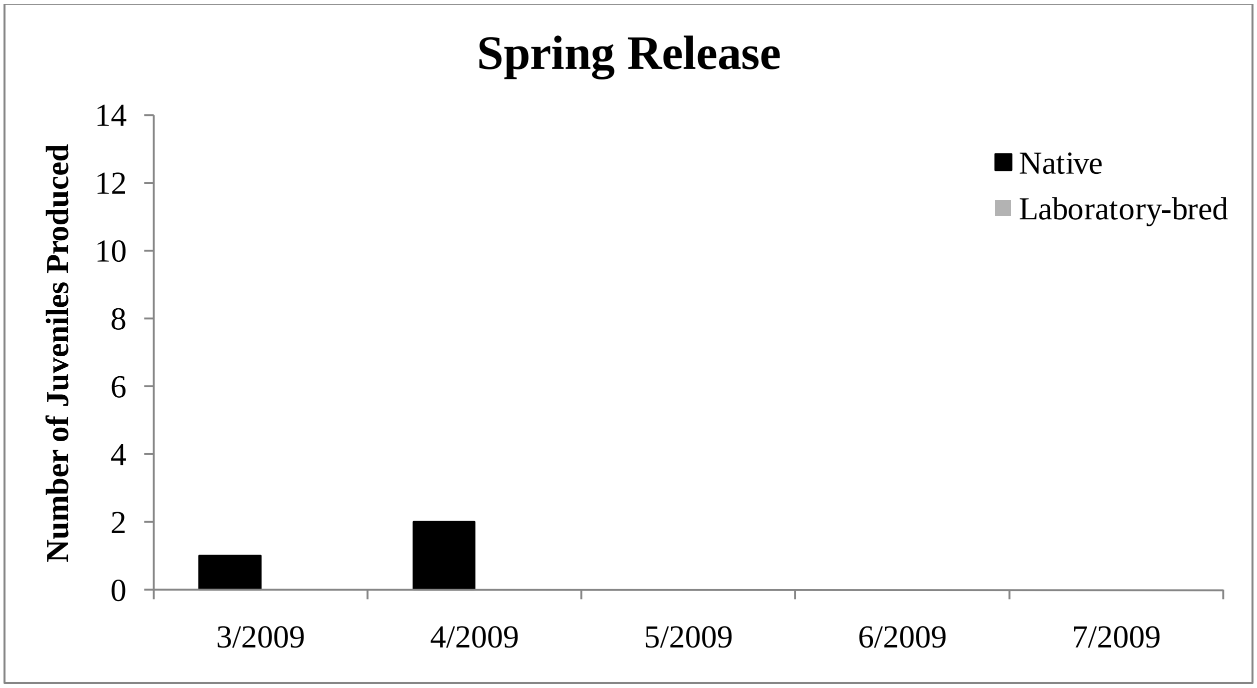

Spring Release
Number of Juveniles Produced
14
12
10
8
6
4
2
0
■ Native
■ Laboratory-bred
3/2009
4/2009
5/2009
6/2009
7/2009

Figure 3.7 – Reproductive activity during autumn release (2 November 2009) of laboratory-bred *O. nuttalli*. Native *O. nuttalli* were more productive early in the breeding season; however, laboratory-bred *O. nuttalli* produced more young from January 2010 to March 2010.

