

COEXISTENCE OF THE WHITE-FOOTED MOUSE, *PEROMYSCUS LEUCOPUS*, AND THE GOLDEN MOUSE, *OCHROTOMYS NUTTALLI*, IN A SOUTHEASTERN FORESTED PENINSULA: A REMOVAL STUDY

by

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(Under the direction of Gary W. Barrett)

ABSTRACT

Much attention has been devoted to interactions among similar coexisting species. Most of this literature, however, concerns negative interactions such as competition, whereas there is less information concerning positive interactions, especially mutualistic interactions, among similar small mammal species. This investigation addresses interactions between two similar small mammal species, the white-footed mouse, *Peromyscus leucopus*, and the golden mouse, *Ochrotomys nuttalli*, and seeks to determine how positive and negative interactions, integrated with community interactions such as vegetative cover and food resources, function in population and community regulation. *Peromyscus leucopus* was removed from 4 experimental grids within the study site to assess the removal effects on population dynamics of *O. nuttalli*. Following removal of *P. leucopus*, *O. nuttalli* showed no difference in population density, but showed a change in habitat use by extending use of vertical habitat. I believe that abundant

resources (e.g., *Quercus nigra* mast crop) precluded extreme competition between these species.

INDEX WORDS: Community, Competition, Landscape, Mutualism, Peninsula,

*Peromyscus leucopus*, *Ochrotomys nuttalli*

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## CHAPTER 1

### INTRODUCTION AND LITERATURE REVIEW

Interactions between and among similar sympatric species have long been of interest to population and community ecologists. Most investigations of coexisting species have concentrated on competitive interactions between species, especially how these negative interactions function to regulate community structure (Gause 1934, Park 1954, MacArthur 1960, Harper 1977, Conner and Simberloff 1979, Abramsky et al. 1979, Deuser and Hallet 1980, Pontin 1987).

Other, more positive interactions such as mutualism are as important as competition as mechanisms of community and ecosystem regulation. There are, however, few examples of investigations that address positive interactions among small mammal species, and few that integrate empirical information with ecological theory (Boucher 1985, Bronstein 1994, Herre et al. 1999, Hoeksema and Bruna 2000). Most studies that concern mutualism focus either on plant-animal interactions, or on identifying the mutualists of a particular species of interest, biased approaches not appropriate to developing a general theory of mutualism (Bronstein 1994). There is therefore a need to design investigations that quantify interactions between and among plant and animal species, and to investigate these interactions in terms of both competitive and mutualistic

relationships that function as mechanisms of regulation across levels of organization, instead of focusing on one solitary interaction.

The evolution of mutualism between insects and their plant hosts is currently a subject of much interest and much debate (Doebeli and Knowlton 1998, Baalen and Jansen 2001). Undoubtedly, this approach is a first step towards the development of a general theory of mutualism between different species, much like Hamilton's rule for mutualism within a single species (Hamilton 1964, Herre et al. 1999, Morris et al. 2001). Comparable studies focusing on animal species relationships, however, are still grossly unrepresented. This is, perhaps, because few models consider mutualism evolutionarily stable, and transmission of mutualism from one generation to the next is still not well understood (Herre et al. 1999, Wilkinson 2001).

Positive interactions between small mammal species have been greatly neglected in the literature. For example, communal nesting is common within small mammal species (Hayes 2000), but little has been reported on communal nesting between small mammal species. Group nesting within a species, for example, can provide energetic benefits to nest mates by lowering their metabolic requirements (Glaser and Lustik 1975, Springer et al. 1981, Vogt and Lynch 1982, Perret 1998). This benefit has been demonstrated in both communally nesting *P. leucopus* and *O. nuttalli* (Springer et al. 1981, Glaser and Lustik 1975, Vogt and Lynch 1982). Additionally, both these small mammal species tend to occupy intraspecific communal nests or build larger, better nests during winter months as compared to summer months (Frank and Layne 1992,

Wolff and Durr 1986). It has been noted, however, that use of terrestrial nests is higher in summer, and arboreal nest use highest in the winter (Goodpaster and Hoffmeister 1954). Thus, it appears that communal nesting is seasonally dependent.

Multifactorial investigations are needed that address small mammal population and community structure (e.g., plant community structure, species assemblages and apportionment, species abundance, and communal nesting) and function (e.g., dispersal and homing behavior, bioenergetics, parasitism, and three-dimensional use of habitat space). A better understanding of how these factors interact should increase our understanding of the coexistence of animal species in natural communities, ecosystems and landscapes. Factors including top-down (predator-mediated), bottom-up (resource-mediated) approaches, and behavioral interactions such as predation/parasitism, commensalism, and amensalism, must be viewed in an integrative manner in order to increase our understanding of small mammal diversity and population regulation (Barrett and Odum 2000; Barrett 2001).

Because species with extreme niche overlap and similar life histories are not predicted to coexist indefinitely due to competitive exclusion (Gause 1934), the coexistence of similar species of small mammal in the same spatial and shared temporal habitat (use of same habitat at the same time) provides an opportunity to examine both negative and positive interactions between species. It has been argued that small mammals provide model species to address processes that transcend levels of organization (Barrett and Peles 1999). The

current study seeks to examine and quantify interactions between the white-footed mouse and the golden mouse co-occurring in a southeastern forested bottomland peninsula. These two species share many life history traits, including shared food and nest resources, similar body mass and bioenergetics, overlapping home ranges, and similar behavioral attributes such as periods of activity and arboreality (Goodpaster and Hoffmeister 1954, Linzey 1968, Randolph 1980, Lackey et al. 1985, Linzey and Packard 1977). The following chapter outlines an integrative approach at investigating the competitive and mutualistic interactions between these two small mammal species, and attempts to discuss how these interactions function to structure a small mammal community. In addition, the bottom-up and top-down forces involved in the coexistence of these two species will be addressed. Hopefully, this multifactorial and integrative approach, accompanied with a replicated experimental design, will serve as a model leading to future investigations along this line.

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## CHAPTER 2

COEXISTENCE OF THE WHITE-FOOTED MOUSE, *PEROMYSCUS*  
*LEUCOPUS*, AND THE GOLDEN MOUSE, *OCHROTOMYS NUTTALLI*, IN A  
SOUTHEASTERN FORESTED PENINSULA: A REMOVAL STUDY<sup>1</sup>

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<sup>1</sup>Cory C. Christopher and Gary W. Barrett. To be submitted to *Ecology*



## ABSTRACT

Much attention has been devoted to interactions among similar coexisting species. These range from strictly negative (competition) to positive (mutualism) interactions and may also include a mixture of positive and negative interactions (commensalism and amensalism). This investigation attempts to address the positive and negative interactions between two similar small mammal species, the white-footed mouse, *Peromyscus leucopus*, and the golden mouse, *Ochrotomys nuttalli*, and seeks to determine how these interactions, integrated with plant community interactions such as vegetative cover and food resources, function in small mammal population and community regulation. *Peromyscus leucopus* was removed from 4 experimental grids within the study site to assess the effect on population dynamics of *O. nuttalli*. After removal of *P. leucopus*, *O. nuttalli* showed no change in population size, but showed a change in home range by extending their use of three-dimensional habitat. It is believed that abundant resources (e.g., *Quercus nigra* mast crop) precluded competition between these two species, despite extreme niche overlap.

INDEX WORDS: Community, Competition, Landscape, Mutualism, Peninsula, *Peromyscus leucopus*, *Ochrotomys nuttalli*

## INTRODUCTION

The coexistence of species with similar life histories and community functions has long been of interest to ecologists. Understanding this topic has spanned many different animal and plant species, temporal and spatial scales, and mechanisms of coexistence. For example, studies at the microcosm scale

such as those with *Paramecium* protozoans (Gause 1934), *Tribolium* beetles (Park 1954), *Trifolium* clover (Harper 1977), and at larger scales such as those with American warblers (MacArthur 1957, MacArthur 1960), generalist and specialist species (MacArthur 1955), and competition among trophic levels (Hairston et al. 1960, Grime 1977), have provided valuable ecological theory regarding competitive interactions occurring among coexisting species. These classic investigations have led to the formulation of concepts such as competitive exclusion, the role of life history morphologies in competition, the effects of abiotic conditions on competition, and the significance of resource partitioning. These earlier studies also successfully demonstrated that competition can contribute to population regulation and community structure.

Despite the importance of competition in regulating both plant and animal systems (Gause 1964, Conner and Simberloff 1979, Abramsky et al. 1979, Pontin 1982), other mechanisms, including mutualism, may be equally important. Empirically, positive relationships have received less attention regarding their function in regulating animal, especially small mammal, communities. In fact, there is no general theory for understanding interspecific mutualism between individuals such as Hamilton's rule for understanding positive density-dependent habitat selection among related individuals (Hamilton 1964, Herre et al. 1999, Morris et al. 2001). Additionally, few investigations have been designed to incorporate ecological theories of mutualism into empirical tests (Boucher 1985, Bronstein 1994, Herre et al. 1999, Hoeksema and Bruna 2000). It is important to note that while studies addressing mutualism are not rare, most have sought to

identify one particular species' mutualist, a biased approach not appropriate to developing a general theory of mutualism (Bronstein 1994). Thus, there is a need to address not only mutualistic relationships occurring between and among different animal species, but also to analyze their efficacy as evolutionary mechanisms of community regulation. There also exists the need to quantify the role and intensity of these interactions in a multifactorial manner.

