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Effects of Changes in the Everglades on Two Indicator Species: Sigmodon Hispidus and Oryzomys Palustris

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UNIVERSITY OF MIAMI

EFFECTS OF CHANGES IN THE EVERGLADES ON TWO INDICATOR SPECIES: *SIGMODON HISPIDUS* AND *ORYZOMYS PALUSTRIS*

By

Miguel Fernandes

A DISSERTATION

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
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EFFECTS OF CHANGES IN THE EVERGLADES ON TWO INDICATOR SPECIES: *SIGMODON HISPIDUS* AND *ORYZOMYS PALUSTRIS*

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The Everglades, a wetland ecosystem unique to southern Florida has been degraded by the loss of nearly half of its area to urban and agricultural development as well as by alterations to Florida's hydrology. Modifications to the flow of water to the Everglades have altered the remaining portion of the Everglades. Most prominent among these changes in the remaining Everglades is the loss of tree islands with a disproportionately greater loss of larger tree islands. Despite their significance as "keystone habitats", our understanding of how changes to Everglades tree islands will affect fauna is poor. In the work presented, 16 study tree islands of Rock Reef Pass, Everglades National Park, Homestead, FL, were classified into three size classes (large, medium and small) and used animal capture histories collected between February 1994 and December 2005 to investigate the relationship between tree island size classes and indirect indicators of adult female hispid cotton rat (*Sigmodon hispidus*) and marsh rice rat (*Oryzomys palustris*) fitness and reproduction. Adult female *S. hispidus* and *O. palustris* body weights were used as an indicator of adult female fitness and compared among tree island size classes. The proportions of reproductively active females, the proportions of captures of individuals in the juvenile age class and the number of juveniles per female were used as indirect indicators of female reproduction and compared among island size classes.

Animal capture histories were also used to perform multi-state mark-recapture analyses, where sates were defined as three island size classes, to draw inferences about state-specific rates of survival and state transition probabilities for *Oryzomys palustris* and *Sigmodon hispidus* as a function of the most salient features of the Everglades ecosystem, namely, its tree islands and its seasonal wet and dry periods. Specifically, Akaike's, information criterion (AIC) was used to make inferences about factors influencing survival and transition probabilities by comparing the relative fit among models where survival and transition rates are described as functions of tree island size classes and as a function of environmental variables that distinguish seasonal periods (monthly water levels, total monthly rainfall, mean air temperature, days dry, days inundated). The probabilities of individuals remaining within the same island size class were interpreted as an indirect indicator of size-class specific tree island use. Results indicated that greater proportions of *S. hispidus* adult females were reproductively active and had higher fitness on larger islands than females on smaller islands. The body weights of *S. hispidus* adult females, the proportions of individuals in the juvenile age class and the number of juveniles per female, were positively correlated with tree island area while the proportions of reproductively active *S. hispidus* females were not. When compared among tree island size classes, *S. hispidus* females recaptured on the same large island weighed more than females recaptured on the same and medium or small island suggesting that females with greater fitness are found on larger tree islands. The proportions of reproductively active *S. hispidus* females and of individuals in the juvenile age class were greater on larger tree islands than on smaller islands, although the number of juveniles per females did not differ among tree islands. The results also indicated that

differences in the fitness and reproductive condition of *O. palustris* females are not as distinct among females on different size tree islands. The body weights *O. palustris* adult females, the proportions of juveniles and the number of juveniles per female were not correlated with island area, while the proportions of reproductively active females were negatively correlated with tree island area. The body weights of *O. palustris* adult females recaptured on the same large tree island were higher than those of females on smaller islands while the proportions of females that were reproductively active and the proportions of captures of juveniles were higher on small islands than on large islands. Mark-recapture analysis provided evidence that overall, *Sigmodon hispidus* survival rates were higher on larger islands than on smaller islands. Evidence was not found that *Oryzomys palustris* survival rates differed among size classes, perhaps due to the limited spatial scale of this study relative to the spatial sale of *O. palustris* habitat use. Both species' survival probabilities differed between seasons with *Oryzomys palustris* having higher survivorship during wet seasons and *Sigmodon hispidus* during the dry season. Both *Oryzomys palustris* and *Sigmodon hispidus* were more likely to remain on large island than on smaller islands.

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Many people have assisted in various aspects of this work and I must thank all of them. Foremost, I must thank my advisor, Don DeAngelis, without whose help and tolerance I would not have completed this task. I also thank the other members of my committee, Dr. Steven Greene and Dr. Michael Gaines. Dr. Greene's statistics advice and detailed editing was of great help. I would especially like to thank Dr. Michael Gaines for giving me the opportunity to attend the University of Miami and for giving me the opportunity to analyze the data used in this dissertation. I must also thank Dr. James Nichols for his time and especially for his hospitality at the Patuxent Wildlife Research Center. The mark-recapture analyses in this work would not have been possible without the generous help of James Hines of the Patuxent Wildlife Research Center.

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The completion of this work was also made possible thanks to the help of my family, my mother, Amelia Vieira, my father, Jose de Sousa Fernandes and my stepmother, Kathy Fernandes. The work ethic and the perseverance of my parents and of my grandmother, Maria Aduzinda Fernandes, through the many great challenges that our family has overcome, were, and always will be an inspiration to me.

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Despite my best efforts and the highest of animal care ethics by Dr. Gaines, on occasion, animals were injured or killed during trapping. It is my hope that I will have the opportunity to continue my effort to contribute to the preservation of species so that I may repay in some measure the lives of the animals that were lost during this work.

The completion of this work would not have been possible without the support and kindness of my wife-to-be, Katrina Herring. I hope that a lifetime of love and companionship will be sufficient to repay her for what she sacrificed so that I may have finished this humble work.

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INTRODUCTION

The Everglades, a wetland ecosystem unique to southern Florida, refers to an aggregate of fresh water marshes characterized by slow moving waters and broad expanses of sawgrass (*Cladium jamaicense*) wet prairies with thousands of tree islands interspersed throughout its landscape. The tree islands of the Everglades form on topographic elevations of limestone bedrock (van der Valk and Sklar, 2002) and provide much of the permanently dry habitat available to terrestrial species in the seasonally flooded Everglades. Nearly half of the more than 400,000 ha of the original Everglades have been lost to agricultural and urban development. The remaining portion of the Everglades has been fragmented and its natural flow of water altered. The construction of water impoundment areas and of an extensive system of canals and levees over the past 50 years has altered the characteristic sheet water flow of this wetland and has further fragmented the Everglades and changed its hydrology.

The inundation of the Everglades during southern Florida's wet season is a fundamental characteristic of the Everglades ecosystem. The duration of these inundation periods, referred to as hydroperiods, have increased in some areas, affecting the plant communities by inhibiting seed germination (Sklar and van der Valk 2002), while in other areas the reduction or the absence of hydroperiods has allowed woody species to encroach into marshes and sloughs (Olmstead *et al.* 1980, Sklar and van der Valk 2002), especially by invasive exotic species. Alterations in the flows of water to the Everglades and in its hydroperiods have also affected the processes associated with the maintenance of sloughs, ridges and tree islands, leading to an overall decrease in the number and size of tree islands and increased distances between islands (Hofmackel

1999, Patterson and Fink 1999, Wetzel *et al.* 2005). Despite their significance as "keystone habitats" described as both "nutrient" and biodiversity "hotspots" (Orem *et al.* 2002; Jayachandran *et al.* 2004), there have been few studies of fauna on tree islands. Our understanding of how changes to Everglades tree islands will affect fauna is at best sketchy (Sklar and van der Valk 2002). The loss of tree islands in the Everglades will continue into the foreseeable future and may increase due to rising sea levels (Michener *et al.* 1997). To have some understanding of how the loss of tree islands has affected and will continue to affect Everglades fauna, it is necessary to have prior knowledge about the species that use and occupy tree islands.

Studies of animal taxa that use and occupy tree islands and whose changes in numbers and distribution in the Everglades are likely to cause corresponding changes in other animal and plant taxa are an important research priority. I believe that Everglades rodents are a prominent example of such a taxon. Rodents are thought to be the most widely distributed mammals throughout the Everglades. Although relatively few tree islands have been sampled for rodents, it is generally assumed that tree islands that remain dry throughout the year will be utilized or occupied by rodents. Although rodents are thought to be the most widely distributed mammals throughout the Everglades, and likely to have one of highest, if not the highest, terrestrial vertebrate biomass in the Everglades, little is known about the ecology of rodents in the Everglades. To the best of my knowledge there are no reference historical data on rodents available for comparison and, to date, only two peer reviewed studies on Everglades small mammals on tree islands have been published (Smith and Vrieze 1979 and Smith 1980).

The ecological role of rodents in the Everglades ecosystem is non-trivial. Rodents, with their characteristically high biomass turnover rates, are a significant source of food for predators even when present at low densities (Golley *et al.* 1975). As prey, herbivorous and omnivorous small mammals also link primary production and secondary consumers (Hayward and Phillipson, 1979). In addition, rodents provide non-redundant ecological services as predators of both seeds and animals. A greater understanding of rodent ecology in the Everglades is relevant to our understanding of one of the Everglades most abundant animals and to our understanding of how changes in tree islands and hydrology may affect this taxon.

Given the paucity of knowledge about rodent ecology in the Everglades, a first and fundamental step is to investigate how rodents are influenced by the most salient characteristics of the Everglades, namely its hydrology and tree islands. Size is a fundamental characteristic of tree islands that determines how much habitat is available to rodents and that influences animal abundance and distribution throughout the Everglades. Considering that the loss of tree islands has not been uniform across island sizes (Wetzel *et al.* 2005) and that disruptions to the historical flow of water to the Everglades continues to alter tree island size, understanding the relationship between rodent ecology and tree island size is relevant to describing the ecology of rodent species in the Everglades and gaining some insights into how changes in the tree island sizes might influence Everglades rodents.

Between February 1994 and December 2005, mark-recapture data were collected on small mammal species found on 16 tree islands at Rock Reef Pass, Everglades National Park, Homestead, FL. In the work presented here, I use these capture histories to investigate the relationship between tree island size and traits associated with adult female fitness and reproduction for the hispid cotton rat (*Sigmodon hispidus*) and the marsh rice rat (*Oryzomys palustris*), the most common rodents on tree islands at Rock Reef Pass and throughout the Everglades. I also used these mark-recapture data in multi-state analyses, where strata were defined as island size classes, to model the survival, transition and recapture probabilities of *O. palustris* and *S. hispidus* as a function of island strata, sex and environment covariates associated with the wet and dry seasons of the Everglades.

Animals, generally, make greater use of habitats that provide more favorable conditions and that increase individual fitness, over habitats with less favorable conditions. At Rock Reef Pass, as with most of the Everglades wetland, the habitats that are primarily available to rodents are tree islands, and thus I expected *S. hispidus* and *O. palustris* to make greater use of tree islands with more favorable conditions over those tree islands with less favorable conditions. I made the assumption that, if habitat suitability differs with tree island size, adult female fitness and reproduction should be positively correlated with the island size that provides the most suitable conditions. A positive correlation between island size and adult female fitness and reproductive condition, implies these traits are influenced by some property of tree island size, or that, conversely, females of a given fitness and reproductive condition are more likely to use islands of a particular size. Regardless of which of these best exemplifies the relationships between adult females and tree islands, so long as a relationship exists between tree island size and adult female condition and reproduction, it is relevant to the understanding of both rodent ecology and the potential impacts of changes in tree island size on rodents. I chose to examine the relationship between tree island size and female traits, because female habitat use and distribution are more likely to be influenced by the distribution of resources, while male habitat use and distribution are often more influenced by the distribution of females (Fleming 1979). Although male habitat use is relevant to the description of these species' ecology, I felt that female fitness and reproduction would be more likely to be influenced by the conditions on the islands where they were captured than male fitness would.

To make statistical analyses and the interpretation of statistical tests tractable, I classified the 16 study islands into three size classes, large, medium and small. Traits associated with adult female fitness and reproduction were then described and compared among the tree island size classes. Body weight has been shown to be an indicator of individual fitness and is positively associated with reproductive success, dominance status and survival (Fleming 1979). The body weights of adult females were used as an indication of the relative fitness of adult females captured on different tree island size classes. I correlated the body weights of adult females at the time of last recapture with tree island area and also compared the weights of females among the tree island size classes. Direct measures of fecundity are difficult to quantify in field studies, especially for inconspicuous animals such as rodents, whose young are seldom captured. Because few *O. palustris* and *S. hispidus* juveniles were captured, I used the proportions of captured females that were reproductively active, the proportions of captured individuals that were juveniles and the number of juvenile individuals per adult female, as indirect indicators of rodent reproduction.

I expected that the higher plant diversity (Sklar and van der Valk 2002) on larger islands would provide greater cover and variety of resources for both *O. palustris* and *S. hispidus* females, especially during pregnancy and the rearing of young. Larger islands also have larger more mature trees whose roots reach the water table, maintaining larger tree islands verdant during the dry season when the marsh surrounding tree islands is dry and open. In comparison, at the Rock Reef Pass study site, the vegetation on small tree islands often became dry and sparser during the dry season providing less cover and food for both *O. palustris* and *S. hispidus.*

I predicted that overall, adult female weight, the proportions of reproductively active females, the proportions of individuals in the juvenile age class, and the proportion of juveniles per female, would be positively correlated with tree island area and the described proportions would be greater on larger islands than on smaller islands for both *O. palustris* and *S. hispidus.*

I also predicted that relative to *O. palustris, S. hispidus* female weight and reproductive traits would be more strongly positively associated with tree island size. I expected that relative to *S. hispidus*, the diet and habitat use of *O. palustris* would diminish the influence of individual tree islands on the fitness of *O. palustris* individuals. *O. palustris* are primarily carnivorous and in the Everglades they forage for insects and crustaceans in the marshes surrounding tree islands and are thus less dependent on tree islands for prey. *S. hispidus* are primarily herbivorous and are thought to feed mostly on tree island vegetation, making them more susceptible to conditions on tree islands. In addition, *O. palustris* are known to use wet-refugia during the dry season, further decreasing the influence of tree island conditions on *O. palustris* fitness.

In addition to comparing traits associated with female fitness and reproduction among tree islands size classes, I also used a multi-state mark-recapture analysis approach that allows for the estimation of sampling rates (capture probabilities) and population changes (survival and transition probabilities) (Williams *et al*. 2002) as state-specific rates. The estimation of state specific, or as in my case, tree island size class-specific survival and transition probabilities, allowed me to address the questions: Are there differences in survival rate, or in movement rates among the three island size classes and do these differ between males and females? Further, might any differences that are apparent be associated with seasonal hydroperiods? I also constructed mark-recapture models describing survival and transition probabilities as a function of the other most salient feature of the Everglades ecosystem, its seasonal inundations, referred to as hydroperiods. I used time-specific measurements of water levels, rainfall, and duration of wet and dry periods, among others, to describe the changes in environmental conditions that most distinguish the wet and dry periods. Sex was included as a covariate to examine differences in males and females by grouping individuals by gender. The inclusion of hydrology covariates allowed me to address questions related to hydroperiods. Are there differences in survival rate, movement rate or recapture rate between wet and dry hydroperiods, and do these differ between males and females? Further, might any differences that are apparent be associated with water-levels or duration of wet and dry periods? This approach is more likely to realistically model the combined influence of tree island size and environmental variables on animal demography.