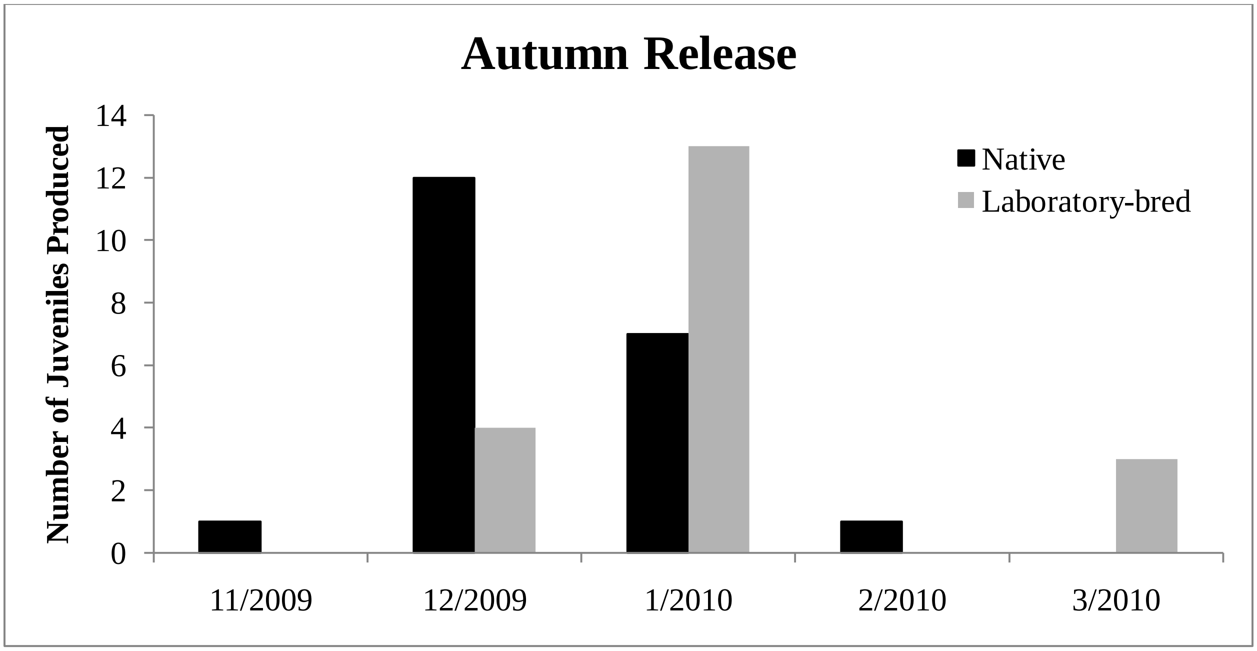

Autumn Release
Number of Juveniles Produced
14
12
10
8
6
4
2
0
11/2009
12/2009
1/2010
2/2010
3/2010
■ Native
■ Laboratory-bred

Figure 3.8 – Comparison of reproductive activity of native *O. nuttalli* compared with laboratory-bred *O. nuttalli*. Winter indicates breeding from November 2009 – March 2010. Spring depicts breeding from March 2009 – July 2009.

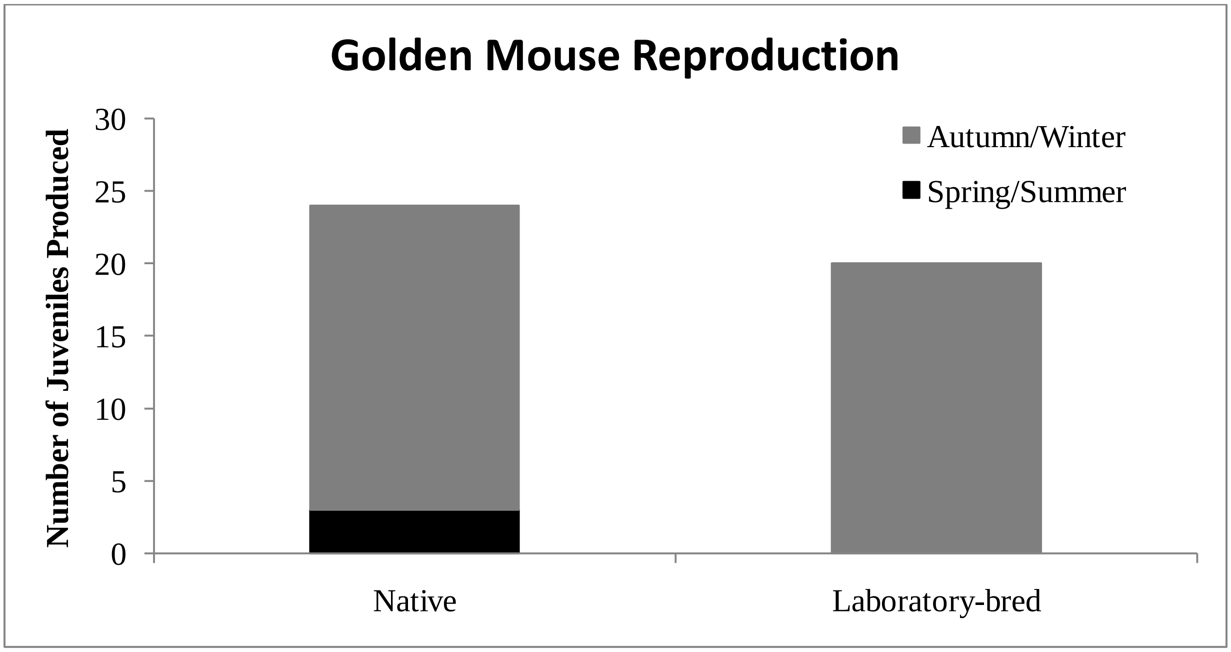
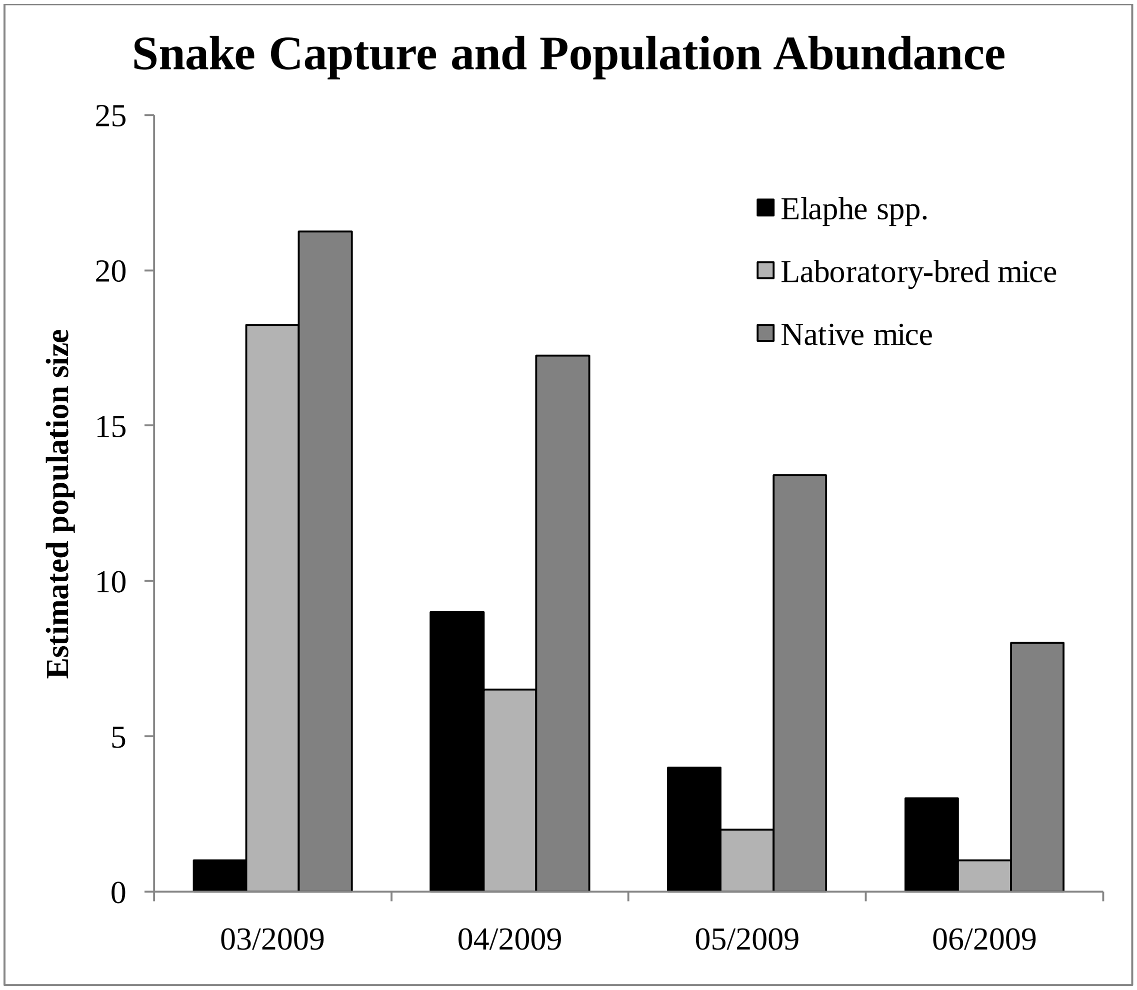