In recent literature, theories of mutualistic interactions, such as those between insects and plants, have been reexamined in terms of the evolution of the interaction and the cost/benefit trade-offs of the mutualists (Doebeli and Knowlton 1998, Baalen and Jansen 2001). While this is a step forward in developing a theory of mutualism, there have been no similar investigations of mutualistic interactions between animal species. For example, there remains a paucity of information addressing interspecific mutualism between small mammal species, and a lack of investigations that focus on the role of mutualism as an important community regulatory mechanism. This is, perhaps, because there are few models that consider mutualistic interactions evolutionarily stable, and the transmission (genetic or otherwise) of mutualism from one generation to the next is not well understood (Herre et al. 1999, Wilkinson 2001). The coexistence of similar species of small mammals in the same spatial and temporal habitat provides an opportunity to examine both positive and negative interactions between the species, and processes that transcend levels of organization (population, community, ecosystem, and landscape).

For example, the life histories of two species of small mammals, the white-footed mouse (*Peromyscus leucopus*) and the golden mouse (*Ochrotomys nuttalli*), suggest highly overlapping niches. Both have similar body masses, nest-site preferences, food choices, home range sizes, and similar behaviors such as periods of activity and arboreality (Goodpaster and Hoffmeister 1954, Linzey 1968, Lackey et al. 1985, Linzey and Packard 1977, Knuth and Barrett 1984). It has been suggested that small mammals are model species for investigating both competitive and mutualistic interactions at higher temporal and spatial scales (Barrett and Peles 1999).

We designed a replicated, multifactorial investigation addressing small mammal community structure (e.g., plant and animal community structure, species diversity and apportionment, home range size and overlap, and communal nesting) and population/community function (e.g., dispersal and homing behavior, parasitism, and three-dimensional use of space) as factors impacting the relationships between species inhabiting similar habitats. We do not attempt to review the wealth of studies focusing on these individual factors, rather present a rationale of why we investigated these major factors, and suggest how structure and function must be viewed in an integrative manner (Barrett and Odum 2000, Barrett 2001) if we are to understand the regulation of small mammal populations at greater temporal and spatial scale.

Predicting the number and composition of species within a particular habitat or ecosystem is important in estimating the total diversity (e.g., species, genetic, habitat) of that system (Cole and Wilson 1996). Investigations of

diversity often utilize metrics which attempt to quantify diversity such as the Shannon-Weaver (Shannon and Weaver 1949) and Simpson (1949) indices. MacArthur's (1960) theory of species apportionment is based on the fact that the number of each species is dependent on how many other species, including the abundance of each species, are already present. He suggests that a decrease in one species will be met by a correlated increase in another, and vice versa. Bersier and Sugihara (1991) elaborated on this hypothesis by adding that because habitat is divided into niches, each species entering the habitat assumes one niche until the habitat is full. However, in cases where mutualistic interactions between similar species filling the same niche might occur, an increase in one species should meet with the likewise increase in their mutualist, until some threshold is reached. Therefore, we hypothesized that the species apportionment will not adhere to MacArthur's broken-stick model, and proportions of species will be significantly different than the proportions predicted by MacArthur's theory. MacArthur's (1960) attempt at estimating species apportionment is a simple estimate of community composition, yet ignores multiple interactions occurring simultaneously. It is now important for new indices to be developed which are temporally plastic, and capable of dealing with multiple interactions occurring together at multiple levels of organization.

Home range estimates are typically based on two-dimensional (planar) measurements, and have tended to ignore three-dimensional, or volumetric, home ranges when estimating home range overlap of species (Diffendorfer et al. 1999, Krohne and Hoch 1999, Bowne et al. 1999). Szacki et al. (1993) suggested

that home ranges of small mammals are more complex than live-trapping techniques or radio telemetry techniques can estimate, but failed to consider three-dimensionality in their study. A parallel study within the present field site has suggested that two-dimensional techniques for estimating home ranges of small mammals in forest communities be abandoned, and more appropriate three-dimensional or vertical approaches be further developed if we are to better understand home range size and overlap among small mammals (Pruett et al. personal communication).

Use of three-dimensional habitat by some species may serve as a mechanism for the coexistence of similar species in the same planar area (Meserve 1977). Cameron and Kincaid (1982) utilized removal of the hispid cotton rat, *Sigmodon hispidus* and the fulvous harvest mouse, *Reithrodontomys fulvescens*, and found that *R. fulvescens* utilized greater three-dimensional habitat in grids where *S. hispidus* had been removed, indicating that interspecific competition had an effect on three-dimensional habitat use (Cameron and Kincaid 1982). The present study was designed to analyze three-dimensional or vertical use of habitat space as a potential mechanism of community regulation in addition to the more traditional analysis of two-dimensional or planar measurements of home range size of both species.

An example of a mutualistic interaction known to occur between small mammals is communal nesting (Hayes 2000). Group nesting can serve to reduce the metabolic requirements of the nesting organisms, and could increase survival through periods of decreased food or temperature (Glaser and Lustik 1975,

Springer, et al. 1981, Vogt and Lynch 1982, Perret1998). Both *P. leucopus* and *O. nuttalli* are known to inhabit communal, arboreal nest sites at least part of the year (Goodpaster and Hoffmeister 1954, Linzey and Packard 1977, Lackey, et al. 1985, Wolff and Hurlbutt 1982). Springer, et al. (1981) found that communal nesting by *O. nuttalli* resulted in bioenergetic benefits because rates of metabolism of those mice living in communal nests tended to be lower than mice living individually. Decreased metabolism lowers their caloric requirements, which would be an advantage to communal mice during colder months when less food is available (Springer et al. 1981). Heavier nest construction (Frank and Layne 1992), and greater use of arboreal nests by *O. nuttalli* have also been reported to occur during this time (Goodpaster and Hoffmeister 1954, Packard and Garner 1964, Dietz and Barrett 1992).

Similar trends have been shown for *P. leucopus*. Glaser and Lustik (1975) demonstrated that communally nesting *P. leucopus* have an energetic savings of up to 29% as compared to solitarily nesting mice, and Vogt and Lynch (1982) found a savings up to 74% in communally nesting *P. leucopus*. Additionally, both *O. nuttalli* and *P. leucopus* nest singly in arboreal nests during the summer months, and in communal nests during the winter months (Wolff and Durr1986). These behaviors appear to be adaptations to decreased winter temperatures or reduced food supplies. This seasonal influence on communal nesting may tend to balance competitive and mutualistic interactions.

The homing ability of *Peromyscus* species has been investigated several times, and many investigations have found individuals to travel relatively long

distances (Murie 1963, Furrer 1973, Teferi and Millar 1993). A related investigation conducted as a part of the current study addressed the homing behavior of *P. leucopus* that had been removed from the riverine peninsula and relocated across the 5<sup>th</sup> order river barrier (Klee et al. personal communication). This study, like a previous study by Cooke and Terman (1977), found that distance removed and homing ability were not necessarily negatively correlated. The homing ability of small mammals across landscape barriers is an important component of population and community structure, because the genetic diversity of the species can be affected by restricted movement of organisms across a landscape barrier.

Parasitism is another important component of population regulation of small mammals (Taitt and Krebs 1983, Norrdahl and Korpimaki 1996). The effects of predation on small mammal dispersal and population density have been noted by Barrett and Peles (2001), yet few studies have investigated how predation or parasitism affects coexistence of small mammal species. We will depict how the botfly *Cuterebra fontinella* could function in the coexistence of *P. leucopus* and *O. nuttalli* by specializing on *P. leucopus* significantly more often than *O. nuttalli* and how this could provide niche segregation.

Deuser and Hallet (1980) found sufficient evidence of competition between *O. nuttalli*, *P. leucopus*, and *Tamias striatus* (eastern chipmunk), and found *O. nuttalli* to be not only the best competitor of the three, but also a habitat specialist, as reported by numerous investigators (King 1968, Linzey and Packard 1977, Deuser and Hallet 1980, Knuth and Barrett 1984, Seagle 1985).



Feldhamer and Maycroft (1992) proposed that *P. leucopus* excluded *O. nuttalli* by affecting trap use and probability of capture of *O. nuttalli*. Deuser and Hallet (1980) suggested that a removal experiment be performed to test the validity of statistical regressions of competition, because no experimental manipulation had been performed in their study. Because *P. leucopus* is known to function as a habitat generalist as compared to the specialist *O. nuttalli* (Lackey et al. 1985), we hypothesized, as did Seagle (1985), that the removal of a specialist species would not likely increase the generalist's niche breadth because it presumably already occupies most of the available habitat space before removal of the specialist. Thus, removal of the generalist species would more likely result in niche breadth expansion of the specialist species if significant competition exists between the two species (Seagle 1985). For these reasons, we elected to remove the generalist, rather than the specialist, small mammal species from this bottomland forest habitat. We view and discuss niche breadth in terms of such parameters as home range size, three-dimensional use of habitat space, rates of bioenergetics, frequency of parasitism, population densities, and nesting and trapping behavior.