Given that *O. palustris* is thought to primarily forage in marshes rather than on tree islands, I predicted that, if *O. palustris* survival rates differ with island size class, survival rates would be lower on small islands, where the sparser cover can potentially increase the risk of predation. Because much of the *O. palustris* diet appears to be composed of aquatic prey, I also predicted that covariates associated with dry seasonal periods would negatively influence *O. palustris* survival and conversely, covariates associated with the wet season will positively affect *O. palustris* survival rates. I expected that nest building and rearing of young would favor *O. palustris* female site fidelity on larger tree islands where females presumably can find more resources than on smaller tree islands. I also expected that, during dry seasons, when the prairie is dry and offers less cover for animals moving across the prairie between tree islands, *O. palustris* would be less likely to move because between islands than in the wet season, when the marsh grasses over animals cover.

Because *S. hispidus* are predominantly herbivorous and that plant diversity and resilience are positively associated with tree island area, I predicted that large islands would have a positive effect on *S. hispidus* survival rates, while small islands would have a negative effect on survival. Given that *S. hispidus,* unlike *O. palustris,* is not a semi-aquatic species, I also predicted that covariates associated with wet seasons would have a negative effect on survival rates, while covariates associated with dry seasons would have a positive effect on *S. hispidus* survival. I predicted that for *S. hispidus,* similar to *O. palustris*, nest building and rearing of young would also favor greater site fidelity on larger tree islands relative to the smaller medium and small tree islands, especially during the dry season, when larger islands provide green vegetation and greater cover than on small tree islands.

CHAPTER ONE

TRAITS ASSOCIATED WITH *Sigmodon hispidus* AND *Oryzomys palustris* FEMALE FITNESS AND REPRODUCTION AMONG DIFFERENT SIZE CLASSES OF TREE ISLANDS OF THE EVERGLADES

BACKGROUND

The size (land area) of habitat patches has been shown to directly influence animal fitness and fecundity (Morrison *et al.* 1992). The disproportionate loss of larger tree islands in substantial portions of the Everglades (Wetzel *et al.* 2005) could potentially influence the demographic performance of the rodent species found throughout the tree islands of the Everglades. In the work presented here, I investigated the relationship between tree island size and traits associated with adult female fitness and reproduction of the two most common rodent species on the tree islands of Rock Reef Pass, the hispid cotton rat (*Sigmodon hispidus*) and the marsh rice rat (*Oryzomys palustris*). Although the use of tree island size is an anthropogenic choice of which of the islands' characteristics is relevant, I feel that, at least for tree islands with a tropical hardwood hammock plant community of similar seral maturity, tree island size is not only the most conspicuous abiotic property of islands, but is also the most relevant, since it likely encompasses the underlying effects of vegetation structure and composition on rodent species. Between February 1994 and December 2005, mark-recapture data were collected on small mammal species found on 16 tree islands at Rock Reef Pass, Everglades National Park, Homestead, FL. This data set constitutes one of the few long-term mark-recapture studies for a mammal species in the Everglades and the first description of rodents on tree islands located on what is referred to as the "Rocky

Glades", a karstic wet-prairie unique to the Everglades. These data provide a unique opportunity to understand better the ecology of rodents in the Everglades.

Animals generally make greater use of habitats that provide more favorable conditions than of habitats with less favorable conditions. At Rock Reef Pass, as with most of the Everglades wetland, the habitats that are primarily available to rodents are tree islands, and thus I expected *S. hispidus* and *O. palustris* to make greater use of tree islands with more favorable conditions over those tree islands with less favorable conditions. I made the assumption that, if habitat suitability differs with tree island size class, the likelihood of adult females staying on the island sizes with the most suitable habitat should be positively correlated with traits indicative of fitness and reproduction. This implies that adult female fitness and reproductive condition are influenced by some property of tree island size, or, conversely, that females of a given fitness and reproductive condition are more likely to use islands of a particular size. Regardless of which of these best exemplifies the relationships between adult females and tree islands, so long as a relationship exists between tree island size and adult female condition and reproduction, it is relevant to the our understanding of both rodent ecology and the potential impacts of changes in tree island size on rodents.

Direct measures of fitness and reproduction are difficult to quantify in field studies, especially for inconspicuous animals such as rodents, whose young are seldom captured and very rarely observed. For these reasons I evaluated indirect indicators of female fitness and reproduction and compared them among tree island size classes and across tree island area. Body weight has been shown to be a fitness component in rodents (e.g., Krackow 1992) and was used as an indicator of adult female condition within tree islands. The proportions of captured females that were reproductively active, the proportions of captured individuals that were juveniles and the number of juvenile individuals per adult female were used as indirect indicators of rodent reproduction.

METHODS

STUDY SITE

The Rocky Glades, a karstic wetland habitat unique to the Everglades National Park, is characterized by a highly irregular surface of Miami limestone outcroppings and solution holes. The Rocky Glades is primarily a seasonally flooded, short hydroperiod marl prairie with thousands of tree islands, typically ranging in size between 0.1 and 3 ha (Loope and Urban 1980). These islands occur on limestone outcrops raised up to 1 m above the surrounding marsh (Armentano *et al*. 2002) with vegetation classified as tropical hardwood hammock dominated by Gumbo-limbo (*Bursera simaruba*), willow bustic (*Sideroxylon salicifolium*), strangler fig (*Ficus aurea*), pigeon plum (*Coccoloba diversifolia*) and poisonwood (*Metopium toxiferum*). Geographic Information Systems software (ArcView 3.0, Redlands, CA, USA) was used to measure the areas of 16 selected tree islands at Rock Reef Pass, an area of the Rocky Glades, from aerial photographs. The areas of the 16 tree islands ranged in size from 4.2 m^2 to 1,110 m^2 (Figure 1.1).

Identifying patterns of tree island occupancy and rodent fitness is challenged by a high degree of movement among tree islands and by relatively short residency times on any single island by individual animals. To help us identify the relationship between tree island size and indirect indicators of fitness, rodent captures from across the 16 study tree islands were clustered into three island size classes, small, medium and large. This clustering of the data helped to identify patterns between animal fitness traits and island size that otherwise would not be detectable. Cluster analysis (k-means) of tree island areas was used to assign tree islands into three size classes with significantly different mean areas (ANOVA, $F = 100$, $df = 13$, $P < 0.001$) (Figure 1.2). Hereafter, values given as means are followed by plus or minus the standard error of the values whose mean is given ($\bar{x}$ = mean ± standard error). The mean areas for the tree size classes are: three large ($\bar{x} = 938$ m^2 ± 94 m^2, 1,110 m^2 - 785 m^2); four medium ($\bar{x} = 374$ m^2 ± 44 m^2, 432 m^2 - 245 m^2), and nine small islands ($\bar{x} = 77$ m^2 ± 21 m^2, 194 m^2 – 4 m^2) (Table 1.1).

SMALL MAMMAL TRAPPING

From February 1994 to August 1994, trapping was conducted for two consecutive nights approximately every two weeks ($\bar{x} = 13$ days ± 0.7 days) on a total of 13 trapping sessions. After August 1994, trapping was conducted for three consecutive nights. Between August 1994 and June 2003 trapping was conducted on a total of 107 trapping sessions approximately every four weeks ($\bar{x} = 28$ days ± 1.4 days), with the exception of a 165 day interruption due to storm damage starting in March of 1998. From June 2003 to December 2005 trapping was conducted more sporadically on a total of 13 trapping sessions with an interruption in trapping of 203 days starting in November 2004. Animals were sampled at Rock Reef Pass on a total of 75,656 trapnights. [Trapnights are the total numbers of 'nights' traps were open and available to capture animals: {13 (trapping sessions) x 2 (consecutive trapnights) + 120 (trapping sessions) x 3 (consecutive trapnights)} x 196 (traps) = 75,656 trapnights.] Small mammals were live-trapped using 7.6 x 8.9 x 22.9 cm, aluminum Sherman traps (H.B. Sherman, Tallahassee, FL) covered by a piece of plywood. Traps contained rolled oats bait and cotton balls. Traps were placed in an evenly spaced grid with a single trap every 10 m. Trapping grids encompassed the area of each tree island and extended onto the surrounding marsh by a maximum of 10 m. A total of 196 traps were used across 16 islands; 92 traps were placed on large islands (47%), 64 on medium islands (33%) and 40 traps (20%) on small islands. At capture, animals were identified to species, sexed, and their reproductive conditions were noted. The trap and island where animals were captured were also recorded. New animals were ear-tagged with a uniquely numbered fingerling tag. Body mass was used to classify *O. palustris* into three age classes, juveniles (< 31 g), subadults (31 - 50 g) and adults (> 50 g) (Wolfe 1985). *S. hispidus* were similarly assigned into three age classes, juveniles (< 60 g), subadults (60 - 95 g) and adults (> 95 g) (Cameron and Kruchek 2005).

SMALL MAMMAL SPECIES

Five species of small mammals were captured: hispid cotton rat (*Sigmodon hispidus*), marsh rice rat (*Oryzomys palustris*), cotton mouse (*Peromyscus gossipynus*), short-tailed shrew (*Blarina brevicauda*), and least shrew (*Cryptotis parva*). Since *P. gossipynus, B. brevicauda, and C. parva* were rarely captured, the work presented here includes only *S. hispidus* and *O. palustris*. *S. hispidus* is generally found in grass-dominated habitats from southern North America to northern South America. It feeds primarily on grasses but it may eat insects seasonally (Cameron and Spencer 1981). Although *S. hispidus* is capable of swimming, its fur is less water repellent than *O. palustris* and it quickly becomes waterlogged (Esher *et al.* 1978). *O. palustris* is a semi-aquatic species found in freshwater marshes, swamps and wetlands throughout the southeastern U.S. *O. palustris* is predominantly carnivorous, feeding on insects and crustaceans (Wolfe 1982).

DATA AND STATISTICAL ANALYSES

The total number of traps in each of the tree island size classes was not the same, because the number and size of tree islands in each tree islands size class differed. Because trapping effort was not equal among tree islands, I compared adult female and juvenile captures within and among the tree island size classes as proportions of captures. Adult female and juveniles captures were quantified as the number of unique individuals present during the three consecutive days of trapping on each island for every month that *S. hispidus* or *O. palustris* were captured. Captures within each tree island were described as a monthly proportion of individuals by age class and reproductive condition and grouped by island size class. These monthly proportions, as well as mean monthly adult female weights, were combined for each island size class and compared across the three tree island size classes using a non-parametric Kruskal-Wallis tests for which the calculated x^2 test statistic is reported. If a significant difference was present among tree island size classes, pair-wise comparisons were then made using non-parametric Conover-Inman tests reported as a *t* statistic. Correlation analyses were also conducted between the calculated adult female and juvenile monthly values for each island and tree islands area and are reported as an r value. Sex ratios were compared using a binomial test of equal probabilities. Statistical analyses were conducted using Systat 13.0 (Systat Software, Inc., Chicago, IL, USA). Mean monthly values are shown as “$\bar{x}$ ” and are followed by plus or minus standard error. These mean values reported for proportion values do not add to one since each is calculated from monthly proportions for individual islands that each sum to one. In other words, the proportions that sum to one are the proportions for each island for every month animals were trapped on that island. When proportions are compared by island size class, the monthly proportions for each island are clustered by size class.

ADULT FEMALE BODY WEIGHT

Animal weights were recorded at first capture and at the first recapture of each monthly sampling period. The mean body weights of *S. hispidus* and *O. palustris* adult females were calculated by month for each tree island and grouped by island size class. It was first determined whether the body weights of adult females differed for different island size by comparing the body weights of all adult females captured each month on large, medium and small islands. The body weights of males and females were averaged by adult individual and compared using an independent-samples *t* test. Body weights were also compared among tree island size classes using a non-parametric Kruskal-Wallis tests for which the calculated x^2 test statistic is reported. If a significant difference was present among tree island size classes, pair-wise comparisons were then made using non-parametric Conover-Inman tests reported as a *t* statistic.

To determine if there was a difference in fitness or condition between *S. hispidus* and *O. palustris* adult females that remained on an island and those that moved between islands, I compared the monthly body weights of adult females at time $t + i$ (where $i \geq 1$ month(s)) that were on same tree island at time t and t + i, versus those females on different tree islands at time t and $t + i$. The weights of females that were recaptured on a different tree island were quantified as the island-specific weights for the island on which the female had been previously captured; that is, from which it had moved. The weights of these females (*i.e.;* females recaptured on the same or on a different island) were also grouped by island size class and compared among size classes to determine if the body weights of females that stay on the same island or that move from it, differ with island size class. Body weights were compared among tree island size classes using a non-parametric Kruskal-Wallis tests for which the calculated x^2 test statistic is reported. If a significant difference was present among tree island size classes, pair-wise comparisons were then made using non-parametric Conover-Inman tests reported as a t statistic. Body weights were also correlated to the areas of the tree islands where adult females were last recaptured. The interval between a female's captures on a given island and its subsequent recapture, either on the same or on a different island, was for most (75 %; N = 48) *S. hispidus* and (72 %; N = 43) *O. palustris* adult females, a single month.

ADULT FEMALE REPRODUCTIVE CONDITION

Female reproductive traits were recorded at first capture and at the first recapture of each monthly sampling period. Information on the captures and reproductive condition of both adult and subadult females was used, since subadult females are capable of being reproductively active. Multiple captures within the same three day sampling period were not included, so as not to count individual females more than once. Three female reproductive traits were recorded: nipple size, if the vagina was perforate or closed and whether the pubic symphysis was slightly open, open or closed. Females were classified as reproductively active if at the time of capture nipple size was large, vagina was perforate or if pubic symphysis was open. The monthly proportions of reproductively active females within each tree island were calculated and correlated with tree island area. The monthly proportions of reproductively active females within each tree island were also grouped by island size class and compared among large, medium and small tree island size classes. To examine if tree island use differs with reproductive condition, I examined separately where reproductively active and non-reproductive females were captured. Subadult and adult female captures were described as a monthly proportions of all females in each tree island that were reproductively active and that were not reproductively active. These island-specific proportions were then combined by tree island size class. The proportions of reproductively active and non-reproductively active females were then separately compared within large, medium and small tree island size classes.

JUVENILES CAPTURES

Proportion of juveniles

The proportions of captures that were juveniles, were described as monthly proportions of individuals captured that were in the juvenile age class within each tree island. This was recorded for every month that any animal was captured on that tree island. The monthly proportions of juveniles within each tree island were correlated to tree island area, grouped by tree island size class, and compared among tree island size classes.

Juveniles per female

The number of juveniles per female was calculated for each tree island as the number of juvenile individuals per adult and subadult female for every month that females were captured on a tree island.

CAPTURE RATES

Inferences about animal ‘populations’ made from the animal capture data are influenced by the underlying biological processes of interest to wildlife biologists, and by process or sampling variation, which confounds such inferences. The incorporation of capture probabilities into the interpretation of capture data can reduce the confounding influence of inherent differences in animal trappability. Using a preliminary mark-recapture analysis, I did not find evidence that recapture rates differed between reproductive and non-reproductive females. Recapture rates did differ among tree island size classes, however, since it is the proportion of both reproductive and non-reproductive females that was estimated, the use of island size class-specific recapture probabilities would have changed the number of females but not the proportions within individual islands. There were too few juveniles captured to estimate useful capture probabilities or to be able to detect differences in the capture probabilities among island size classes. In addition, use of capture rates would not have provided information of the body weights of females not captured. This use of capture rates is fundamental to making reliable inferences about animal populations. In the work I present here, I limited my analyses to the use of animal data that were appropriate given that capture rates were not incorporated in statistical analyses.