Golden Mouse Reproduction
Number of Juveniles Produced
30
25
20
15
10
5
0
Autumn/Winter
Spring/Summer
Native
Laboratory-bred

Figure 3.9 – Snake capture and population abundance of *O. nuttalli*. Increased snake capture was associated with decreased population density for laboratory-bred and native *O. nuttalli*.


Snake Capture and Population Abundance
25
20
15
10
5
0
Estimated population size
03/2009
04/2009
05/2009
06/2009
■ Elaphe spp.
■ Laboratory-bred mice
■ Native mice

CHAPTER 4

CONCLUSIONS

Patterns of reproductive activity varied consistently for *O. nuttalli* and *P. leucopus* across the sympatric portion of their geographic ranges. There exists a geographic isothermal transition point around 35° North latitude, where mean annual temperature shifts below 60°F (15.6°C) to the north and above 60°F (15.6°C) to the south. The reproductive strategy for *P. leucopus* and *O. nuttalli* changes from winter breeding in the south to summer breeding in the north. This trend is hypothesized to be the result of increased predation and parasitism in the southern portion of the ranges of both species during the warmer summer months. Whereas, the northern pattern for summer season of reproduction is likely the result of colder winter months, during which reproductive activity is prohibited by climatic factors. This geographic trend has not been previously investigated and warrants further research to determine whether an isothermal transition point exists for other small mammal species.

The effects of laboratory-inbreeding on survival and reproduction in *O. nuttalli* appear to be mitigated largely by season-of-release. Laboratory-bred mice released into a natural environment survived at a rate similar to that of native *O. nuttalli* in the same habitat during the winter; however, laboratory-bred mice released during spring did not survive and failed to produce any offspring. Although it is unclear whether the effects of laboratory-inbreeding in *O. nuttalli* are different from those in *P. leucopus,* our study suggests that *O. nuttalli* is better able to compensate with the effects of laboratory-inbreeding based upon reproductive activity and survival rates. Further investigation is needed to determine whether the background rate of inbreeding for *O. nuttalli* differs from that of *P. leucopus*.

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