If competition exists between the two species, then a significant increase in *O. nuttalli* population densities should occur following removal of *P. leucopus*. Conversely, if a mutualistic relationship (e.g., communal nesting) exists between these two very similar small mammal species, then the density of *O. nuttalli* would likely decrease with *P. leucopus* removal. A positive interaction, however, was not predicted regarding interspecific communal nesting, because this

behavior occurs most frequently during winter months, and this study was conducted during spring, summer, and fall months. Many primary food resources (e.g., mast crop, privet fruit, and hickory fruit) are most abundant during fall months (Koenig et al. 1994), and thus competition for these food resources should be at its peak in the summer months, when mast crops should be at their lowest. Because both species have similar food and nesting requirements (Goodpaster and Hoffmeister 1954, Linzey 1968, Lackey et al. 1985, Linzey and Packard 1977), there should be strong competition for both food resources and summer nesting sites.

In a concurrent study, O'Malley et al. (personal communication) found that *P. leucopus* ingested and assimilated up to twice as much food as *O. nuttalli*, and exhibited twice the metabolic rate. This finding suggests that *P. leucopus* would need to forage more often, and thus should be strong competitors for resources. Therefore, we hypothesized that the population density of *O. nuttalli* in removal grids would increase following removal of *P. leucopus* in comparison to nonremoval treatments. It is only from replicated, experimental studies of this design that community interactions and relationships will become better quantified.

## Materials and Methods

### *Experimental site*

This study was conducted at the HorseShoe Bend Ecological Research Site (HSB) located in Clarke County near Athens, Georgia (37 ° 57' N, 83°19'W). The site is a 14.2-hectare (35-acre) riverine peninsula created by the meandering

North Oconee River (Fig. 1) and is composed of two habitat types: an upland deciduous forest and bottomland deciduous forest prone to flooding. However, due to recent droughts across much of the southeastern United States, no floods occurred during the 2000-2001 study period. Both sites contain an abundance of greenbrier (*Smilax* spp.) and honeysuckle (*Lonicera* spp.). These species have been shown to provide important food, cover, and nesting material for both species, but especially for *O. nuttalli* (Goodpaster and Hoffmesiter1954, Linzey and Packard 1977). Water oaks (*Quercus nigra*) and Chinese privet (*Ligustrum sinense*) also dominated both habitat types, whereas white oaks (*Q. alba*) were abundant in upland habitats, and river birch (*Betula nigra*) were populous mainly in lowland regions.

Preliminary data for this investigation were collected from 15 March –15 November 2000. The main focus of this study is from 29 March –16 November 2001. We periodically refer to the 2000 data to enhance or refine certain aspects of this investigation. Based on preliminary findings, for example, the number of experimental grids was increased from 4 to 8 to increase the replication during 2001.

### *Research Design*

Eight trapping grids were established in the two habitat types (N=4 each). Each grid, was approximately 0.12 hectares. Each grid consisted of a 2 x 6 pattern of small mammal trapping stations (Fig. 1) consisting of two Sherman live traps, one positioned on an L-shaped wooden platform 1.5 m on the trunk of a tree, and the second located on the ground within 1-m of the base of the same

Figure 1. Aerial Photograph of HSB study site depicting the design and arrangement of trapping grids. Trapping grids are to scale.



tree. Trapping stations were 10 meters ( $\pm 2$  meters) apart. Four additional traps were placed in 4 of the trapping stations in each grid, (32 additional traps) on platforms 4.5 meters higher into the canopy to quantify three-dimensional or vertical use of habitat space. No 4.5-m traps were placed on trees located at either end of the trapping grid to avoid edge effects. This three-dimensional grid system was utilized to quantify habitat use by both *P. leucopus* and *O. nuttalli*, since both are often found foraging and nesting arboreally (Goodpaster and Hoffmesiter 1954, Lackey et al. 1985).

#### *Vegetation analysis*

A point-quarter sampling method (Cox 2002) was utilized to estimate plant diversity and describe vegetative cover in each experimental grid. A 60-m transect was established transversing the length of each grid and situated between the two rows of trapping stations in each of the 8 experimental grids. Six point-quarter sampling points were then established at 10-meter intervals along the 60-m transect. Measurements were taken for both trees and privet within each quartile. The distance to the nearest neighbor tree from the point of origin was recorded for tree species  $>2$  cm diameter at breast height (DBH). The same procedure was followed for privet, though no minimum DBH was established. A Shannon-Weaver diversity index (Shannon and Weaver 1949) was calculated for each site using the following equation:

$$H = -\sum p_i \log_e p_i$$

where  $p_i$  is the proportion of each species.

### *Acorn Mast Crop*

To estimate available food resources from *Quercus nigra*, 32 litter traps (0.25 m<sup>2</sup> each) were positioned under trees located in 4 of the 8 experimental grids during the 2000 and 2001 study periods. Eight litter traps were placed in each grid under mature *Quercus nigra* trees. On a bi-weekly basis between 3 October and 5 December 2000 and 2001, litter traps were checked and all fallen mast (acorns) collected. Samples were sorted by location, dried, and weighed to the nearest gram for comparisons between years and of upland versus lowland mast crops.

### *Small Mammal Census Procedures*

Live trapping was conducted twice weekly between 29 March and 17 November 2001, with checking efforts alternating between 0-m (ground) and 1.5-m traps one week, and 4.5-m traps the next. Traps were baited with black oil sunflower seed and set for two consecutive days. Cotton was provided as bedding when temperatures decreased below 10° C (50° F). Traps were set each night at 17:00 h and checked the following morning before 9:00 h. Traps set at 4.5-m heights were checked using a self-designed 5-m PVC pole with a hook attached to one end in order to lower and raise each live trap during setting and checking. Captured animals were identified to species, marked for identification by toe clipping (ASM 1998), sexed, examined for reproductive condition (open or closed vaginal orifice, abdominal versus scrotal testes, pregnant, or lactating), weighed to the nearest gram, checked for overall health (e.g., presence of botflies, wounds), and released at the site of capture.

Removal of white-footed mice from four grids (2 upland and 2 lowland) began on 31 May and continued until 16 November 2001. Hereafter we will refer to removal and nonremoval grids as removal and nonremoval treatments. Each *Peromyscus leucopus* captured in the removal treatments was removed from the riparian peninsula and released in a similar heavily-wooded forest habitat on the opposite side of the North Oconee River. Release sites were located in different areas along the opposite side of the North Oconee River (Fig. 1). The initial grid of capture within the peninsula and the final relocation point on the opposing side of the river were recorded for each animal removed.

Weekly mean population densities were estimated for *P. leucopus* and *O. nuttalli* using the Minimum Number Known Alive (MNKA) method (Krebs 1996). Individuals of both species were highly trappable, thus reducing the negative bias often associated with the use of this method (Krebs 1996, Slade and Blair 2001).

#### *Small Mammal Diversity and Abundance*

The number of individuals for each species captured during the study period was counted and ranked from most to least abundant. An expected number of individuals per species was calculated from the apportionment equation predicted by MacArthur's broken-stick model (MacArthur 1960):

$$\frac{m}{n} \sum_{i=1}^r 1/n - i + 1$$

where  $n$  is number of species captured,  $i$  is the species' ranking with the rarest species = 1, and  $m$  is the total number of individuals. A chi-square test was used to compare expected numbers with observed abundance per species.



### *Parasitism*

Presence and number of botfly larvae were recorded for each individual captured during the 2001 study period. It has been previously confirmed that the botfly species *Cuterebra fontinella* infects *P. leucopus* (Dunaway et al. 1967, Lackey et al. 1985). Additionally, several investigators have noted infections of *Cuterebra* in *O. nuttalli* (Linzey 1968, Linzey and Packard 1977, Dunaway et al. 1967).

### *Data analysis*

Differences in population densities between removal and nonremoval treatments were determined using the estimated MNKA means entered into a SAS repeated measures ANOVA procedure. Differences in small mammal species apportionment based on MacArthur's broken-stick model were analyzed using Chi-Square analysis. A t-test assuming equal variance was performed on Shannon-Weaver index values to compare tree diversity, as well as for distance to nearest neighbor (tree density) and DBH of nearest neighbor for tree and privet species for removal versus nonremoval grids. ANOVA procedures were performed on *Quercus* mast crops to compare upland and lowland habitat types. Rates of infection of bot fly larvae were calculated by comparing known number of infected individuals of a single species per week with the known population of that species in order to quantify percent infection rate per week per species. A repeated measures ANOVA test was utilized to compare the species infection rates. To assess the use of three-dimensional (vertical) habitat, ANOVA and Tukey's tests were performed for removal versus nonremoval grids to determine