RESULTS

Between February 1994 and December 2005, 715 *S. hispidus* individuals were trapped on 2,516 occasions and 777 *O. palustris* individuals were trapped on 1,583 occasions. The majority (N = 485; 68%) of *S. hispidus* were captured on two or more occasions (Figure 1.2). Of the *S. hispidus* individuals that were recaptured, the majority (N = 275; 57 %) were recaptured on a single tree island (Figure 1.3). *S. hispidus* captures were male (1.64:1; $P < 0.001$) biased, with 436 males captured on 1,488 occasions and 266 females captured on 1,028 occasions. *S. hispidus* adult males (N = 243; $\bar{x}$ = 127.21 g ± 1.52 g) were heavier ($t = 3.08$; $df = 317.5$; $p = 0.002$) than adult females (N = 124; $\bar{x}$ = 120.46 g ± 1.58 g).

The majority of *O. palustris* were captured on two or more occasions (N = 443; 57 %) (Figure 1.4). Of the *O. palustris* individuals that were recaptured, most were recaptured on a single tree island (N = 256; 58 %) (Figure 1.5). *O. palustris* captures were male biased (1.47:1; $P < 0.001$) with 455 males were captured on 1,274 occasions and 309 females captured on 906 occasions. *O. palustris* adult males (N = 352; $\bar{x}$ = 79.54 g ± 1.03 g) were also heavier ($t = 7.52$; $df = 475.4$; $p < 0.001$) than adult females (N = 184; $\bar{x}$ = 68.47 g ± 1.06 g). For both species the sex of 13 individuals was either not determined or not recorded.

Consistent with our expectation that juveniles are more likely to remain in their natal tree island, only 10.4 % (N = 24) of *S. hispidus* and 15.6 % (N = 11) of *O. palustris* juvenile individuals were recaptured on a different island from where they were first captured.

ADULT FEMALE WEIGHTS AND TREE ISLAND SIZE

S. hispidus

The body weights of *S. hispidus* adult females at the time of recapture were greater ($t = 2.321$; $df = 453$; $P = 0.021$) for *S. hispidus* adult females recaptured on the same tree island (N = 377; $\bar{x}$ = 124.5 g ± 1.18 g), regardless of tree island size, than for adult females recaptured on a different tree island (N = 78; $\bar{x}$ = 117.97 g ± 2.16 g). When tree island size is included in the analyses of adult female body weight and recaptures, the results suggest that, consistent with our expectation, there exists a relationship between adult female fitness and tree island size. Overall, the body weights of *S. hispidus* adult females were positively correlated to tree island area (ρ = 0.184; P = 0.002) (Figure 1.6).

At the time of recapture, the weights of adult *S. hispidus* females recaptured on the same tree island were positively correlated (ρ = 0.174, P = 0.001) with tree island area (Figure 1.7a) and differed (X^2 = 23.511; df = 2, $P < 0.001$) among females recaptured on the same large (N = 297; $\bar{x}$ = 127.03 g ± 1.35 g), medium (N = 61; $\bar{x}$ = 112.62 g ± 2.17 g) and small (N = 17; $\bar{x}$ = 125.59 g ± 5.19 g) tree islands (Figure 1.8). Adult females recaptured on the same large tree island (t = 4.99; df = 356; $P < 0.001$) were heavier than adult females that were recaptured on the same medium tree island. The body weights of adult females recaptured on the same medium island were in turn greater (t = 2.331; df = 76; P = 0.02) than the body weights of adult females recaptured on small tree islands, while the body weights of adult females recaptured on the same small or large tree island did not differ (t = 0.249; df = 312; P = 0.804).

The body weights of adult *S. hispidus* females recaptured on a different tree island were not correlated (P = 0.74) with the area of the tree island on which adult females were previously captured (Figure 1.7b) and did not differ (X^2 = 0.276; df = 2; P = 0.871) among large (N = 23; $\bar{x}$ = 119.61 g ± 4.81 g), medium (N = 33; $\bar{x}$ = 116 g ± 2.84 g) and small tree islands (N = 22; $\bar{x}$ = 119.2 g ± 4.07 g) (Figure 1.8).

O. palustris

The adult *O. palustris* female condition, as indicated by body weight, was not as strongly associated with island size as it was for *S. hispidus* females. The body weights of adult *O. palustris* females did not differ ($t = 0.431$; $df = 402$; $P = 0.667$) between females recaptured on the same tree island (N = 247; $\bar{x} = 67.70$ g ± 0.85 g) or those recaptured on a different tree island from where they were last captured (N = 157; $\bar{x} = 67.15$ g ± 0.83 g). Overall, the body weights of all *O. palustris* adult females were not correlated ($P = 0.132$) with tree island area (Figure 1.9), nor were the body weights of *O. palustris* adult females recaptured either on the same tree island ($P = 0.196$) (Figure 1.10a), or on a different tree island ($P = 0.431$) (Figure 1.10b), correlated with tree island area.

When the body weights of adult *O. palustris* females recaptured on the same tree island were clustered and compared by island size class, their weights differed ($X^2 = 13.528$; $df = 2$; $P = 0.001$) among females recaptured on the same large (N = 110; $\bar{x} = 64.91$ g ± 1.38 g), medium (N = 60; $\bar{x} = 71.27$ g ± 1.33 g) and small (N = 77; $\bar{x} = 69.49$ g ± 1.46 g) tree island (Figure 1.11). Adult *O. palustris* females recaptured on the same large tree island weighed more than adult females recaptured on the same medium ($t = 3.706$; $df = 168$; $P < 0.001$) or adult females recaptured on the same small tree island ($t = 2.042$; $df = 185$; $P = 0.042$). The difference in the body weights of adult females recaptured on the same medium or small tree islands did not differ ($t = 1.693$; $df = 135$; $P = 0.092$) (Figure 1.11).

For adult *O. palustris* females recaptured on a different tree island, their weights did not differ ($X^2 = 0.44$; $P = 0.82$) among females that in their previous capture been found on large (N = 38; $\bar{x}$ = 68.37 g ± 1.78 g), medium (N = 41; $\bar{x}$ = 66.42 g ± 1.48 g) or small tree islands (N = 78; $\bar{x}$ = 66.95 g ± 1.31 g) (Figure 1.11).

REPRODUCTIVELY ACTIVE FEMALES AND TREE ISLAND SIZE

S. hispidus

Overall, the proportions of reproductively active *S. hispidus* females captured each month were not correlated (*P* = 0.264) to the area of the tree islands where they captured (Figure 1.12). When the proportions of reproductively active females captured on each island were clustered by island size and compared among tree island size classes, the proportions of reproductively active females differed ($X^2 = 9.6$; *df =2; P* = 0.008) among females captured on large (N = 227; $\bar{x}$ = 0.79 ± 0.03), medium (N = 98; $\bar{x}$ = 0.63 ± 0.05) and small (N = 63; $\bar{x}$ = 0.73 ± 0.06) size class tree islands (Figure 1.13). The proportions of females that were reproductively active on large tree islands were greater (*t* = 3.126; *df* = 159; *P* = 0.0019) than on medium islands but did not differ between large and small tree islands (*t* = 0.95; *df* = 323; *P* = 0.343) or between females captured on medium and small tree islands (*t* = 1.502; *df* = 288; *P* = 0.134) (Figure 1.13).

To determine if *S. hispidus* females' use of tree islands differed with reproductive condition, the monthly proportions of where reproductively active and non-reproductively active females were captured each month were grouped by island size class and the two proportions were compared within large, medium and small tree islands (Figure 1.14). Greater proportions (*t* = 4.24; *df* = 529; *P* < 0.001) of the reproductively active *S. hispidus* females (N = 351; $\bar{x}$ = 0.23 ± 0.016) than non-reproductively active females (N = 180; $\bar{x}$ = 0.17 ± 0.024) were captured on large islands. On medium ($N_{\text{reproductive}}$ = 468; $\bar{x}$ = 0.042 ± .006) ($N_{\text{non-reproductive}}$ = 300; $\bar{x}$ = 0.068 ± 0.012) and small (N

$_{\text{reproductive}}$ = 1053; $\bar{x}$ = 0.015 ± 0.003) (N $_{\text{non-reproductive}}$ = 480; $\bar{x}$ = 0.018 ± 0.006) tree islands these proportions did not differ (t_{medium} = 0.346; *df* = 766; *P* = 0.73) (t_{small} = 1.307; *df* = 1,531; *P* = 0.192) (Figure 1.14).

O. palustris

The monthly proportions of *O. palustris* females captured on each tree island that were reproductively active were negatively correlated (ρ = - 0.134; *P* = 0.009) to tree island area (Figure 1.15). The proportions of females captured each month that were reproductively active within each tree island approached a significant difference (X^2 = 5.92; *df* = 2; *P* = 0.052) among females captured on large (N = 141; $\bar{x}$ = 0.53 ± 0.039), medium (N = 89; $\bar{x}$ = 0.53 ± 0.052) and small (N = 144; $\bar{x}$ = 0.65 ± 0.04) tree islands (Figure 1.16). Because the differences among these proportions approached statistical significance, I preceded with pairwise comparisons of the proportions of reproductively active females by tree island size classes. The proportions of reproductively active *O. palustris* females on small tree islands were greater (*t* = 2.207; *df* = 283; *P* = 0.028) than on large islands, while they did not differ between medium and large (*t* = 0.031; *df* = 228; *P* = 0.975) tree islands nor between females captured on small and medium (*t* = 1.908; *df* = 283; *P* = 0.057) tree islands (Figure 1.16).

As with *S. hispidus*, the monthly proportions of where reproductively active and non-reproductively active *O. palustris* females were captured each month were grouped by island size class and the two proportions were compared for large, medium and small tree islands (Figure 1.17). The proportions of where reproductively active and non-reproductive *O. palustris* females were captured differed only on small tree islands, where greater (*t* = 3.572; *df* = 1,528; *P* < 0.001) proportions of reproductively active female captures (N = 774; $\bar{x}$ = 0.045 ± 0.006) occurred than those of non-reproductive females (N = 756; $\bar{x}$ = 0.033 ± 0.006). These proportions did not differ for females on medium ($N_{reproductive}$ = 344; $\bar{x}$ = 0.046 ± 0.008) ($N_{non\text{-}reproductive}$ = 336; $\bar{x}$ = 0.061 ± 0.010) (*t* = 0.322; *df* =678; *P* = 0.77) or large tree islands ($N_{reproductive}$ = 258; $\bar{x}$ = 0.137 ± 0.016) ($N_{non\text{-}reproductive}$ = 252; $\bar{x}$ = 0.155 ± 0.018) (*t* = 0.284; *df* = 508; *P* = 0.78) (Figure 1.17).

PROPORTIONS OF JUVENILES AND JUVENILES PER FEMALE

S. hispidus

The monthly proportions of *S. hispidus* individuals captured within each tree island that were in the juvenile age class were not correlated (ρ = 0.07*;* *P* = 0.08) (Figure 1.18) with tree island area but did not differ (X^2 = 4.9; *df* = 2; *P* = 0.086) among large (N = 320; $\bar{x}$ = 0.33 ± 0.036), medium (N = 169; $\bar{x}$ = 0.23 ± 0.038) and small (N = 133; $\bar{x}$ = 0.2 ± 0.035) tree islands (Figure 1.19). Because the proportions of juvenile captures nearly differed among tree island size classes, I proceeded with pair-wise comparisons of the proportions of juvenile captures between tree island size classes. A greater proportion (*t* = 1.96; *df* = 451; *P* = 0.05) of individuals captured on large tree islands were in the juvenile age class than individuals captured on small tree islands but did not differ (*t* = 1.61; *df* = 487; *P* = 0.108) from the proportion of juveniles captured on medium islands. The proportions of juveniles also did not differ (*t* = 0.42; *df* = 300; *P* = 0.672) for individuals captured on medium and small tree islands.

The numbers of *S. hispidus* juveniles per adult and subadult female for every month on which either or both juveniles and females were captured on the same island were positively correlated (ρ = 0.096, *P* = 0.038) (Figure 1.20) with tree island area. When compared among tree island size classes, the number of juveniles per adult and subadult female did not differ ($X^2 = 4.243$; $df = 2$; $P = 0.12$) among large (N = 255; $\bar{x} = 0.565 \pm 0.06$), medium (N = 123; $\bar{x} = 0.354 \pm 0.058$) or small (N = 89; $\bar{x} = 0.3 \pm 0.052$) tree islands (Figure 1.21).

O. palustris

The monthly proportions of *O. palustris* individuals captured within each tree island that were in the juvenile age class were not correlated ($P = 0.065$) with tree island (Figure 1.22) area but differed ($X^2 = 6.085$; $df = 2$; $P = 0.048$) among large (N = 236; $\bar{x} = 0.075 \pm 0.018$), medium (N = 201; $\bar{x} = 0.057 \pm 0.014$) and small (N = 296; $\bar{x} = 0.055 \pm 0.013$) size class tree islands (Figure 1.23). Greater ($t = 2.467$; $df = 530$; $P = 0.014$) proportions of *O. palustris* captured on small tree islands were in the juvenile age class than those captured on large tree islands, while the proportions of juveniles captured did not differ between small and medium ($t = 1.402$; $df = 495$; $P = 0.162$) nor between medium and large tree islands ($t = 0.885$; $df = 435$; $P = 0.377$).

The numbers of *O. palustris* juveniles per adult and subadult female captured within each tree island were not correlated (Figure 1.24) with the area of the tree island ($P = 0.265$) on which they were captured and did not differ ($X^2 = 4.373$; $df = 2$; $P = 0.112$) among large (N = 156; $\bar{x} = 0.19 \pm 0.035$), medium (N = 100; $\bar{x} = 0.18 \pm 0.04$), and small (N = 160; $\bar{x} = 0.13 \pm 0.028$) tree islands (Figure 1.25).

DISCUSSION

In the work presented here, I investigated the relationship between tree island size and traits associated with adult female fitness and reproduction of *S. hispidus* and *O. palustris*. Tree island use by *S. hispidus* and *O. palustris* adult females were broadly described by comparing the relative proportions of adult females recaptured either on the same island or on a different island from where they were last captured. The comparisons of these proportions were not intended to describe the movement patterns of adult females between tree islands, but rather only to examine whether indirect indicators of animal fitness and reproduction differ with island size class and whether they differ for females that were either recaptured on the same or on a different tree island. A more robust and efficient analysis of species' tree island use and movement between tree island size classes would include tree size class-specific animal capture probabilities. In this chapter I use a multi-state mark-recapture analysis (e.g., Brownie et al. 1993) that incorporates capture probabilities in estimates of animal transition probabilities between tree island size classes. In the work presented here, I assumed that if habitat quality differed among tree island size classes, then adult females captured on tree islands of a size class that offered more favorable conditions would be more likely to have greater fitness than females captured on islands of a size class with less favorable conditions. This approach also assumed that sufficient numbers of adult females were able to move between islands, so that differences in female fitness were not merely due to the limitations imposed by the quality of the island where females were born or by their limited ability to occupy islands that may differ in quality. Sixty-eight percent of *S. hispidus* and 57 % of *O. palustris* were recaptured on at least a second occasion. Of these, 43 % of *S. hispidus* and 57 % of *O. palustris* were captured on two or more tree islands. These captures likely underestimated the true proportion of animals that moved between islands, since trapping limits our information to a relatively small number of individuals over a short period on 16 out of the thousands of tree islands in the

Everglades. Nonetheless, these trapping data inform us that *S. hispidus* and *O. palustris* adult females are able to move between islands and thus have the opportunity to either remain on the tree island they occupy or move to another.

Overall, our results suggest that the use of tree islands, irrespective of size, by *S. hispidus* adult females is best characterized by females that primarily remain on the same tree island, while the use of tree island by *O. palustris* adult females is best characterized by females that are as likely to move to another island as they are to stay on the same island.