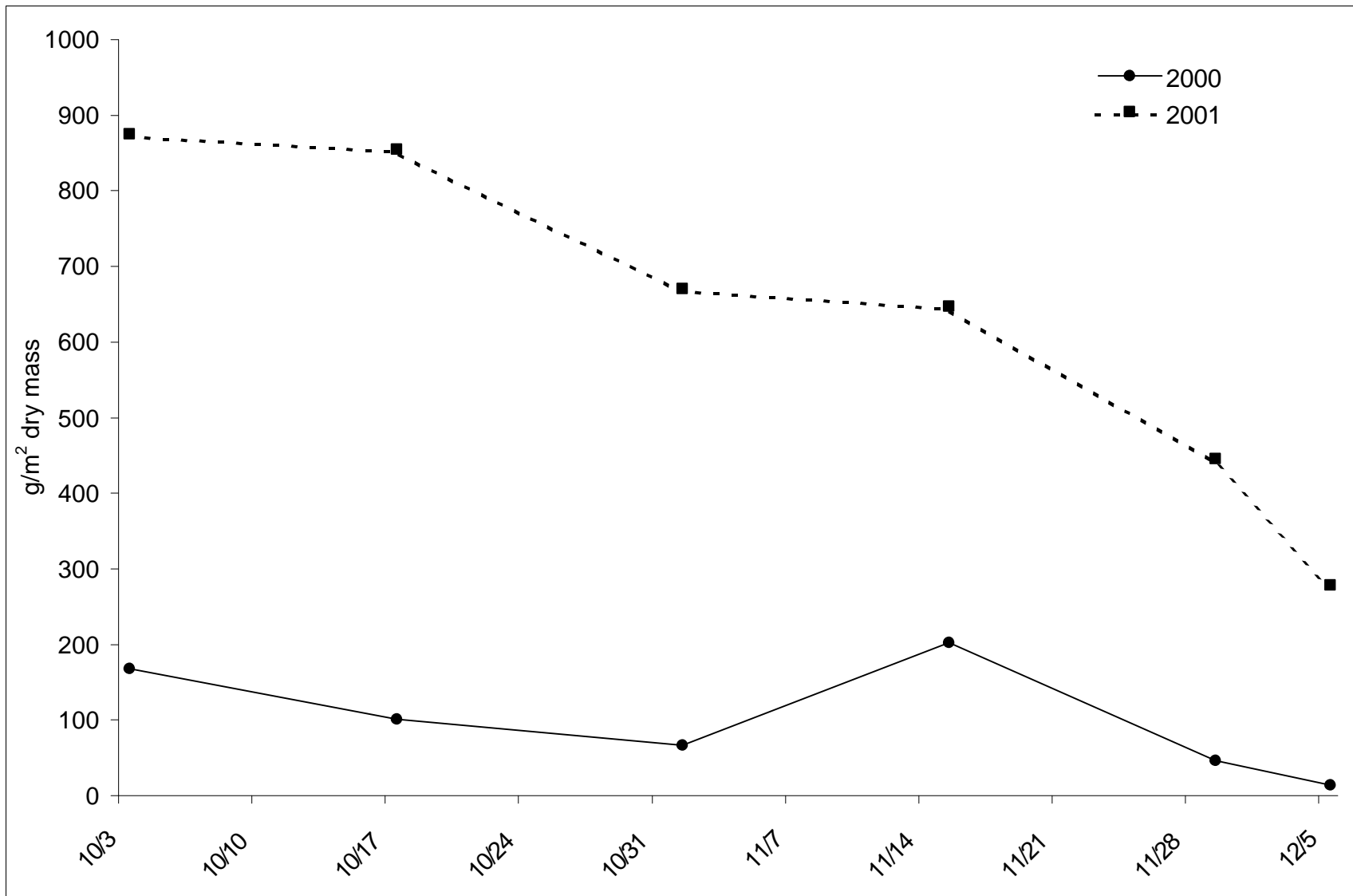
differences in height of capture for each species between preremoval and postremoval periods. An  $\alpha$  value of 0.05 was used for all statistical tests.

## Results

### *Vegetation surveys*

Dominant tree species in lowland habitat grids were water oaks (*Quercus nigra*), Chinese privet (*Ligustrum Sinense*), and ironwood (*Carpinus caroliniana*). Upland habitat grids were dominated by water oak, sweet gum (*Liquidamber styraciflua*), and Chinese privet. Shannon-Weaver Index values revealed no significant difference in vegetative diversity between the removal and nonremoval grids ( $T = 0.259$ ,  $P = 0.91$ ). There was also no difference between removal and nonremoval grids regarding tree density (ANOVA,  $df = 7$ ,  $F = 0$ ,  $P = 0.96$ ), privet density (ANOVA,  $df = 7$ ,  $F = .70$ ,  $P = 0.44$ ), or in mean tree DBH (ANOVA,  $df = 7$ ,  $F = 1.28$ ,  $P = 0.30$ ). Repeated measures ANOVA of *Quercus nigra* mast crop ( $\text{g}\cdot\text{m}^{-2}$ ) revealed a significant difference between upland and lowland habitat grids, with a greater crop in lowland sites (ANOVA,  $df = 5$ ,  $F = 24.72$ ,  $P = 0.004$ ). Upon comparing 2000 mast crop to 2001 mast crop, it was found that 2001 had a significantly higher mast crop than 2000 (ANOVA,  $df = 5$ ,  $F = 37.88$ ,  $P = 0.002$ ) (Fig. 2).

Figure 2. Comparison of *Quercus nigra* mast crop from 2000 and 2001. Mass measurements represent g dry mass·m<sup>-2</sup>.



### *Small mammal species apportionment*

Nine species of small mammals were captured at HSB during 2001. Ranked from most to least abundant, the total number of individuals of each species captured was *Peromyscus leucopus* (254), *Ochrotomys nuttalli* (121), *Glaucomys volans* (67), *Tamias striatus* (35), *Blarina brevicauda* (4), *Neotoma floridana* (1), *Mus musculus* (1), *Rattus rattus* (1), and *Sciurus carolinensis* (1). The predicted proportions of these species according to MacArthur's broken-stick model (MacArthur 1960) were as follows, respectively: 152: 98: 71: 54: 40: 29: 20: 13: 6. Observed proportions of each species captured were as follows: 254: 121: 67: 35: 4: 1: 1: 1: 1. Chi-square analysis showed a significant difference ( $df = 8$ ,  $P < .001$ ) between observed and predicted values, and thus refutes the predictions of the model. The dominant species (*P. leucopus* and *O. nuttalli*) were more abundant than predicted, and the rarer species (*B. brevicauda*, *N. floridana*, *M. musculus*, *R. rattus*, and *S. carolinensis*) were less abundant than expected.

### *Population densities and Peromyscus leucopus removal*

Population densities of both *P. leucopus* and *O. nuttalli* decreased over time in both removal and nonremoval habitat grids (Fig. 3 and 4). Mean population density decreases of *O. nuttalli* in the nonremoval treatments did not differ from the decreases in the removal treatments (ANOVA,  $df = 33$ ,  $F = 0.02$ ,  $P = 0.39$ ). As expected, populations of *P. leucopus* differed between removal and nonremoval treatments (ANOVA,  $df = 33$ ,  $F = 1.74$ ,  $P < 0.0001$ ).

Figure 3. Mean Densities of *P. leucopus* populations in both removal and nonremoval treatments. MNA refers to minimum number of mice known to be alive at each sampling date.

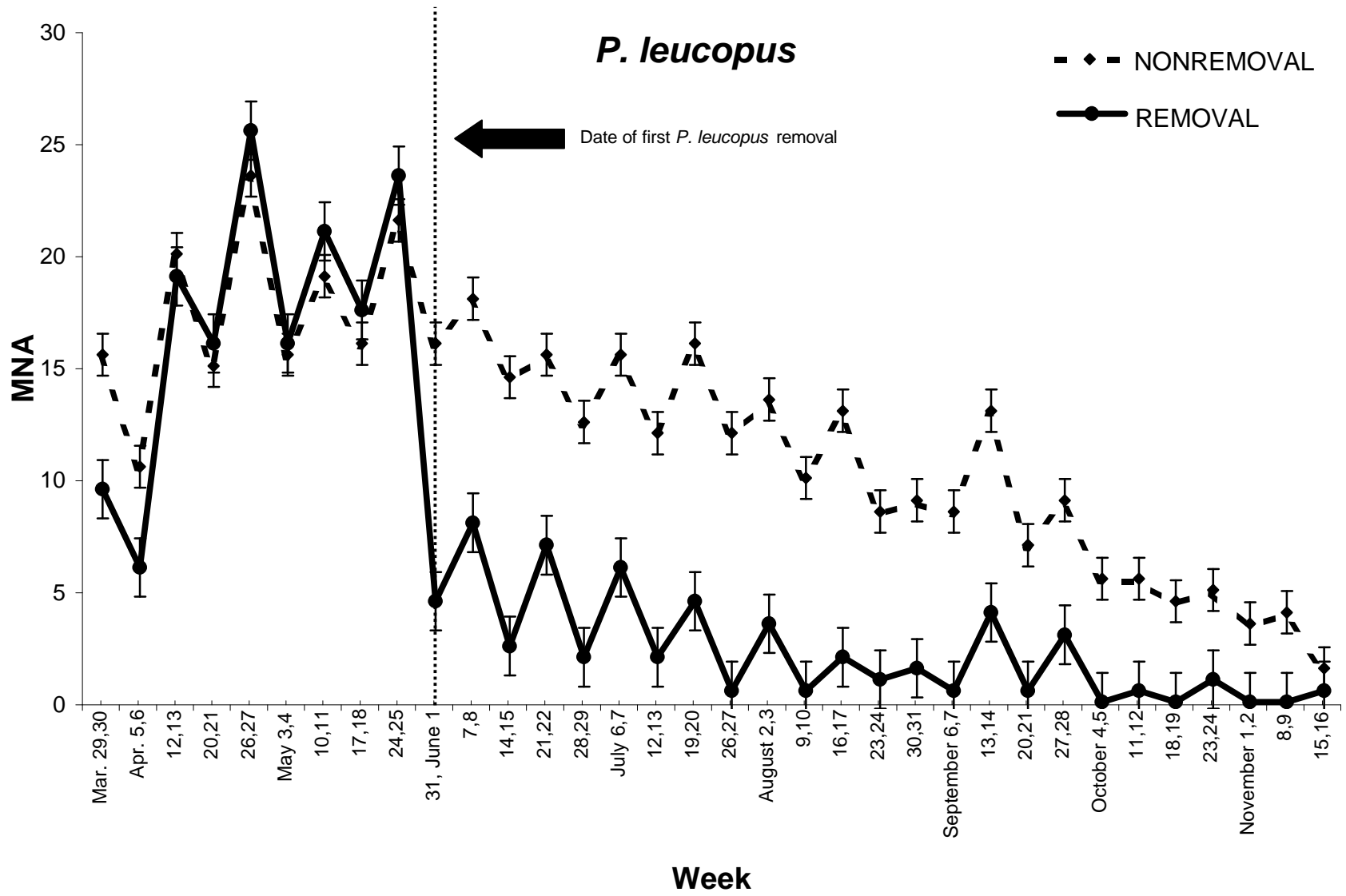
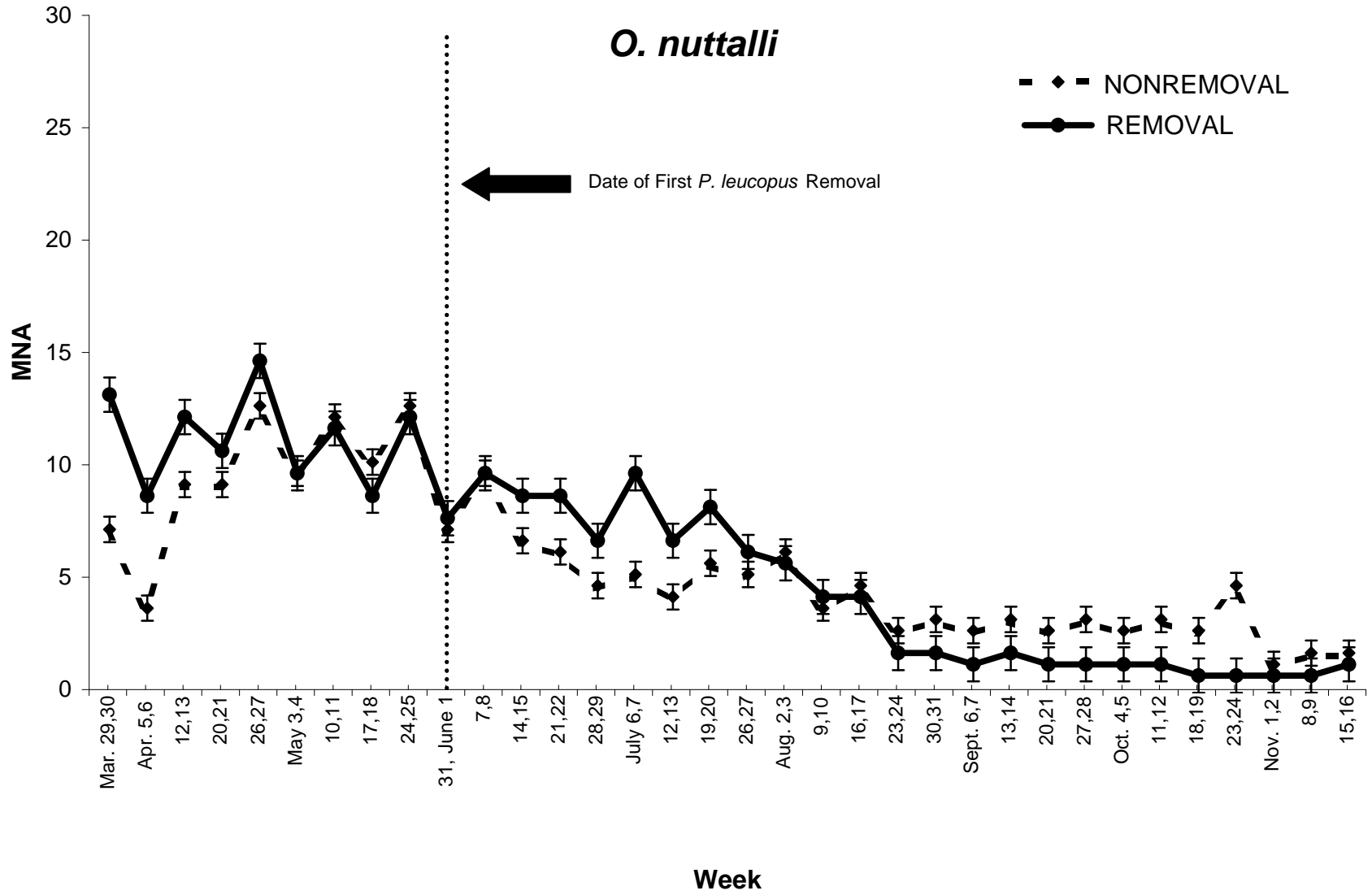


Figure 4. Mean densities of *O. nuttalli* populations in both removal and nonremoval treatments<sup>a</sup>. MNA refers to minimum number of mice known to be alive at each sampling date.





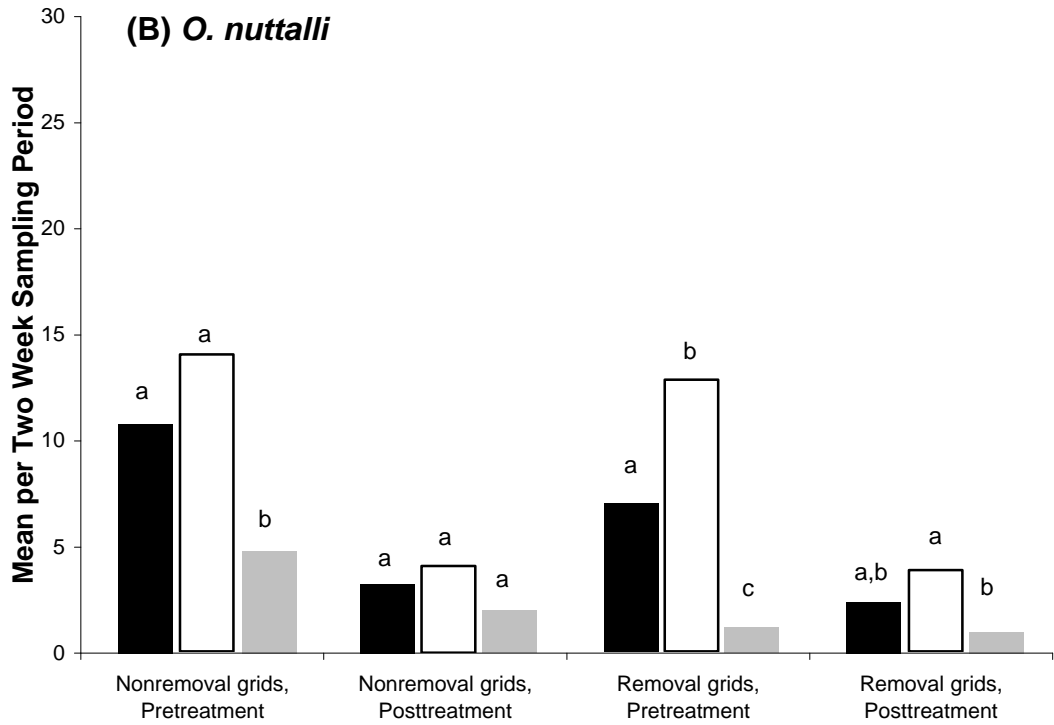
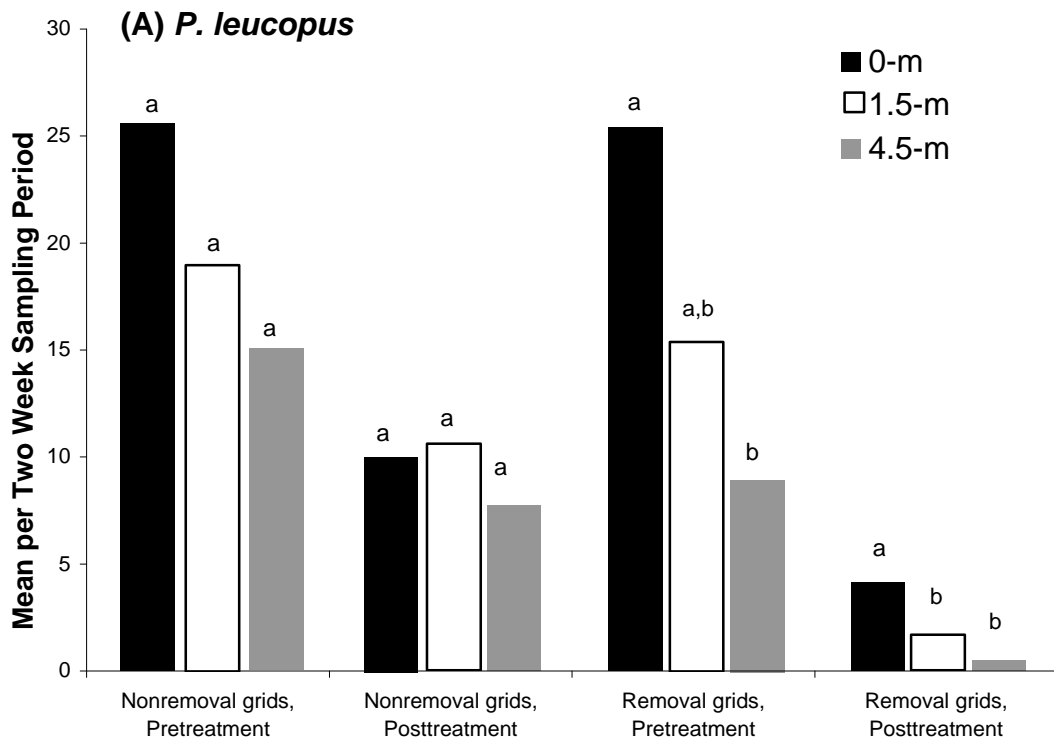
Interestingly, populations of *P. leucopus* differed between upland and lowland grids (ANOVA,  $df = 33$ ,  $F = 46$ ,  $P < 0.001$ ), as did populations of *O. nuttalli* (ANOVA,  $df = 33$ ,  $F = 5.3$ ,  $P < 0.03$ ). Therefore, additional independent repeated measures ANOVA analyses were performed for upland removal versus upland nonremoval and for lowland removal versus nonremoval treatments. Using these additional analyses, there were differences between removal and nonremoval grids for *P. leucopus* in uplands (ANOVA,  $df=33$ ,  $F=0.2$ ,  $P = 0.02$ ) and in lowlands (ANOVA,  $df = 33$ ,  $F = 2.5$ ,  $P < 0.001$ ). *Ochrotomys nuttalli* population density in the upland removal treatments was greater than in the upland nonremoval treatments (ANOVA,  $df= 33$ ,  $F=0.21$ ,  $P = 0.01$ ), but no difference was found between removal and nonremoval treatments for *O. nuttalli* in lowland grids (ANOVA,  $df= 33$ ,  $F=0.02$ ,  $P = 0.43$ ).