The positive correlation between the proportions of *S. hispidus* and *O. palustris* adult females that remained on the same island, would suggest that there may be some benefit to occupying large islands. If such benefits exist, they might be exhibited as a positive association between increased adult female fitness and island area. Because of the difficulty of quantifying direct measures of individual fitness in a field-study of free-living animals, I instead quantified traits that have been shown to be associated with individual fitness, adult body weight and reproductive condition (e.g., Krackow 1992), and examined their relationship to island area.

The body weights of all adult *S. hispidus* females captured were positively correlated with island area (Figure 1.6). For *S. hispidus* recaptured on the same island, their body weights were positively correlated with tree island area, while the body weight of *S. hispidus* females recaptured on a different tree island were not correlated with tree island area (Figure 1.7b). The absence of a significant correlation between the weights of *S. hispidus* females with tree island area is not surprising, given that females recaptured on different islands diminish differences in animal weights across tree islands. The monthly proportions of females captured on each tree island that were reproductively active were also not correlated to tree island area (Figure 1.12), which was also not surprising, given that rodents are r-selected species whose demographic strategy favors a short-term investment in reproduction (Fleming 1979), because of their limited lifespan. When body weights and the proportions of reproductively active females were grouped by island size classes and compared in pair-wise combinations of island size classes, the weights of all *S. hispidus* females captured, the weights of females recaptured on the same tree island, as well as the proportions of reproductively active females, were greater on large islands than on medium islands (Figures 1.8 and 1.14), while female weights and reproductive state did not differ between *S. hispidus* females captured on large and small islands nor between those captured on small and medium islands (Figures 1.8 and 1.14). In addition, the proportions of reproductively active female captures that occurred on large tree islands were greater than the proportions of non-reproductively active female captures that occurred on large islands, suggesting that reproductively active females make greater use of large islands than non-reproductive females (Figure 1.14). The absence of significant differences in body weight and reproductive condition between *S. hispidus* females captured on large and small tree islands was likely due to the physical distribution of study islands in the landscape that increased the temporary occupancy of some small islands by *S. hispidus* females from the adjacent large size class tree islands. In addition, the small proportions of *S. hispidus* females recaptured on the same small tree island suggest that adult females occupying these islands are primarily transitory and, therefore, that it is less likely that their body weight and reproductive condition are influenced by conditions on small islands. Despite the similarities between *S. hispidus* females on large and small tree islands, our results provide evidence that on large size class tree islands the body weights and proportions of reproductively active *S. hispidus* females were consistent with the interpretation that, relative to smaller tree islands, large islands provide more favorable conditions for *S. hispidus* adult females.

For *O. palustris* females, the relationship between tree island area and both adult weight and proportion of reproductively active females were not consistent with an interpretation suggesting a direct relationship between female fitness and island area. No correlations were found between the weights of females recaptured either on the same or on a different tree island and tree island area (Figures 1.10a and 1.10b), while the proportions of reproductively active *O. palustris* females were negatively correlated with tree island area (Figure 1.15). When the body weights and proportions of reproductively active *O. palustris* adult females on each island were grouped by tree island size class and compared among island size classes, the only differences found were that females recaptured on the same medium island were heavier than females recaptured on the same large island (Figure 1.11) and that the proportions of reproductively active *O. palustris* females were greater on small islands than on large tree islands (Figure 1.16).

The absence of stronger and more consistent relationships between tree islands size and both *O. palustris* adult female body weight and the proportions of reproductively active females was most likely due to the high number of *O. palustris* that moved between tree islands. Thirty-one percent of adult females were captured on two or more tree islands, meaning that nearly one third of adult females contributed to the estimated mean weights and to the reproductive condition of females on two or more islands. This movement likely homogenized potential differences in adult female reproductive condition and body weight across the tree islands of the study site, potentially masking the relationship between tree islands and animal traits. Studies conducted over greater spatial scales may be able to detect potential relationships between *O. palustris* and tree islands that operate at spatial scales beyond the Rock Reef Pass Study site.

Quantifying reproductive output is difficult in field studies, especially for inconspicuous taxa such as rodents, whose young can only be evaluated by trapping once they emerge from the natal burrow or nest. This meant that fecundity could not be quantified. It was also not possible to calculate the relative contribution of females on different islands to population recruitment, since most tagged juveniles dispersed out of the study site, not to be seen again. Therefore, the source of new individuals in the population could not be determined. However, I felt that for this study the count of the juveniles in different islands already encompasses potential differences in fecundity for females on different tree islands. In addition, once juveniles disperse out of the natal tree island, they likely have similar survivorships, since they face identical hazards, regardless of which island they were born in, and, therefore, it is the number of offspring produced that is most likely to influence the relative contribution of females on different size tree islands to population recruitment.

Thirty two percent (N = 226) of all *S. hispidus* individuals captured were juveniles. The monthly proportions of juvenile captures were not correlated with the area of the tree island on which they were captured (Figure 1.18). However, when compared among tree island size classes, the proportions of *S. hispidus* juveniles on large islands were greater than those on small islands (Figure 1.19). The numbers of *S. hispidus* juveniles per adult and subadult female within each tree island were positively but weakly correlated with tree island area and did not differ among tree island size classes (Figure 1.20). The greater proportions of *S. hispidus* juveniles within large islands is interpreted as an indication that the production of *S. hispidus* offspring on large islands is greater than on smaller tree islands. In addition, because the number of juveniles per female was positively but weakly correlated with tree island area and did not differ among tree island size classes, these results are interpreted as an indication that the production of *S. hispidus* on large islands is higher because there are more females producing offspring, rather than that each female produced more offspring.

In comparison to *S. hispidus,* relatively few *O. palustris* were captured. Only 9.78% (N = 76) of *O. palustris* individuals captured were juveniles. This small sample size of *O. palustris* juveniles likely tended to weaken the relationship between juvenile captures and tree islands. The proportions of individuals captured that were juveniles were not correlated with tree island area (Figure 1.22), and when captures were clustered and compared among pairs of island size classes, the proportions of juveniles on small tree islands were greater than on large tree islands (Figure 1.23). The numbers of *O. palustris* juveniles per adult and subadult female were not correlated with the tree island area and did not differ among large, medium, and small tree islands (Figures 1.24 and 1.25).

Differences in the captures, condition and reproduction of *O. palustris* and *S. hispidus* adult females on tree islands, are necessarily in part a reflection of differences in these species' movement rates among tree islands and their diets. *O. palustris* are primarily carnivorous. During the wet season, the semi-aquatic *O. palustris* forages for insects and crustaceans in the marsh surrounding tree islands. In the dry season, most *O.*

palustris at Rock Reef Pass disappear, presumably moving to wet refugia provided by water in solution holes in the limestone substrate. The diet of *O. palustris* and use of multiple islands, as well as their use of wet refugia outside of the study site, increases the spatial scale of habitat use by *O. palustris,* making them less susceptible to conditions on any one tree island thus diminishing the influence of local conditions. The absence of a significant difference in the body weight of adult females recaptured on the same island and those recaptured on another island is likely the result of this life-history strategy, which, unlike that of *S. hispidus,* does not favor or confer the advantages of greater body weight, to females that remain on the same island over those that move between islands. The decreased reliance on individual tree islands, relative to *S. hispidus*, is also supported by the weaker correlations between *O. palustris* female recaptures and island area and the fewer instances where there were significant differences among tree island size classes in the *O. palustris* female traits compared in this study.

In contrast, *S. hispidus* are primarily herbivorous and feed on tree island vegetation. Although *S. hispidus* can swim and at Rock Reef Pass *S. hispidus* do move between islands during the wet season, their fur quickly becomes water-logged. *S. hispidus'* greater dependence on tree island vegetation for its diet and its diminished ability to move between tree islands makes *S. hispidus* more susceptible than *O. palustris* to conditions on the tree islands they occupy and thus increasing the influence of local conditions on *S. hispidus*.

A comparison of our findings with those of Smith and Vrieze's (1979), conducted at Taylor Slough, a wet prairie marsh of the Everglades, located approximately 17 km southeast of Rock Reef Pass, shows that rodent species composition is not uniform throughout the tree islands of the Everglades. While at our Rock Reef Pass study site's tree islands, few cotton mice (*Peromyscus gossipynus*) were captured, at Taylor Slough, *P. gossipynus* was the most abundant rodent on tree islands. Population turnover rates between wet seasons also differ between the two sites. At Taylor Slough there is a complete turnover of rodents between seasons, whereas at Rock Reef Pass a complete turnover of rodents generally takes two seasons to occur. During the dry season, Taylor Slough was described by Smith and Vrieze's (1979) as a "dusty plain," while at Rock Reef Pass limestone solution holes provide sources of water during the dry season. During the wet season water levels on Taylor Slough's prairie are higher than at Rock Reef Pass, and Taylor Slough lacks the limestone outcroppings that at Rock Reef Pass provide rodents with waypoints between tree islands that are covered with emergent vegetation. The absence of limestone outcroppings and deeper water levels at Taylor Slough make movement between tree islands more perilous, not only because animals need to swim farther with less cover, but also because the deeper water levels and the lack of rock outcropping allow alligators to move easily across the flooded marsh, as evidenced by the dense alligator trails crisscrossing the sawgrass (personal observation). Conditions restricting the movement of rodents between tree islands should favor smaller species like the much smaller *P. gossipynus*, which are better able to persist when restricted to a smaller area.

CONCLUSIONS

Overall, the work reported here indicated that on the tree islands at Rock Reef Pass, there was relationship between tree island area and *S. hispidus* adult female body weight, a fitness trait, and indicators of female reproduction. The relationship between the described traits and tree island area and size classes, suggested that *S. hispidus* females on larger tree islands had higher fitness than females on smaller islands. For *O. palustris* females, the relationship between fitness and reproduction traits and tree island area and size classes was less distinct. While *O. palustris* females recaptured on the same large island weighed more than females that were recaptured on the same medium or small island, the proportions of reproductively active females and of juveniles in *O. palustris* captures, were both higher on small islands. *O. palustris* adult females on large islands were heavier than those on smaller islands, suggesting that it is possible that females with higher fitness make greater use of larger islands.

If the higher body weight of females on large islands is an indication that relative to medium and small islands, rodents on large islands have higher fitness, them it would be also be expected that the demographic rates of rodents on large tree islands, would be consistent with expectation that more fit individuals should also have higher survival rates than rodents on medium and small islands.

In Chapter Two, *S. hispidus* and *O. palustris* survival probabilities were estimated as island size class-specific rates and as non-stratified rates. A model selection approach was then used to determine which survival model is best supported in the data. This approach allows for the estimation of survival probability, a fundamental demographic rate, as a function of tree island size class and as a function of environmental covariates for wet and dry seasons, which are both fundamental features of the Everglades ecosystem studied. In addition, in Chapter Two, I also estimated the transition probabilities among tree island size classes, which can provide insights into the use of tree islands in the Everglades.

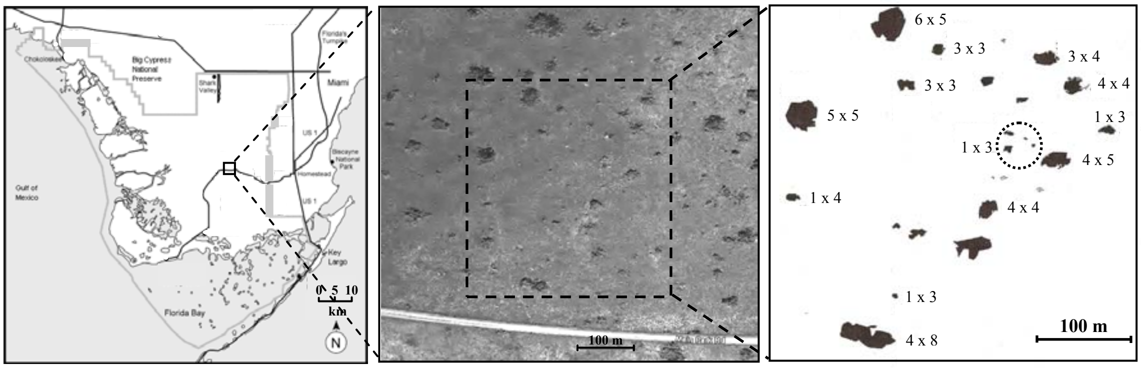


Figure 1.1. (a) Study was conducted in the Everglades National Park, Homestead, FL, in an area commonly known as Rock Reef Pass. (b) The study site was located just north of the main Park road, 17 kilometers from the main National Park entrance. (c) The 16 tree islands of varying sizes were selected for small mammal live-trapping and are indicated by the trapping grid size shown adjacent to each tree island.

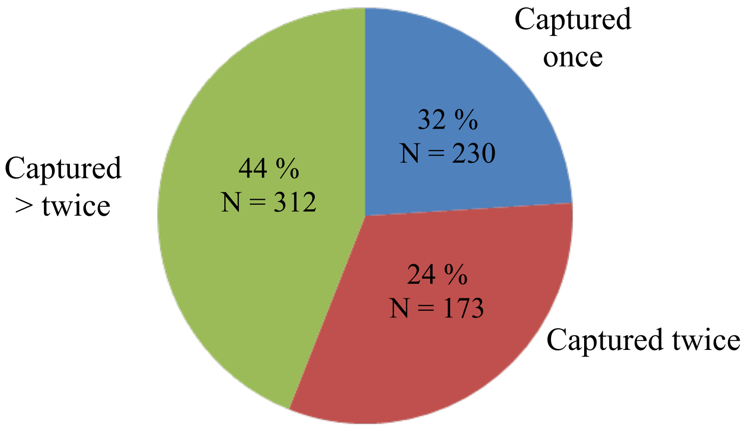


Figure 1.2. Thirty-two percent (N = 230) of *S. hispidus* were captured once and not seen again. Twenty-four percent (N = 173) were captured on two occasions. The remaining 44 % (N = 312) of *S. hispidus* were captured on more than two occasions ($\bar{x}$ = 6.3 ± 1.2).

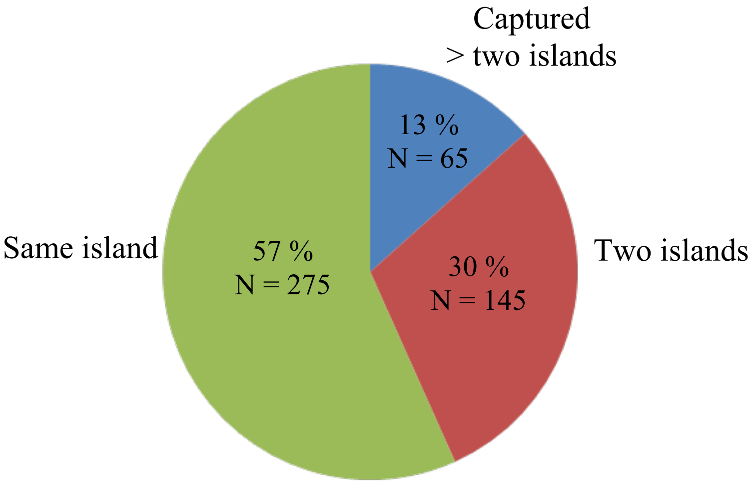


Figure 1.3. *S. hispidus* individuals were captured on a mean of 1.4 (± 0.8) tree islands. Of the *S. hispidus* individuals that were recaptured (N = 485), 57 % (N = 275) were recaptured on the same island, 32% (N = 145) were recaptured on two different tree islands and 13% (N = 65) were recaptured on more than two tree islands ($\bar{x}$ = 3.5 ± 0.9).