#### *Differential use of habitat space*

Before removal of *P. leucopus*, *O. nuttalli* utilized 1.5-m trap heights more often than 0-m (ground) and 4.5-m trap heights in removal grids (ANOVA,  $df = 2$ ,  $F=24.7$ ,  $P < 0.0001$ ); in nonremoval grids, the species utilized 0-m and 1.5-m to the same extent, though both more often than 4.5-m heights (ANOVA,  $df = 2$ ,  $F = 11.73$ ,  $P < 0.001$ ) (Fig. 5).

Following the removal of *P. leucopus*, *O. nuttalli* in removal grids continued to use 0-m and 4.5-m to the same extent, but utilized 1.5-m trap heights significantly more often than 4.5-m heights (ANOVA,  $df = 2$ ,  $F=5.9$ ,

Figure 5. Mean number of captures for *P. leucopus* (A) and *O nuttalli* (B) per two week sampling period before *P. leucopus* removal began as compared to mean number of captures after removal began. Sampling periods span two weeks since 0-m / 1.5-m traps and 4.5-m traps were checked on alternating weeks.



$P < 0.006$ ). In nonremoval grids, *O. nuttalli* utilized all heights equally (ANOVA,  $df = 2$ ,  $F = 1.05$ ,  $P = 0.36$ ) following removal (Fig. 5).

Before removal began, *Peromyscus leucopus* utilized all traps heights equally in nonremoval treatments (ANOVA,  $df = 2$ ,  $F = 1.28$ ,  $P = 0.31$ ); in removal grids, however, the species utilized 1.5-m and 4.5-m traps equally, but utilized 0-m traps significantly more often than 4.5-m traps after removal (ANOVA,  $df = 2$ ,  $F = 6.34$ ,  $P = 0.01$ ).

Following removal, *P. leucopus* in nonremoval treatments used all heights equally (ANOVA,  $df = 2$ ,  $F = 0.78$ ,  $P = 0.46$ ). In removal treatments, the species utilized 0-m traps more often than both 1.5-m and 4.5-m traps, which were used equally (ANOVA,  $df = 2$ ,  $F = 7.34$ ,  $P < 0.01$ ).

#### *Frequency of double captures*

Simultaneous captures during live trapping refer to the capture of two individuals in the same trap at the same time. During the 2000 and 2001 trapping seasons, there were 47 double captures of *P. leucopus*, 10 double captures of *O. nuttalli*, and 7 double captures of *P. leucopus* and *O. nuttalli* (Table 1). Double captures of females (♀♀) and males (♂♂) of *P. leucopus* were more frequent (21:1) than double captures of these sexes for *O. nuttalli*.

#### *Homing*

During the removal, there were 101 *P. leucopus* removed from within the peninsula and released on the opposite side of the North Oconee River. Six of these individuals were recaptured within the peninsula; 3 in their original grid of capture. The minimum and maximum distances traveled were 250-m and 1750

Table 1. Summary of Sex Combinations of Each Double Capture

Sex Combination	<i>P. leucopus</i>	<i>O. nuttalli</i>	<i>P. leucopus</i> / <i>O. nuttalli</i>
Female / Female	13	0	1
Male / Male	8	1	3
Female / Male	26	9	3
Total	47	10	7

-m ( $\pm 728$ -m), respectively (Klee et al., personal communication). No fallen logs or debris were observed that could have provided a means of crossing the river, which averages  $28.0 \pm 1.8$ -m wide.

### *Parasitism*

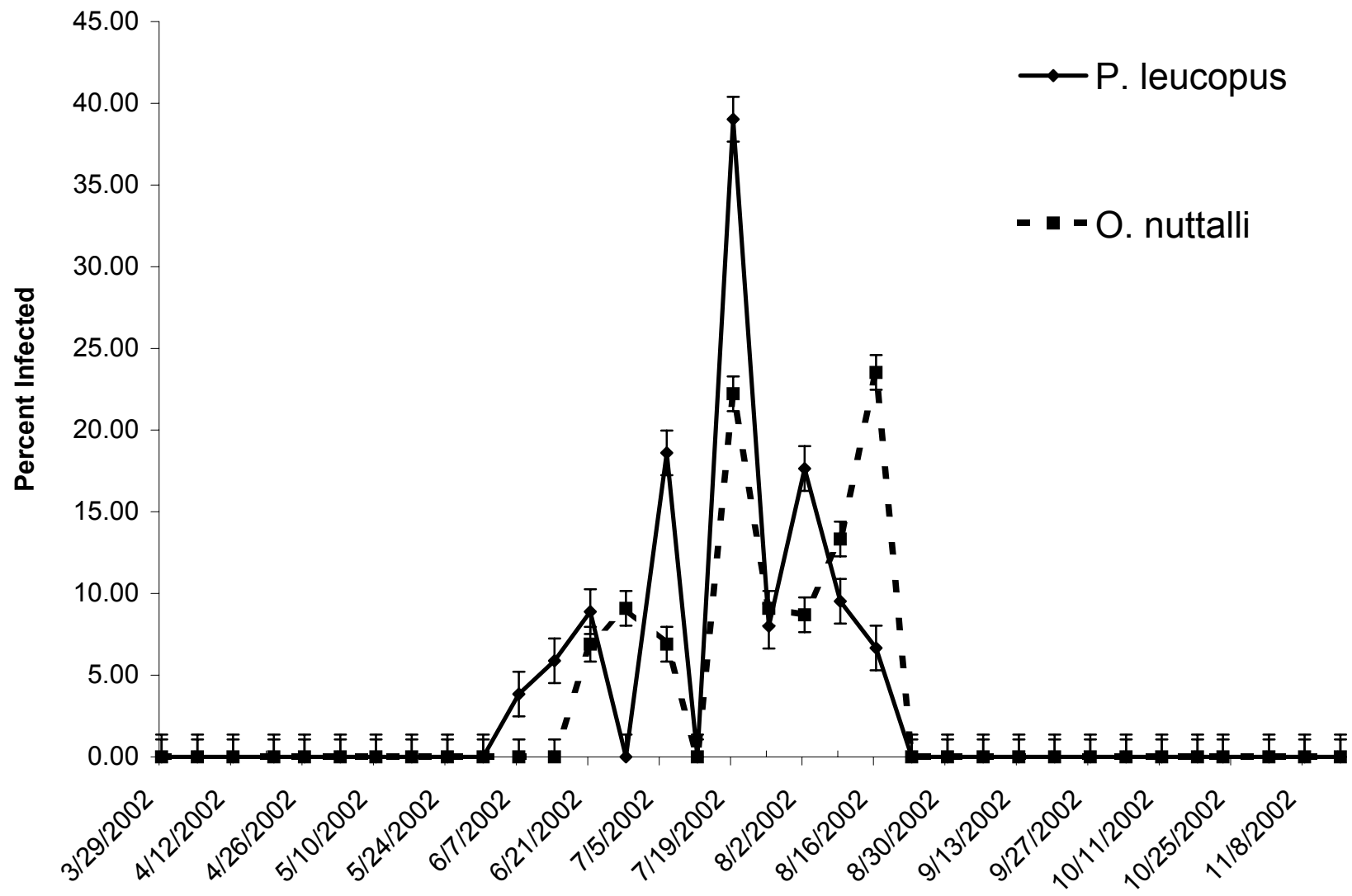
Infections of the botfly larvae *Cuterebra fontinella* observed during live trapping were quantified for *P. leucopus* and *O. nuttalli* (Fig. 6). A total of 18 infections were observed in 16 *P. leucopus* (8 female, 8 male) and 5 infections in 4 *O. nuttalli* (1 female, 3 males). Assuming equal infections rates predicted for each species, and correcting for the differential populations of *P. leucopus* and *O. nuttalli*, a repeated measures ANOVA revealed that *P. leucopus* were infected more often than *O. nuttalli* ( $F = .2403$ ,  $df = 33$ ,  $P < .01$ ). Peak rates of infections occurred on 29 July 2001 when at least 8 individuals were infected by *Cuterebra fontinella* larvae (Fig. 6).