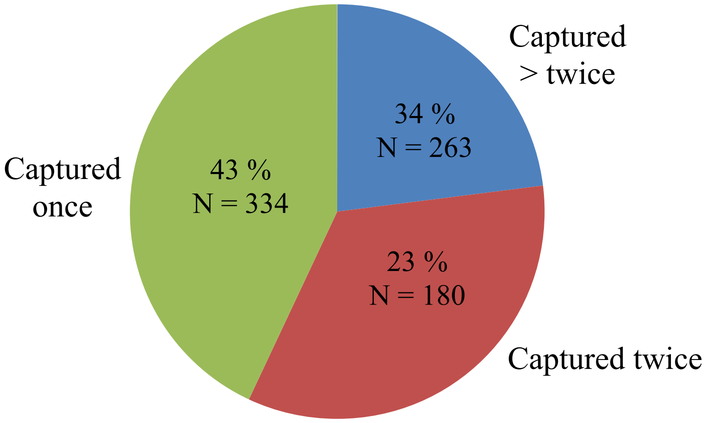


Figure 1.4. Forty-three percent (N = 334) of *O. palustris* were captured once and not seen again. Twenty-three percent (N = 180) of *O. palustris* were captured on two occasions and the remaining 34 % (N = 263) were captured on more than two occasions ($\bar{x}$ = 5.7 ± 0.14).

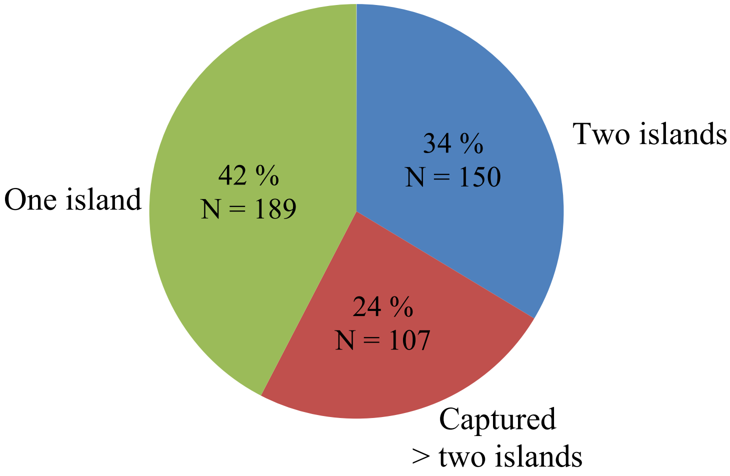


Figure 1.5. *O. palustris* individuals were captured on a mean of 1.6 (± 0.04) tree islands. Of the *O. palustris* individuals were recaptured (N = 443), 42 % (N = 189) were recaptured on the same tree island, 34% (N = 150) were recaptured on two islands and 24 % (N = 107) were recaptured on more than two islands ($\bar{x}$ = 3.9 ± 0.04).

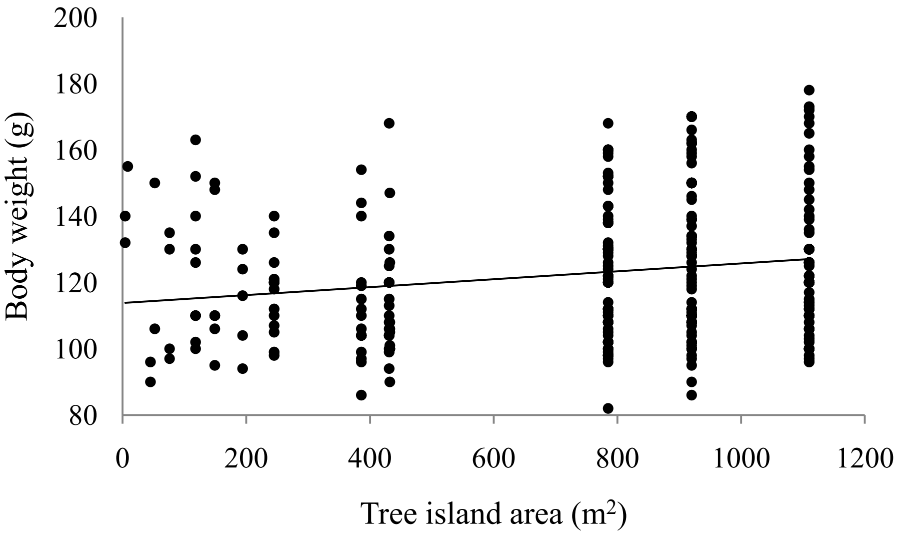
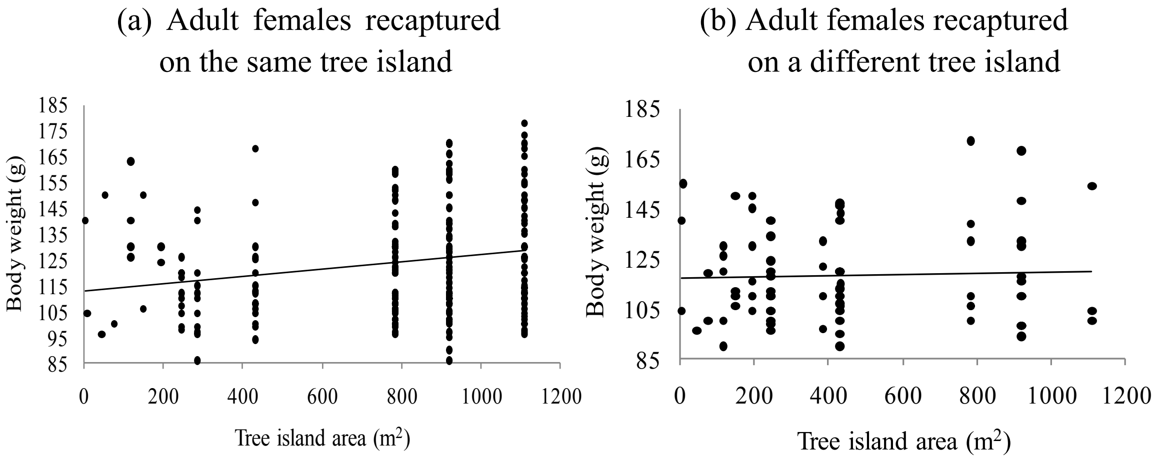


Figure 1.6. The body weights of *S. hispidus* adult females were positively correlated to tree island area ($\rho = 0.184$; $P = 0.002$). Animal body weights were recorded on the first captured/recapture of each month and not on subsequent recaptures within the same month.


(a) Adult females recaptured on the same tree island

(b) Adult females recaptured on a different tree island

Figure 1.7. **(a)** The weights of adult *S. hispidus* females at the time of recaptured on the same tree island were positively correlated ($\rho = 0.174$, $P = 0.001$) with tree island area, **(b)** while the body weights of adult *S. hispidus* females recorded at the time of recapture on a different tree island were not correlated ($\rho = - 0.017$, $P = 0.88$) with the area of the tree island on which adult females were previously captured. Body weights were recorded at the time of recapture, either on the same or on a different tree island. The interval between recaptures was one or more months. Of the *S. hispidus* adult female individuals that were recaptured, 75 % (N = 43) were recaptured the following month.

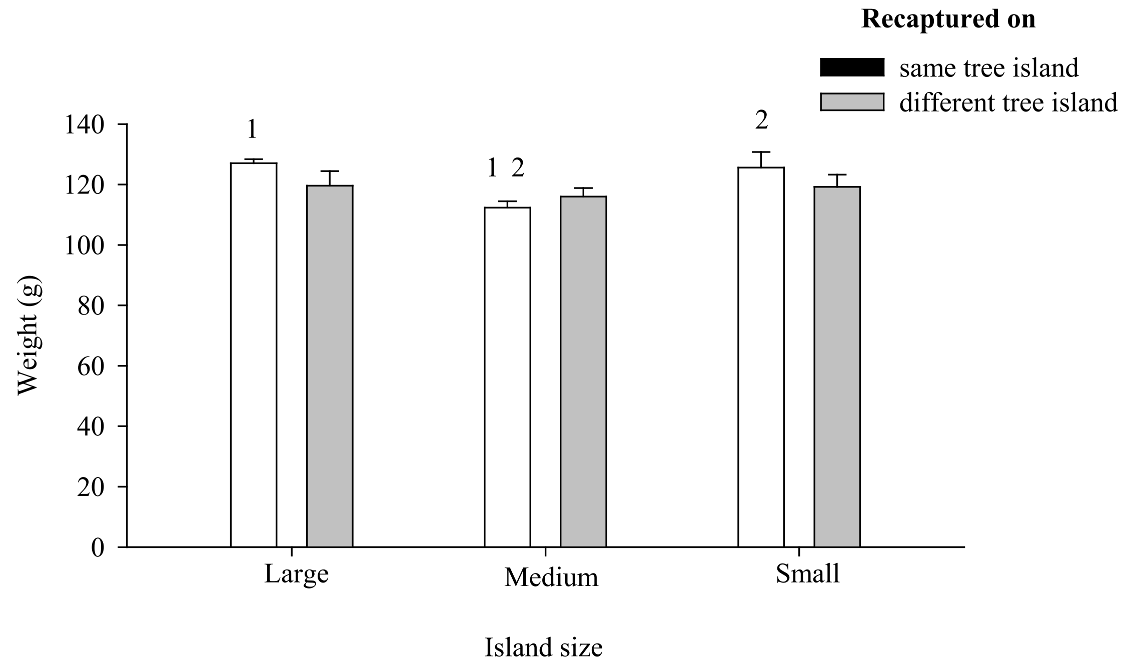


Figure 1.8. Comparison of *S. hispidus* body weights for adult females recaptured either on the same tree island or on a different tree island. Body weights were recorded at the time of recapture, either on the same or on a different tree island. The weights of females recaptured on the same islands, were grouped by the size class of the tree island where they were recaptured. The weights of females recaptured on a different tree island, were grouped by size class of the island where an individual had been previously captured (i,e.; the island the female ‘moved’ from). The weights of adult females were tested for equal weights on islands for the three size classes. These comparisons were conducted separately for *S. hispidus* recaptured on the same tree island and for *S. hispidus* recaptured on a different tree island. The body weights of adult *S. hispidus* adult females recaptured on the same tree island differed ($X^2 = 23.511$; $df = 2$; $P < 0.001$) among females recaptured on the same large (N = 297; $\bar{x} = 127.03$ g ± 1.35 g), medium (N = 61; $\bar{x} = 112.62$ g ± 2.17 g) and small (N = 17; $\bar{x} = 125.59$ g ± 5.19 g) tree islands. Adult females recaptured on the same [1] large tree island ($t = 4.99$; $df = 356$; $P < 0.001$) were heavier than adult females recaptured on the same medium tree island. Adult females recaptured on the same [2] medium island weighed more ($t = 2.331$; $df = 76$; $P = 0.02$) than adult females recaptured on the same small tree island, while the body weights of adult females recaptured on the same small or the same large tree island did not differ ($t = 0.249$; $df = 312$; $P = 0.804$). The body weights of adult *S. hispidus* females recaptured on a different tree island did not differ ($X^2 = 0.276$; $df = 2$; $P = 0.871$) among females that in their previous captured had been found on large (N = 23; $\bar{x} = 119.61$ g ± 4.81 g), medium (N = 33; $\bar{x} = 116$ g ± 2.84 g) and small tree islands (N = 22; $\bar{x} = 119.2$ g ± 4.07 g). The interval between recaptures was one or more months. Of the *S. hispidus* adult female individuals that were recaptured, 75 % (N = 48) were recaptured the following month.

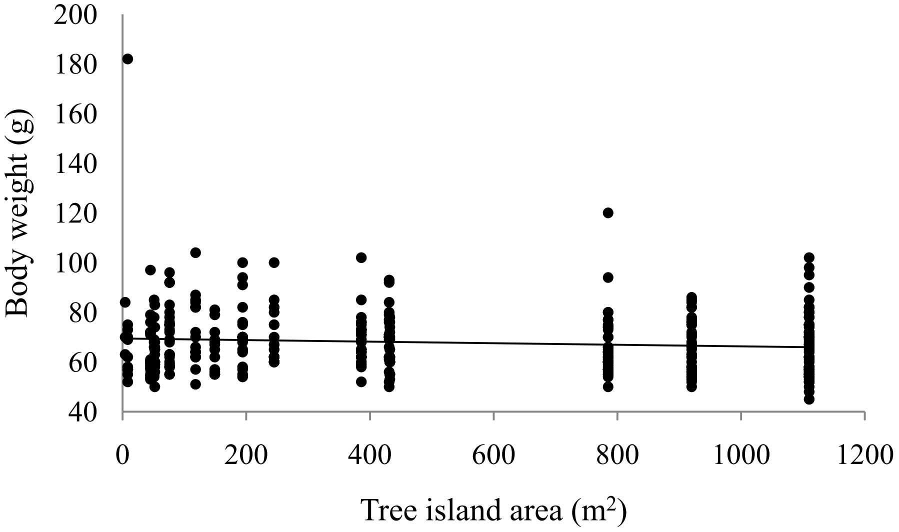


Figure 1.9. The body weights of adult *O. palustris* adult females were not correlated (ρ = - 0.083, P = 0.13) with the area of the tree island they were captured. Animal body weights were recorded on the first captured/recapture of each month.

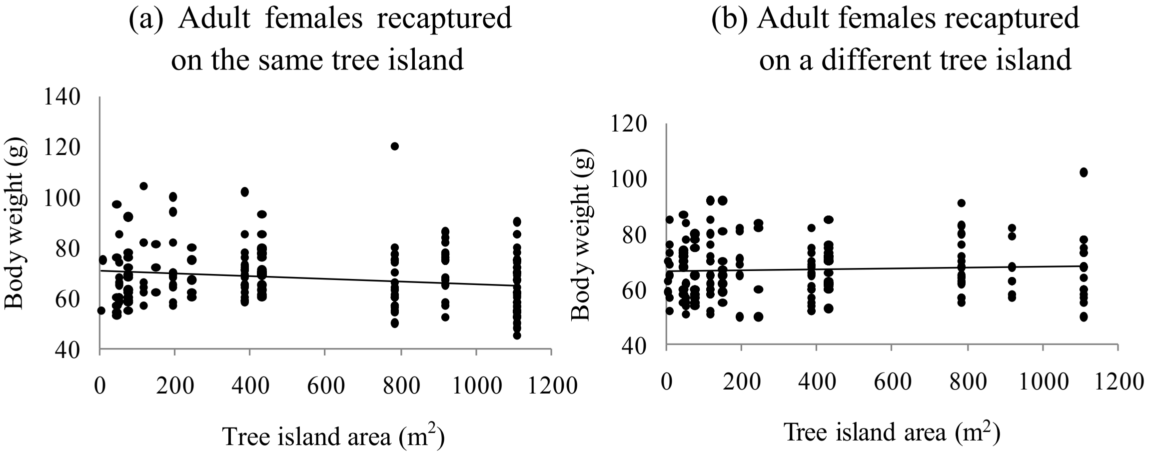


Figure 1.10. **(a)** The body weights of adult *O. palustris* adult females were not correlated to tree island area for adult females recaptured either on the same tree island (ρ = - 0.018, P = 0.067) or for **(b)** adult females recaptured on a different tree island (ρ = 0.07, P = 0.39) from that on which they were last captured. Animal body weights were recorded on the first recapture of each month, either on the same or on a different tree island. The interval between recaptures was one or more months. Of the *O. palustris* adult female individuals that were recaptured, 72 % (N = 43) of these females were recaptured the following month.

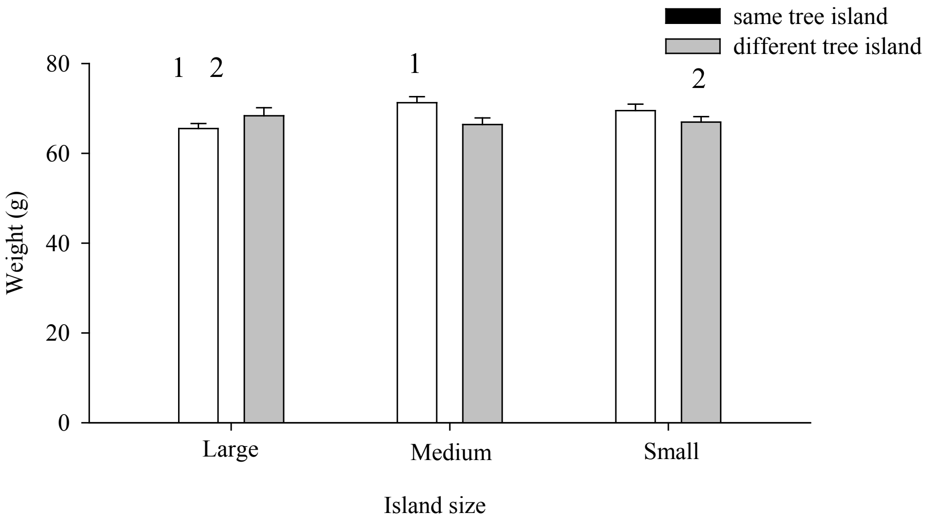


Figure 1.11. Comparison of *O. palustris* body weights for adult females recaptured either on the same tree island or on a different tree island. Body weights were recorded at the time of recapture, either on the same or on a different tree island. The weights of females recaptured on the same islands were grouped by the size class of the tree island where they were recaptured. The weights of females recaptured on a different tree island were grouped by size class of the island where an individual had been previously captured (*i,e.*; the island the female 'moved' from). The weights of adult females were tested for equal weights on islands for the three size classes. These comparisons were conducted separately for *O. palustris* recaptured on the same tree island and for *O. palustris* recaptured on a different tree island. The body weights of *O. palustris* adult females recaptured on the same tree island differed (X^2 = 13.528; *df* = 2; *P* = 0.001) among adult females recaptured on the same large (N = 110; $\bar{x}$ = 64.91 g ± 1.38 g), medium (N = 60; $\bar{x}$ = 71.27 g ± 1.33 g) and small (N = 77; $\bar{x}$ = 69.49 g ± 1.46 g) tree island. Adult *O. palustris* females recaptured on the same $^{\mathbf{1}}$ large tree island weighed more than adult females recaptured on the same medium (*t* = 3.706; *df* = 168; *P* < 0.001) or adult females recaptured on the same $^{\mathbf{2}}$ small tree island (*t* = 2.042; *df* = 185; *P* = 0.042). The difference in the body weights of adult females recaptured on the same medium or small tree islands approached significance (*t* = 1.693; *df* = 135; *P* = 0.092). The body weights of adult females recaptured on a different tree island, did not differ (X^2 = 0.44; *df* = 2; *P* = 0.82) among females that in their previous captured were found on large (N = 38; $\bar{x}$ = 68.37 g ± 1.78 g), medium (N = 41; $\bar{x}$ = 66.42 g ± 1.48 g) or small tree islands (N = 78; $\bar{x}$ = 66.95 g ± 1.31 g). The interval between recaptures was one or more months. Of the *S. hispidus* adult female individuals that were recaptured, 72 % (N = 43) were recaptured the following month.

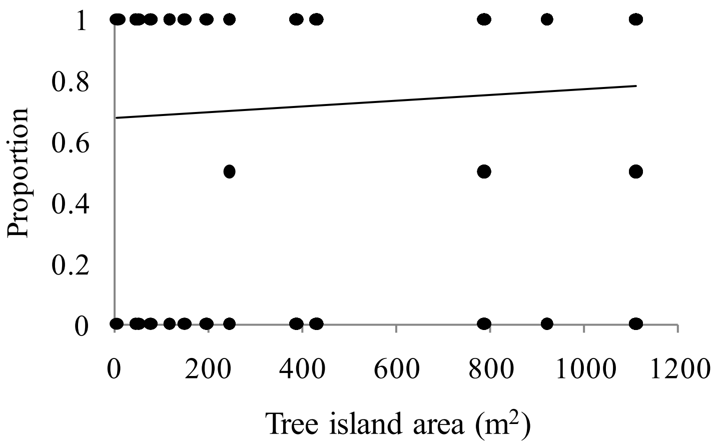


Figure 1.12. The monthly proportions of reproductively active *S. hispidus* females captured on each tree island were not correlated ($\rho = 0.057$, $P = 0.264$) to the area of the tree islands they were captured on.

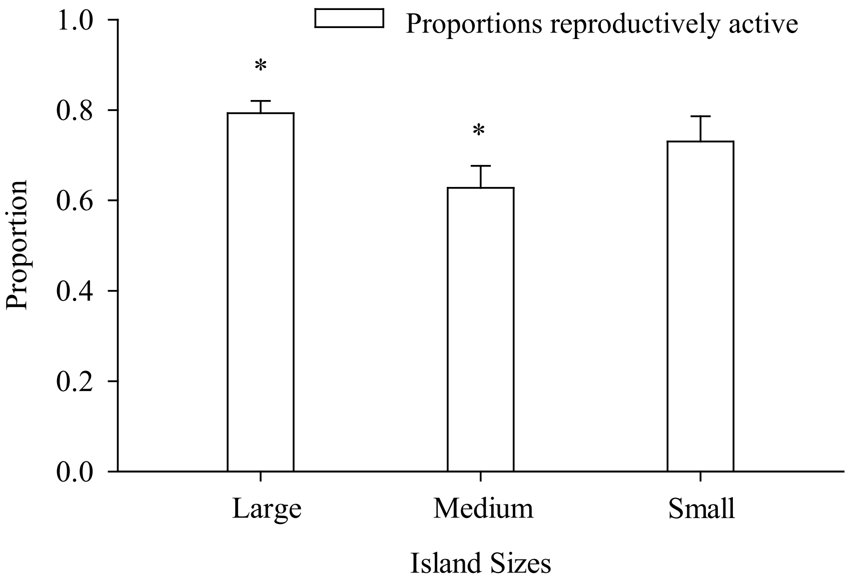


Figure 1.13. The proportion of reproductive active *S. hispidus* females within each tree island was calculated for each month that a female was captured on an island. Monthly proportions were grouped by island size and tested for equal proportions on islands for the three size classes. The monthly proportion of adult *S. hispidus* females that were reproductively active differed ($X^2 = 9.6$; $df = 2$; $P = 0.008$) among females captured on large (N = 227; $\bar{x} = 0.79 \pm 0.03$), medium (N = 98; $\bar{x} = 0.63 \pm 0.05$) and small (N = 63; $\bar{x} = 0.73 \pm 0.06$) size class tree islands. The proportions of females that were reproductively active on * large tree islands were greater ($t = 3.126$; $df = 159$; $P = 0.0019$) than on medium islands but did not differ between large and small tree islands ($t = 0.95$; $df = 323$; $P = 0.343$) or between females captured on medium and small tree islands ($t = 1.502$; $df = 288$; $P = 0.134$).

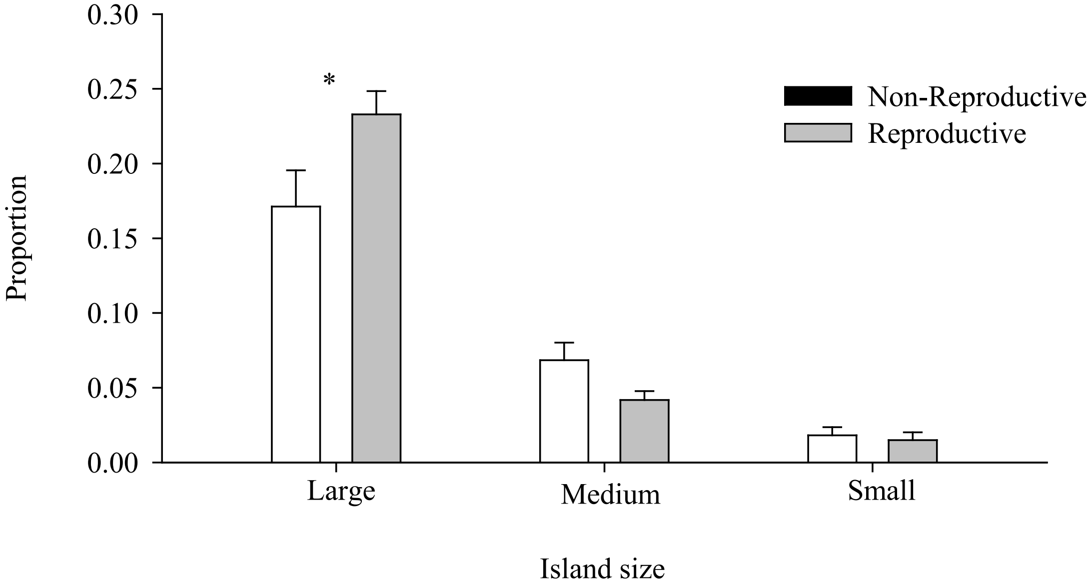


Figure 1.14. Comparisons of the proportions of reproductively active and non-reproductively active *S. hispidus* females among three island size classes. The monthly proportions of reproductively active and non-reproductively active females within each tree islands were quantified for each month that females were captured on an island. Tree island-specific monthly proportions of both reproductive states were grouped separately by island size class and tested for equal proportions of recaptures on islands for the three size classes. Greater proportions (t = 4.24; df = 529; P < 0.001) of the reproductively active *S. hispidus* female captures (N = 351; $\bar{x}$ = 0.23 ± 0.016) occurred on large islands than the proportions of non-reproductively active females ($\bar{x}$ = 0.17 ± 0.32) captures that occurred on large islands. The proportions of reproductively active and non-reproductively active females captures did not differ (t_{medium} = 0.346; df = 766; P = 0.73) (t_{small} = 1.307; df = 1,531; P = 0.192) within either medium ($N_{\text{reproductive}}$ = 468; $\bar{x}$ = 0.042 ± .006) ($\bar{x}_{\text{non-reproductive}}$ = 0.068 ± 0.20) and small ($N_{\text{non-reproductive}}$ = 480; $\bar{x}$ = 0.018 ± 0.006) ($\bar{x}_{\text{non-reproductive}}$ = 0.015 ± 0.08) tree islands.

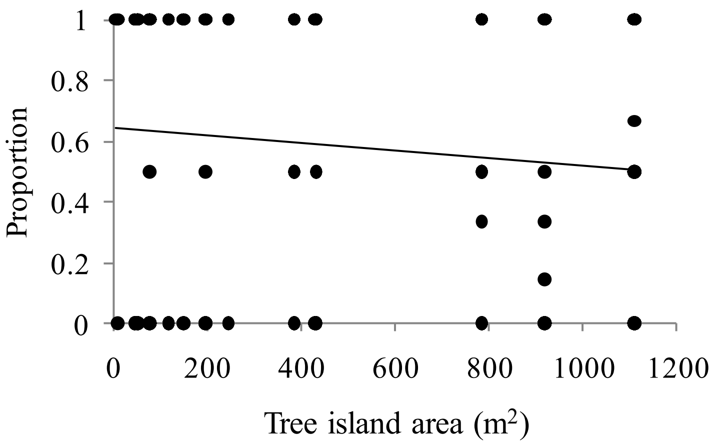


Figure 1.15. The monthly proportions of reproductively active *O. palustris* females captured on each tree island, were negatively correlated (ρ = - 0.134; P = 0.009) to the area of the tree islands they were captured on.

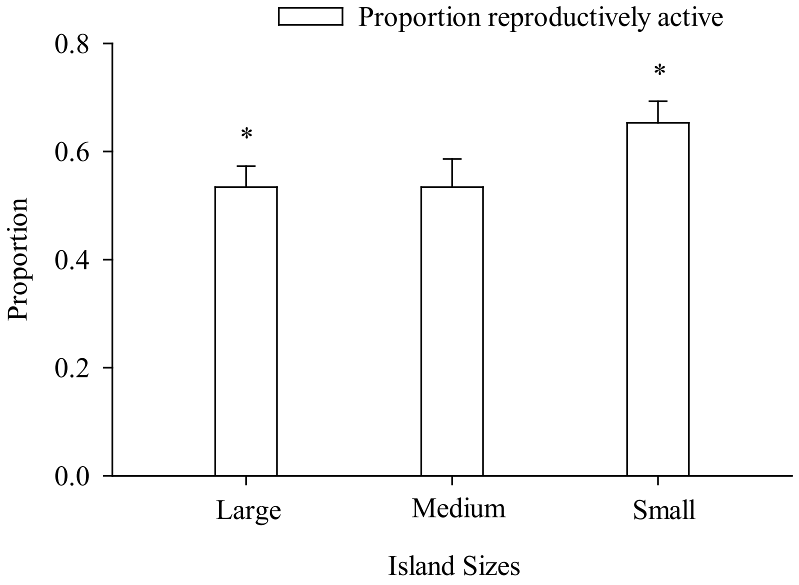


Figure 1.16. The proportion of reproductive active *O. palustris* females within each tree island was calculated for each month that a female was captured on an island. Monthly proportions were grouped by island size and tested for equal proportions on islands for the three size classes. The monthly proportions of reproductively active *O. palustris* females captured on each tree island approached a significant difference (X^2 = 5.92; df = 2; P = 0.052) among females captured on large (N = 141; $\bar{x}$ = 0.53 ± 0.039), medium (N = 89; $\bar{x}$ = 0.53 ± 0.052) and small (N = 144; $\bar{x}$ = 0.65 ± 0.04) tree island size classes. The proportions of *O. palustris* females that were reproductively active on * small tree islands were greater (t = 2.207; df = 283; P = 0.028) than on large islands, while the proportions of reproductively active *O. palustris* females did not differ between medium and large (t = 0.031; df = 228; P = 0.975) tree islands nor between females captured on small and medium (t = 1.908; df = 283; P = 0.057) tree islands.