### DISCUSSION

We investigated the multiple factors involved in the coexistence of similar species of small mammals, using the white-footed mouse, *Peromyscus leucopus*, and the golden mouse, *Ochrotomys nuttalli*. These two small mammal species share many life history traits, and thus served as models for investigating both competitive and mutualistic interactions occurring between similar coexisting species. We attempted to determine the mechanisms by which two species that have greatly overlapping niches are able to coexist in the same temporal and spatial habitat without excessive competition. In order to accomplish this, we

Figure 6. Percent observed botfly infections each week during the 2001 trapping period for *P. leucopus* and *O. nuttalli*.





designed a multifactorial, holistic investigation to address the top-down and bottom-up interactions occurring within the species' habitat. This included quantifying food resources, rates of bot fly parasitism, use of two- and three-dimensional habitat space and movement (homing) behavior, as well as examining the population dynamics of both *P. leucopus* and *O. nuttalli*.

*Quercus nigra* is the most abundant oak species within HSB, and serves as an important food resource for both small mammal species, as demonstrated in a related feeding study (O'Malley et al. personal communication). Thus, this oak species was chosen above other less abundant species to quantify mast crop for 2000 and 2001. Acorns were collected only from nonremoval treatments, so no comparison between removal and nonremoval treatments in terms of mast crop was possible, though there is no reason to expect a difference. There was a higher acorn yield, however, in lowlands versus uplands in 2001, and a significantly higher mast crop in 2001 versus 2000. Thus, 2001 could represent a peak year in a *Q. nigra* mast cycle (Koenig and Knops 2002). Because there was no difference in tree diversity, density, or vegetative cover between removal and nonremoval treatments, it is unlikely that there were more food trees (especially *Q. nigra*) or nest sites in removal or nonremoval treatments.

The predicted species apportionment according to MacArthur's model (1960) was not supported because *P. leucopus* and *O. nuttalli* were more abundant than predicted while all other species captured were less abundant than expected. The high abundance of *P. leucopus* and *O. nuttalli* in 2001 was attributed to a significantly higher mast crop of water oaks (*Q. nigra*) during the

2001 study period than during 2000 (Fig. 2). A notable finding regarding species diversity is that both *Rattus rattus* and *Mus musculus* likely crossed a major 4-lane highway immigrating from a heavy construction area. Neither species had ever been found in the peninsula prior to the beginning of the construction project.

There was no significant increase overall in *O. nuttalli* populations in removal versus nonremoval treatments, as both population densities of *O. nuttalli* decreased over time. There was no significant difference between the rates of decrease in *O. nuttalli* populations in removal grids versus nonremoval treatments. Therefore, the original hypothesis that *O. nuttalli* populations should increase in *P. leucopus* removal grids due to a release from competition was not supported. However, when considering upland and lowland grids separately, we found that *O. nuttalli* population densities in upland grids were higher over time in removal treatments as compared to nonremoval treatments. Considering that the upland habitat had a significantly lower mast crop than the lowland habitat in 2001, it is likely that there was greater food limitation in uplands than in lowlands, and thus, more competition for food resources. Thus, *O. nuttalli* in upland removal treatments responded to competitive release, while those in lowland removal treatments did not.

The finding that there was no effect on *O. nuttalli* populations following *P. leucopus* removal in lowland habitat grids is surprising. Beckerman (2000), however, found similar results with two grasshopper species. In his investigation, the two species shared a food resource, but after food manipulation and

competitor manipulation, there were no signs of competition between the two species that may be influencing their distribution. It was concluded that resources such as vegetative cover and food resources likely had a greater effect on grasshopper survival and distribution than interspecific competition. Shanker (2001) investigated interspecific competition between the black rat (*Rattus rattus*) and the soft furred field rat (*Millardia melitada*) in a montane ecosystem in India, and also found no evidence of competition between the two species, though both species shared food resources. In our investigation, it was believed that microhabitat selection provided sufficient niche segregation to allow the coexistence of the species. In the present study, *P. leucopus* and *O. nuttalli* were likely not food limited due to the abundant acorn crop, and are thus less likely to compete for food resources.

Differential use of three-dimensional habitat space likely contributed to niche segregation. For example, in the *P. leucopus* removal grids, *O. nuttalli* changed its use of three-dimensional (vertical) habitat space after removal of *P. leucopus*. Before removal, *O. nuttalli* utilized traps placed 1.5 meters into the canopy more often than 0-m and 4.5-m heights, but began using 0-m heights to the same extent as 1.5-m and 4.5-m trap heights following removal of *P. leucopus*. *Ochrotomys nuttalli* still utilized 1.5-m traps significantly more often than 4.5-m traps (Fig. 5), however. Thus, it appears that *O. nuttalli* began to use ground level traps in removal grids more frequently after removal of *P. leucopus*. It should be noted, however, that, after removal, the proportions of *O. nuttalli* trap use was very similar in nonremoval grids versus removal grids. Thus, the change in three-

dimensional use of space seems only of minor importance as an indicator of competition between the two species.

The density of Chinese privet (*L. sinense*) and vegetative cover such as honey suckle (*Lonicera* spp.) and greenbrier (*Smilax* spp) at our study site was at its greatest 1.5-m above the ground. The increased cover provides not only protection from predators (Gray et al. 2000, Carey and Wilson 2001), but may also provide increased food and nest resource availability. Chinese privet, honeysuckle, and greenbrier have been shown to be readily used as a food resource by *O. nuttalli* (Goodpaster and Hoffmeister 1954, Linzey and Packard 1977, O'Malley et al. in preparation). Below 1.5-m, there is less foliage in which to seek cover. Because the height of the privet rarely exceeded 4 meters, 4.5-m traps have far less heavy vegetative cover. Although *Ochrotomys nuttalli* chose 1.5-meter heights over ground and 4.5-m heights, this species increased its niche breadth and began using ground traps when competition was removed. This finding supports Gray et al. (2000) in which *M. musculus* was found to prefer more complex enclosures over open enclosures. Thus, it appears that *O. nuttalli* will slightly increase its use of vertical habitat space (i.e., use the forest floor habitat more frequently) after removal of competitors, but, regardless of its highly arboreal nature, does not seem to extend its habitat use higher, likely due to the lack of vegetative cover, or perhaps because there are ample food resources at 1.5-m and increasing habitat use would not provide an additional benefit.

In the nonremoval treatment, *P. leucopus* did not change its use of three-dimensional habitat. In the removal treatment, however, *P. leucopus* utilized 1.5-

m traps less often than during the preremoval period. In the removal treatment, *P. leucopus* always used ground traps significantly more often than 4.5-m heights. In effect, removing conspecifics likely decreased the competitive advantage of *P. leucopus* which allowed *O. nuttalli* to out compete *P. leucopus* at 1.5-m. As noted earlier, *Ochrotomys nuttalli* has been predicted to be a stronger specialist competitor, especially when considering arboreal habitat (Goodpaster and Hoffmeister 1954, Dueser and Shugart 1979). Our findings support this earlier prediction.

Considering the three-dimensional use of habitat space is important not only in regards to its potential role in niche segregation, but also when considering relative home range size of small mammal species. Home ranges are typically quantified with either live trapping or with radio-telemetry techniques (Cameron and Spencer 1985, Krohne and Hoch 1999, Barrett and Peles 1999, Mabry personal communication, Kie et al. 1996). In the case of forest dwelling small mammals, however, this system of quantifying home range size tends to become less accurate. Several investigations, for example, have maintained that *O. nuttalli* displays a relatively small home range size, ranging from 0.05-h to 0.5-h in some reports (Goodpaster and Hoffmeister 1954, Linzey and Packard 1977). It should be noted, however, that these home range size values are typically based on a planar (two-dimensional) perspective and do not take into account the volumetric (three-dimensional) patterns of movement.

In a related study at this site, Pruett et al. (personal communication) found that both *P. leucopus* and *O. nuttalli* moved freely through the forest canopy.