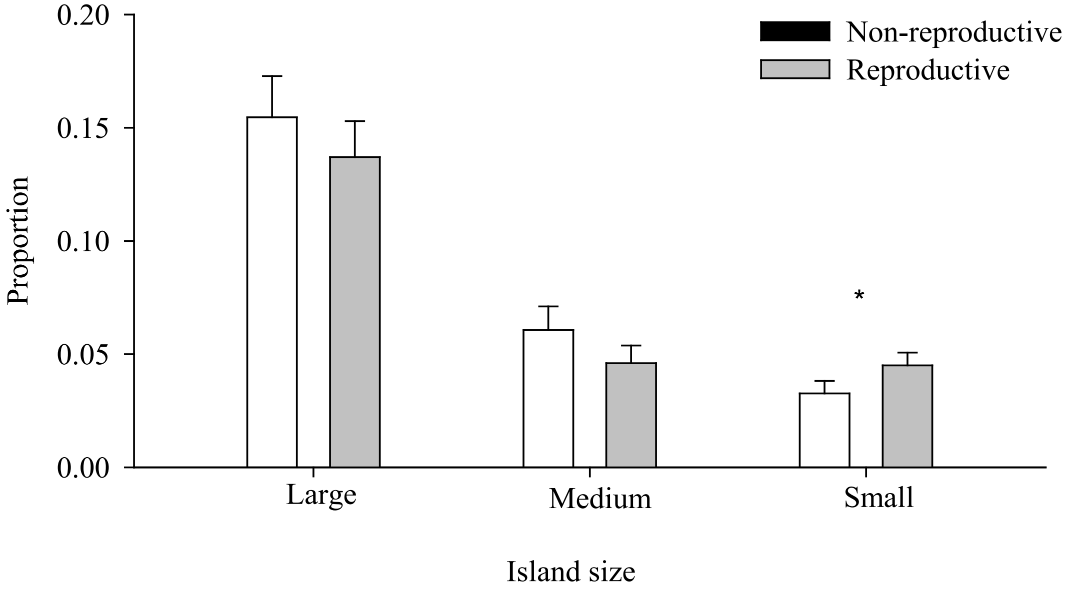


Figure 1.17. Comparisons of the proportions of reproductively active and non-reproductively active *O. palustris* females among three island size classes. The monthly proportions of reproductively active and non-reproductively active females within each tree islands were quantified for each month that females were captured on an island. Tree island-specific monthly proportions of both reproductive states were grouped separately by island size class and tested for equal proportions of recaptures on islands for the three size classes. Comparisons of the monthly proportions of where reproductively active and non-reproductively active adult *O. palustris* female captures occurred for each tree island size class. It was only on small size class tree islands that the proportions of reproductively active and non-reproductively active females differed. On small tree islands the proportions of reproductively active (N = 756; $\bar{x}$ = 0.033 ± 0.006) female captures were greater ($t = 3.572$; $df = 1{,}528$; $P < 0.001$) than the proportions of non-reproductive female (N = 774; $\bar{x}$ = 0.045 ± 0.006) captures that occurred on small islands. The proportions of reproductively active and non-reproductive *O. palustris* female captures did not differ for females captured on either medium ($N_{\text{reproductive}} = 344$; $\bar{x}$ = 0.046 ± 0.008) ($N_{\text{non-reproductive}} = 336$; $\bar{x}$ = 0.061 ± 0.010) ($t = 0.322$; $df = 678$; $P = 0.77$) or large tree islands ($N_{\text{reproductive}} = 258$; $\bar{x}$ = 0.137 ± 0.016) ($N_{\text{non-reproductive}} = 252$; $\bar{x}$ = 0.155 ± 0.018) ($t = 0.284$; $df = 508$; $P = 0.78$).

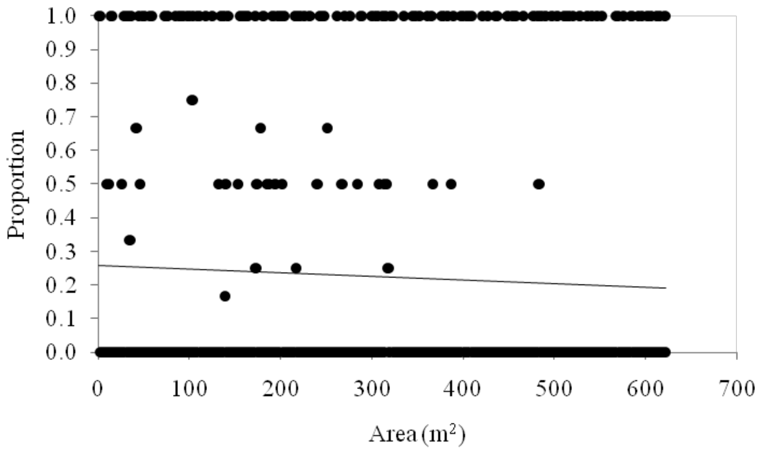


Figure 1.18. The monthly proportions of *S. hispidus* individuals captured within each tree island that were in the juvenile age class were not correlated (ρ = 0.07; P = 0.08) with tree island area.

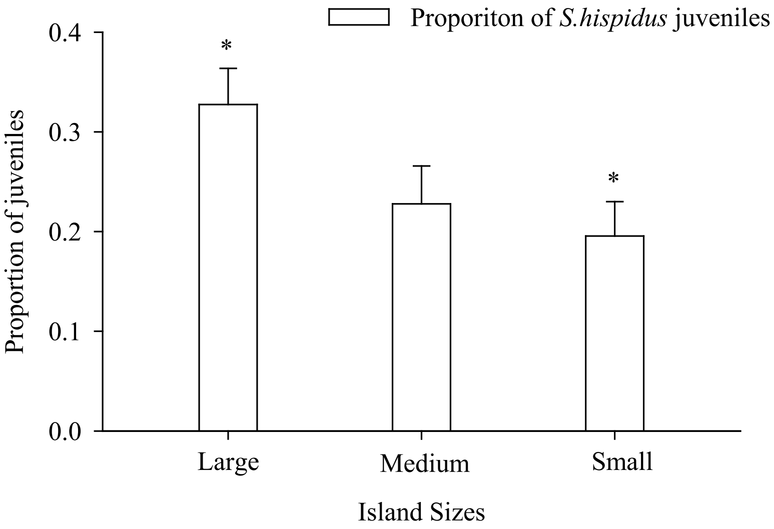


Figure 1.19. The monthly proportions of *S. hispidus* individuals captured within each tree island that were in the juvenile age class were grouped by island size class and tested for equal proportions of recaptures on islands for the three size classes. The proportions of juveniles in captures approached a significant difference (X^2 = 4.9; df = 2; P = 0.086) among *S. hispidus* captures on large (N = 320; $\bar{x}$ = 0.33 ± 0.036), medium (N = 169; $\bar{x}$ = 0.23 ± 0.038) and small (N = 133; $\bar{x}$ = 0.2 ± 0.035) tree islands, so we proceeded with pair-wise comparisons of the proportions of juvenile captures between tree island size classes. * A greater proportion (t = 1.96; df = 451; P = 0.05) of individuals captured on large tree islands were in the juvenile age class than on small tree islands, but did not differ (t = 1.61; df = 487; P = 0.108) from the proportion of juveniles captured on medium islands. The proportions of juveniles also did not differ (t = 0.42; df = 300; P = 0.672) for individuals captured on medium and small tree islands.

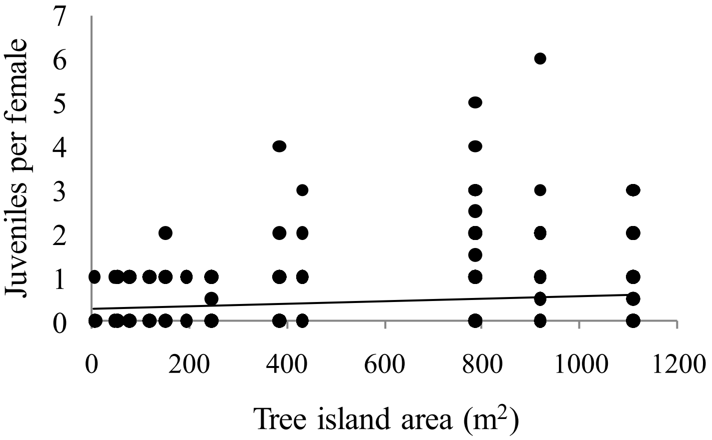


Figure 1.20. The numbers of *S. hispidus* juveniles per adult and subadult female were positively correlated with tree island size ($\rho = 0.096$, $P = 0.038$).

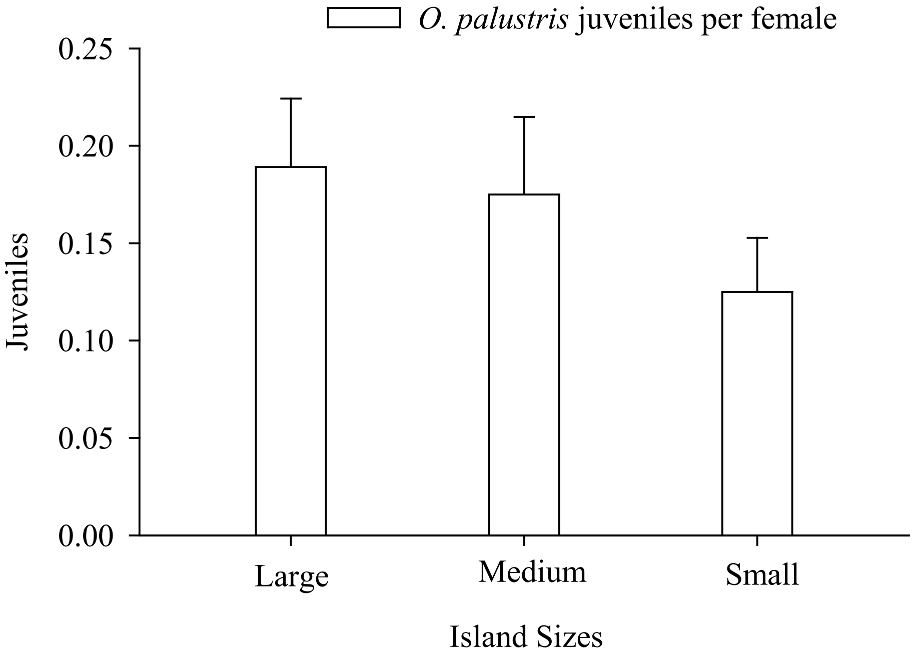


Figure 1.21. The numbers of *S. hispidus* juveniles per adult and subadult female did not differ ($X^2 = 4.243$; $df = 2$; $P = 0.12$) among large (N = 255; $\bar{x} = 0.56 \pm 0.06$), medium (N = 123; $\bar{x} = 0.35 \pm 0.058$) or small (N = 89; $\bar{x} = 0.3 \pm 0.06$) tree islands.

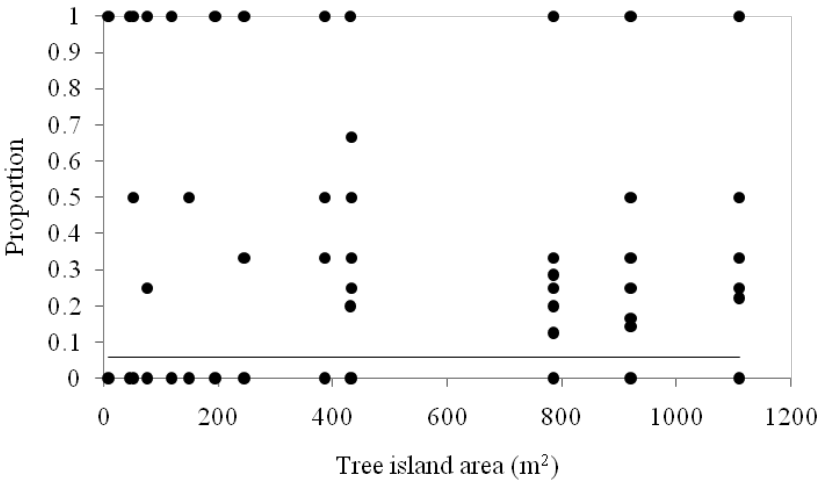


Figure 1.22. The monthly proportions of *O. palustris* individuals captured within each tree island that were in the juvenile age class were not correlated ($\rho = 0.068$, $P = 0.065$) with the area of the tree island where individuals were captured.

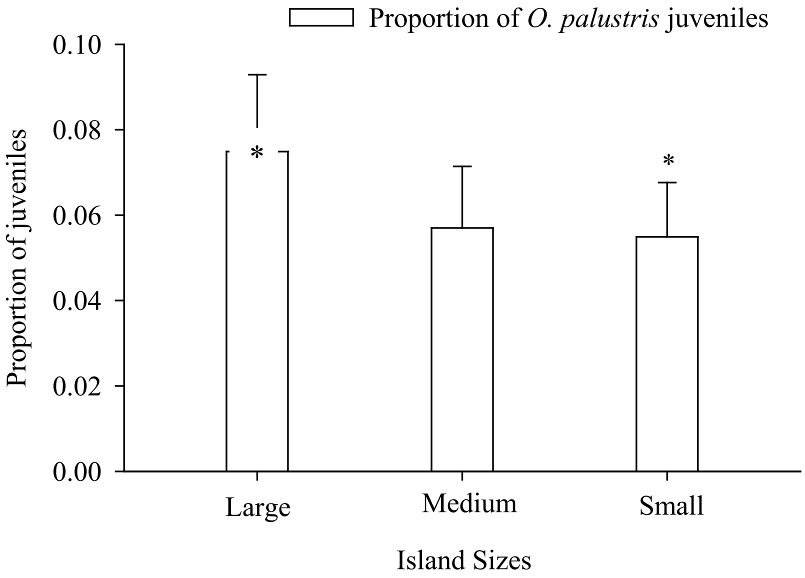


Figure 1.23. The monthly proportions of *O. palustris* individuals captured within each tree island that were in the juvenile age class were grouped by island size class and tested for equal proportions of recaptures on islands for the three size classes. The proportions of individuals in the juvenile age class differed ($X^2 = 6.085$; $df = 2$; $P = 0.048$) among large ($N = 236$; $\bar{x} = 0.075 \pm 0.018$), medium ($N = 201$; $\bar{x} = 0.057 \pm 0.014$) and small ($N = 296$; $\bar{x} = 0.055 \pm 0.013$) size class tree islands. Greater ($t = 2.467$; $df = 530$; $P = 0.014$) proportions of *O. palustris* captured on small tree islands were in the juvenile age class than those captured on large tree islands, while the proportions of juveniles captures did not differ between small and medium ($t = 1.402$; $df = 495$; $P = 0.162$) nor between medium and large tree islands ($t = 0.885$; $df = 435$; $P = 0.377$).

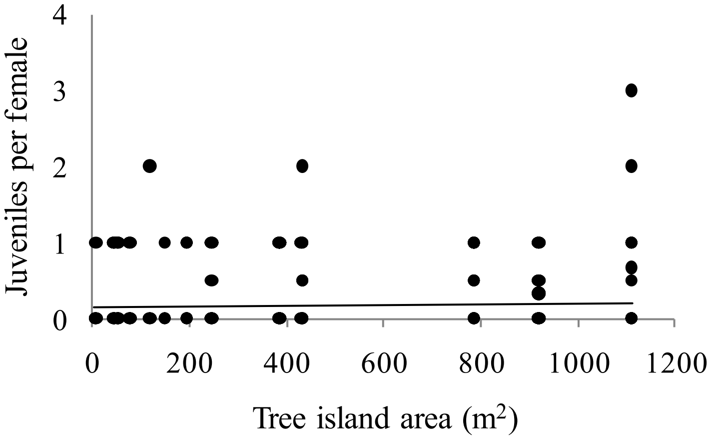


Figure 1.24. The numbers of *O. palustris* juveniles per adult and subadult female captured within each tree island were not correlated with the area of the tree island ($\rho = 0.055$, $P = 0.265$) where they were captured.