Meserve (1977) found that small mammal home ranges are larger when viewed three-dimensionally. In the investigation, it was noted that much three-dimensional use of habitat is linked to food resources (Meserve 1977). This finding could also relate to the bioenergetic needs of the organism. For example, when the metabolic rates of *P. leucopus* and *O. nuttalli* were quantified, it was found that *P. leucopus* ingested and assimilated nearly twice the food resources (*Q. nigra* acorns and *L. sinense* fruit) as *O. nuttalli* (O'Malley personal communication). This high rate of assimilation and respiration in white-footed mice is likely linked its greater use of three-dimensional space (i.e., greater metabolic requirements would require a larger three-dimensional home range size). This generalist behavior and rate of metabolism likely functions not only to help segregate niches between *P. leucopus* and *O. nuttalli*, but also serves to supply the energetic requirements of *P. leucopus* related to greater foraging activities.

Investigations carried out concurrently with the present study estimated the home range size of both *P. leucopus* and *O. nuttalli*. These investigations found no difference between the two species' home range size. These findings lend credence to the need to couple metabolic findings with patterns of movement if one is to understand three-dimensional use of habitat space and the necessary energy costs behind these patterns of movement. Our findings suggest that differential use of habitat space may decrease total (two- and three-dimensional) home range overlap between species living in the same habitat, and thus allow for the coexistence of even very similar species. Future

investigations need to incorporate multiple trapping heights and radio telemetric measurement in their research design in order to more accurately quantify home range size at the landscape level.

Double captures were not unusual during the 2000 or 2001 trapping seasons. Most often, two *P. leucopus* were captured together in the same trap, with one male and one female representing the most frequent combination of capture. Most likely, these individuals were mates, since male *P. leucopus* often cohabit with a mated female until parturition (Wolff 1989). There were often double captures of *O. nuttalli*, and again, these were typically composed of one male and one female, suggesting that these, too, were most likely mates. However, on 7 occasions during 2000 and 2001, we captured 1 *P. leucopus* and 1 *O. nuttalli* in the same trap. We have found a paucity of information regarding this unusual simultaneous capture of different small mammals live trapped in the same trap. It is possible that these simultaneous captures represent shared foraging of the two species. Novak (1983) pointed out that double captures are quite rare, and that their occurrence could be due to random encounters at a single trap ( i.e., the mice were not foraging together, but came upon the same trap at the same time). The two species, however, might also be social. Goodpaster and Hoffmeister (1954) reported finding a *P. leucopus* nest 15 feet away from an *O. nuttalli* nest, and stated that there appeared to be no rivalry between the two species. Regardless of the behavior by which the organisms entered the same trap, double captures of *P. leucopus* and *O. nuttalli* demonstrate that these two species exhibit shared use of both two-dimensional



and three-dimensional habitat, since double captures occurred at 0-m (ground), 1.5, and 4.5-m trapping heights. In cases of mixed species captures, only one individual (*O. nuttalli*) was found dead upon checking the traps. In all other cases of mixed or double captures of the same species, no individuals appeared injured upon release. This suggests a high degree of compatibility, or at the least tolerance, between these two species, even when confined to a single live trap.

The homing ability of *Peromyscus* species has been frequently investigated. Several investigators have found individuals to travel relatively long distances, (Murie 1963, Furrer 1973, Teferi and Millar 1993). The homing ability of removed *P. leucopus* was investigated during the 2001 trapping season at HSB (Klee et al., in preparation). Of the 101 mice removed from within the peninsula, only 6 individuals returned, and of these, 3 individuals returned to their original grid of capture. The ability to cross a large 5<sup>th</sup> order river is important in maintaining gene flow across landscape barriers, and can influence species composition. Klee (personal communication), like a previous study by Cooke and Terman (1977), found that distance removed and homing ability were not necessarily negatively correlated. With homing affecting both genetic, species, and habitat diversity, it should be addressed as an important component of community and population regulation in future investigations.

In the southeast, several of the botfly species (*Cuterebra fontinella*) regularly prey upon small mammal species. Most data of botfly infections concern the physiological effects on the host (Karasov 1993, Bergallo 2000), though some studies have addressed the effects of infection on the population

dynamics of small mammal species (Miller and Getz 1969). It is known that increased exposure to forest edges may increase susceptibility to infection in *P. leucopus* (Wolf and Batzli 2001). The life cycle of the *Cuterebra* involves an adult fly laying eggs near a burrow entrance of small mammals. Once hatched, the first instar larva attaches to the pelage of a small mammal entering the burrow, and enters via the nasal or oral passages, moving subdermally to the inguinal region (Munger and Karasov 1994). Once infected, the physiological effects may include loss of body mass, increased metabolism, increased food intake, and can reduce reproductive output in cases of low food resources, high energetic demands, or in small, isolated populations (Dunaway et al. 1967, Miller and Getz 1969, Munger and Karasov 1994).

An explanation of this difference in susceptibility to bot fly infection can be found in the different nesting behaviors of the species. For example, *Peromyscus leucopus* utilize terrestrial nests (Wolff and Hurlbutt 1982), though the species is known to build and utilize arboreal nests, as well (Lackey et al. 1985). *Ochrotomys nuttalli* tends to nest most often in arboreal nests (Goodpaster and Hoffmeister 1954, Linzey and Packard 1977, Linzey 1968).

Thus, it appears that the nesting behavior of *P. leucopus* is directly related to rates of botfly infection. For example, we found white-footed mice were live-trapped in ground traps more frequently than golden mice, the latter of which preferred 1.5-m trap heights. The significantly higher rate of infection in *P. leucopus* by *Cuterebra fontinella* was attributed to behavioral differences in nesting. The potential decreased fitness may help to prevent this species from

out competing *O. nuttalli*. Thus, the coexistence of these two very similar species with extreme niche overlap may be in part mediated via differential susceptibility to a common parasite.

The present multifactorial study sought to show competition occurring between the white-footed mouse, *Peromyscus leucopus*, and the golden mouse, *Ochrotomys nuttalli*, while simultaneously investigating the many habitat variables that play a role in the coexistence in small mammal species exhibiting extreme niche overlap. We found that coexistence of the two small mammal populations investigated in this study was dependent more on an array of evolutionary changes and interactions such as changes in three-dimensional use of habitat space and differences in rates of metabolism and parasitism, rather than on major competitive changes such as home range segregation, or direct antagonistic behaviors. For this reason, we suggest that multi-factorial, integrative approaches (Lidicker 1988, Barrett 2001), represent a better means to understand processes related to the coexistence of similar species.

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## CHAPTER 3

### CONCLUSIONS

This study attempted to examine the mechanisms by which two similar species of small mammals, the white-footed mouse, *Peromyscus leucopus*, and the golden mouse, *Ochrotomys nuttalli*, are able to coexist in the same temporal and spatial habitat. When defining the mechanisms that govern species composition and ultimately community regulation, it is necessary to consider all levels of organization, including the organismal, population, community, ecosystem, and landscape levels, while at the same time considering all potential symbiotic interactions. We considered both bottom-up interactions, such as acorn mast crop and food resources, and top-down forces, such as parasitism.

There was only minor evidence of competitive interactions in terms of population densities between *P. leucopus* and *O. nuttalli*. For example, there appeared to be a slight change in the use of three-dimensional habitat space by *O. nuttalli* following *P. leucopus* removal. This suggests that there existed, at best, limited competition for habitat space, although probably not strongly related to food (acorn) supply. It appears that these two species have divided habitat space such that *O. nuttalli* specializes in canopy heights  $\approx 1.5$  meters from the ground, where vegetative cover was greatest, whereas *P. leucopus* tends to utilize heights from 0-m (ground) to 4.5-m above the ground equally. This finding

helps to explain why *P. leucopus* had a metabolic rate almost twice that of *O. nuttalli*.

Direct interactions between the species such as overlapping home ranges, and simultaneously captures in the same trap, suggest shared foraging sites between the species. Indirect interactions between the two species are also important in regulating the interactions between them. For example, the botfly *Cuterebra fontinella* parasitized *P. leucopus* significantly more often than *O. nuttalli*.

It was concluded that ample food resources, especially an abundant *Quercus nigra* acorn mast crop in 2001, helped to reduce competition between these two species. Both species are communal nesters, and have been found to occupy the same nest. In addition, it is known that both species are able to lower metabolic requirements via communal nesting, a significant advantage during periods of decreased temperatures or scarce food supplies. Thus, it is important for future studies addressing communal nesting behaviors to incorporate winter trapping schedules (i.e., when temperatures would make communal nesting necessary). Our findings suggest that a suite of minor, yet significant, evolutionary changes, rather than a single major change, best explains the coexistence of these two very similar species.

It was hypothesized that, upon the removal of *P. leucopus* from removal treatments, there would be an increase in the number of *O. nuttalli* in these removal grids as a result of competitive release. This hypothesis was not

supported. Thus direct, antagonistic competition between the species cannot be a dominant force.

Future investigations of interactions between species need to consider multiple levels of organization, as well as considering additional interactions (e.g., commensalisms, amensalism, and predation) occurring between species. We believe that there is rarely only one major interaction occurring between species (e.g., competition for food or nest sites). Indeed, it is likely that seasonal changes effect behavior between and within species, which in turn influence which type of interaction (e.g., competitive or mutualistic) occurs between and within species.

If we are to learn more about the mechanisms governing species diversity, abundance, and coexistence, it is imperative that we design studies that encompass both reductionist and holistic approaches, addressing questions not only at the organismal and population levels of organization, but also at the community, landscape, and ecosystem levels, as well.