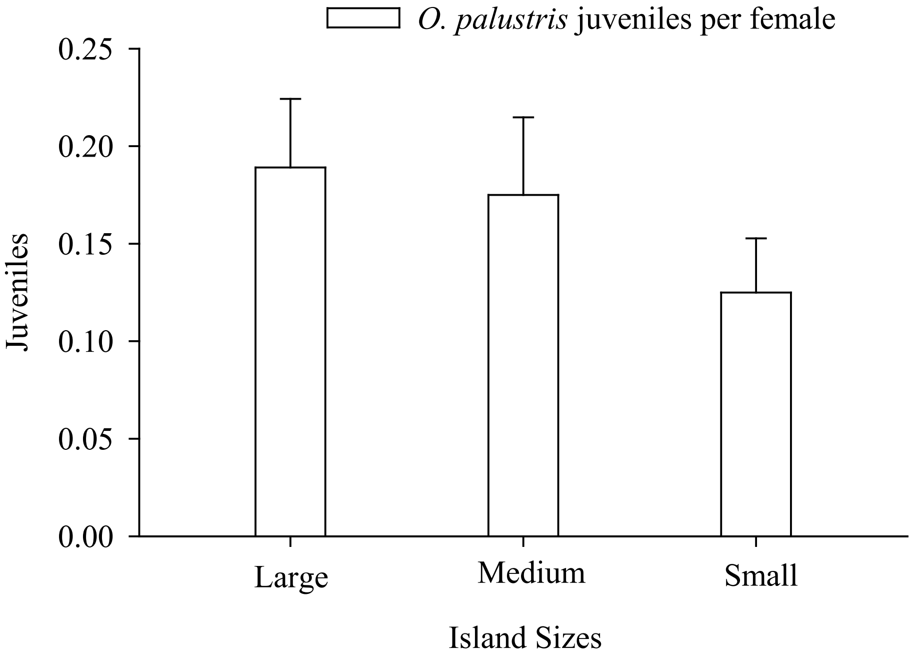


Figure 1.25. The numbers of *O. palustris* juveniles per adult and subadult female captured within each tree island did not differ ($X^2 = 4.373$; $df = 2$; $P = 0.112$) among large (N = 156; $\bar{x} = 0.19 \pm 0.035$), medium (N = 100; $\bar{x} = 0.18 \pm 0.04$), and small (N = 160; $\bar{x} = 0.13 \pm 0.028$) tree islands.

Tree Island Size Classes

Tree island areas (m^2)		
Large	Medium	Small
1,110	432	194
920	431	149
785	386	118
	245	76
		52
		51
		45
		8
		4
$\bar{x}$ = 938 m^2 ± 94 m^2	$\bar{x}$ = 374 m^2 ± 44 m^2	$\bar{x}$ = 77 m^2 ± 21 m^2

Table 1.1. Sixteen study tree islands were classified into large, medium and small island size classes. Cluster analysis (k-means) of tree island areas was used to assign tree islands into size classes with significantly different mean areas (ANOVA, $F = 100$; $df = 13$; $P < 0.001$): three large, four medium and nine small islands.

CHAPTER TWO

THE INFLUENCE OF TREE ISLAND SIZE AND HYDROPERIODS ON SURVIVAL AND TRANSITION PROBABILITIES OF *Sigmodon hispidus* AND *Oryzomys palustris* ON THREE SIZE CLASSES OF TREE ISLANDS OF THE EVERGLADES

BACKGROUND

The distribution and abundance of animal populations are often considered to be primarily determined by the availability and distribution of habitat and resources (Van Horne 1983). For populations in conspicuously patchy habitats (e.g., tree fall gaps in rain forests Beck 2008), resources are distributed in discrete patches that are distinct from the surrounding habitat. In island systems, resources are also distributed in discrete patches of habitat; in islands, however, habitat is primarily fixed in size and location, relative to the time scale of most ecological processes. Because resources vital for animals, such as cover and vegetation, can vary with the physical properties of islands such as area, islands differ in their relative resource value to the animals that use and occupy them. Loss of islands results in permanent loss and altered distribution of habitat. The loss or degradation of islands with greater resource value to animals is likely to have a disproportionately greater effect on animal populations. Understanding the relationship between island habitat and animal populations is of special interest in ecosystems where islands are being degraded and lost, such as in the Everglades.

The Everglades, a wetland ecosystem unique to southern Florida, is characterized by broad expanses of sawgrass (*Cladium jamaicense*) wet prairie with thousands of tree islands interspersed throughout the landscape. These tree islands form on topographic elevations in the Everglades limestone bedrock (van der Valk and Sklar, 2002) and provide much of the permanently dry habitat available to terrestrial species in the seasonally flooded Everglades. Nearly half of the Everglades has been permanently lost to urban and agricultural development. The remaining portion of the Everglades has been degraded by alterations to Florida's hydrology. The inundation of the Everglades during southern Florida's wet season is a fundamental characteristic of the Everglades ecosystem. The duration of these inundation periods, referred to as hydroperiods, have increased in some areas, affecting the plant communities by inhibiting seed germination (Sklar and van der Valk 2002), while in other areas the reduction or the absence of hydroperiods has allowed woody species to encroach into marshes and sloughs (Olmstead *et al.* 1980, Sklar and van der Valk 2002), especially by invasive exotic species. Alterations in the flows of water to the Everglades and in its hydroperiods have also affected the processes associated with the maintenance of sloughs, ridges and tree islands, leading to an overall decrease in the number and size of tree islands and increased distances between islands (Hofmackel 1999, Patterson and Fink 1999, Wetzel *et al.* 2005).

Despite their significance as "keystone habitats" described as both "nutrient" and biodiversity "hotspots" (Orem *et al.* 2002; Jayachandran *et al.* 2004), there have been few studies of fauna on tree islands. Our understanding of how changes to Everglades tree islands will affect fauna is at best sketchy (Sklar and van der Valk 2002). The loss of tree islands in the Everglades will continue into the foreseeable future and may increase due to rising sea levels (Michener *et al.* 1997). To understand how the loss of tree islands affects Everglades fauna, we first need prior knowledge about the species that use and occupy tree islands. Of greater research priority are studies of species or taxa whose changes in numbers and distribution in Everglades tree islands are most likely to have broader ecosystem-level effects. I believe that Everglades rodents are such an example. Although rodents are thought to be the most widely distributed mammals throughout the Everglades, and likely to have one of highest, if not the highest, terrestrial vertebrate biomass in the Everglades, little is known about the ecology of rodents in the Everglades. To the best of my knowledge there are no reference historical data on rodents available for comparison and, to date, only two peer reviewed studies on Everglades small mammals on tree islands have been published (Smith and Vrieze 1979 and Smith 1980).

The ecological role of rodents in the Everglades ecosystem is non-trivial. Rodents, with their characteristically high biomass turnover rates, are a significant source of food for predators even when present at low densities (Golley *et al.* 1975). As prey, herbivorous and omnivorous small mammals also link primary production and secondary consumers (Hayward and Phillipson, 1979). In addition, rodents provide non-redundant ecological services as predators of both seeds and animals. A greater understanding of rodent ecology in the Everglades is relevant to our understanding of one of the Everglades most abundant animals and to our understanding of how changes in tree islands and hydrology may affect this taxon.

Quantifying habitat-specific survival is critical for understanding population dynamics and variation in fitness (Van Horne 1983), especially in degraded ecosystems (Breininger *et al.* 2009) where habitat alterations are often accompanied by decreases in animal fitness. For populations in patchy habitats, such as rodents in the Everglades tree islands, demographic rates may differ with the physical properties of patches, or in this case, tree islands. For these animals, population fitness may be the product of the combined influence of patch-specific demographic rates. If patch-specific demographic rates differ sufficiently among patches, the relative availability and use of those patches that positively influence demographic success become of greater conservation value. Patch-specific use and demographic rates are especially relevant to the study of rodents on Everglades tree islands because of the tree islands that were lost, a disproportionately greater proportion of these islands were larger tree islands (Wetzel *et al.* 2005), which may offer more favorable conditions to rodents than smaller islands.

In Chapter One, I examined the relationship between tree island size and traits associated with fitness and reproduction for the hispid cotton rat (*Sigmodon hispidus*) and the marsh rice rat (*Oryzomys palustris*) adult females captured on 16 tree islands of Rock Reef Pass, Everglades National Park, FL. The comparisons of adult females body weights which have been shown to be a fitness component in rodents (e.g., Krackow 1992), suggested that *S. hispidus* females on larger islands have higher fitness than *S. hispidus* females on smaller islands. For *O. palustris*, differences in adult female weights, and therefore the expected differences in fitness, were not as pronounce among *O. palustris* females captured on different size islands. Differences in adult female body weights and the presumed differences in fitness, should also be reflected in the demographic rates of individuals across different tree islands. In the work presented here I used the same 119 months of rodent capture histories used in Chapter One's analysis of adult *S. hispidus* and *O. palustris* females fitness and reproduction, to perform multi-state mark-recapture multi-state analyses, where states were defined as three tree island size classes. Multi-state models are a generalization of the Cormack-Jolly-Seber (CJS) live captures model that allows individuals in the population to be distributed across multiple sites or among multiple phenotypic states and to stochastically transition between states or sites. However, the multi-state models differ from the CJS, in that homogeneity of all marked individuals in the population does not have to be assumed and variation among animals in different states is permitted. However, homogeneity is still assumed within each state (Williams *et al*. 2002). This approach allows for the estimation of sampling rates (capture probabilities) and population changes (survival and transition probabilities) (Williams *et al*. 2002) as state-specific rates. A state-specific framework is especially relevant to tree islands because islands can be characterized as distinct features. Animals make unambiguous transitions between these states. I used state- transition probabilities to describe *S. hispidus* and *O. palustris* habitat use in tree islands of the Everglades, as a probability of individuals remaining in a given island class. The necessary assumption of this measure of 'habitat use' is that animals are more likely to remain in a habitat that provides favorable conditions and more likely to move when conditions on that habitat are less favorable. I contended this assumption is generally reasonable and that the description of the relative probabilities of *O. palustris* and *S. hispidus* remaining or transitioning between island size classes are a valid, but broad description, of their use of different size tree islands.

The use of multi-state analyses of mark-recapture data made it possible to model the survival, transition and recapture probabilities as a function of island strata, sex and environment covariates and to simultaneously quantify not only state-specific survival probabilities and transition probabilities between states, but also to simultaneously address separate hypotheses about state specificity of survival and conditional transition probabilities (Nichols *et al*. 1994, Nichols and Kendall 1995). This approach is more likely to realistically model the combined influence of environmental variables on animal demography. Another advantage of the multi-state approach is that time- and state-specific survival and capture probabilities can be directly estimated without *a priori* knowledge of the form of the relationship between the estimated population rates and each of the states (Williams *et al.* 2002). The reduced reliance on *a priori* knowledge is advantageous, especially in our case, since little prior information is available on Everglades rodents.

The estimation of state specific, or as in our case, tree island size class-specific survival and transition probabilities, allows us to address the questions about island size motivating this work: Are there differences in survival, or movement rates among the three island size classes? Further, might any differences that are apparent be associated with seasonal hydroperiods?

In addition to constructing island size class-specific models that address questions about tree island size-specific survival rates, I also constructed models where survival and transition probabilities are estimated as a function of hydroperiod covariates. These time-specific hydroperiod covariates included periods in which standing water was present or absent at the study site, calendar-defined wet and dry seasonal periods, mean monthly water levels from the nearest gauging station, and the accumulated days that the study site was either continuously dry or inundated. In addition to these hydroperiod covariates, I also included the additional environmental variables of mean monthly air temperature, and total monthly rainfall. Sex is included as a covariate to examine differences in males and females by grouping individuals by gender. The inclusion of hydrology covariates allowed us to address questions related to hydroperiods. Are there differences in survival, movement rate or recapture rate between wet and dry hydroperiods? Further, might any differences that are apparent be associated with water-levels or duration of wet and dry periods?

METHODS

STUDY AREA

The Rocky Glades, a karstic wetland habitat unique to the Everglades National Park, is characterized by a highly irregular surface of Miami limestone outcroppings and solution holes. The Rocky Glades is primarily a seasonally flooded, short hydroperiod marl prairie with thousands of tree islands, typically ranging in size between 0.1 and 3 ha (Loope and Urban 1980). These islands occur on limestone outcrops raised up to 1 m above the surrounding marsh (Armentano *et al*. 2002) with vegetation classified as tropical hardwood hammock dominated by Gumbo-limbo (*Bursera simaruba*), willow bustic (*Sideroxylon salicifolium*), strangler fig (*Ficus aurea*), pigeon plum (*Coccoloba diversifolia*) and poisonwood (*Metopium toxiferum*). Southern Florida's climate is characterized by pronounced wet and dry seasons, where on average 60% of annual rainfall occurs during the wet season, from June to September, and 25% of rainfall occurs during the six month dry season, from November to April (Duever *et al.* 1994). The Everglades landscape differs dramatically between the wet and dry seasons. During the wet season the Everglades sawgrass prairies are inundated, and tree islands provide most of the above water terrain. During the dry season sawgrass prairies are dry with standing fresh water found primarily in limestone solution holes and alligator ponds. The climate in southern Florida is classified differently according to different systems. In the Köppen classification system, it is classified as *Tropical Savannah* (Lodge 2004); it is most often, however, referred to as semitropical or subtropical. Regardless of how the climate is classified, with a mean monthly temperature of 23.6 C^0 and with few days below freezing, tropical vegetation is abundant. Geographic Information Systems software (ArcView 3.0, Redlands, CA, USA) was used to measure the areas of 16 selected tree islands at Rock Reef Pass, an area of the Rocky Glades, from aerial photographs (Figure 1.1). The areas of the 16 tree islands ranged in size from 4.2 m^2 to 1,110 m^2 (Table 2.1). At Rock Reef Pass, greater numbers of *O. palustris* (Figure 2.2) were captured during the wet season months while greater numbers of *S. hispidus* (Figure 2.3) were captured during wet season months.

RODENT SPECIES

Although relatively few tree islands have been sampled for small mammals, it is generally expected that small mammals are found on most tree islands throughout the Everglades. Our trapping experience at Rock Reef Pass and elsewhere in the Everglades (unpublished) leads us to believe that *S. hispidus* and *O. palustris* are likely to be the most commonly found rodents on tree islands of the Everglades. *S. hispidus* is generally found in grass-dominated habitats from southern North America to northern South America. It feeds primarily on grasses but it may eat insects seasonally (Cameron and Spencer 1981). Although *S. hispidus* is capable of swimming, its fur is less water repellent than *O. palustris* and it quickly becomes waterlogged (Esher *et al.* 1978). *O. palustris* is a semi-aquatic species found in freshwater marshes, swamps and wetlands throughout the southeastern U.S. *O. palustris* is predominantly carnivorous, feeding on insects and crustaceans (Wolfe 1982). In the Everglades, *O. palustris* forage for aquatic macroinvertebrates in the mashes surrounding tree islands. During the dry seasons, *O. palustris* are known to find and use wet refugia. *S. hispidus* is a common associate of *O. palustris* and previous studies have not found a competitive relationship between these two species in the Everglades or elsewhere (Birkenholz 1963, Harris 1953, Joule and Jameson 1972). Seasonal changes in water levels in the Everglades have been shown to influence the relative abundance of both species (Gaines *et al*. 2003, Birkenholz 1963). While *O. palustris* abundance is greater during the wet season months, *S. hispidus* abundance is greater during the dry months.

TRAPPING

Between February 1994 and August 1994, trapping was conducted for two consecutive nights approximately every two weeks ($\bar{x}$ = 13 days) on a total of 13 trapping sessions. After August 1994, trapping was conducted for three consecutive nights. These two and three consecutive days of trapping are hereafter referred to as trapping sessions. Between August 1994 and June 2003 trapping was conducted on a total of 107 trapping sessions approximately every four weeks ($\bar{x}$ = 28 days) with the exception of a 165 day interruption due to hurricane damage starting in March of 1998. From June 2003 to December 2005 trapping was conducted more sporadically on a total of 13 trapping sessions with an interruption in trapping of 203 days starting in November 2004. The periods between trapping sessions are hereafter referred to as trapping intervals.

Animals were trapped at Rock Reef Pass on a total of 75,656 trapnights [Trapnights are the total numbers of ‘nights’ traps were open and available to capture animals: (13 (trapping sessions) x 2 (consecutive trapnights) + 120 (trapping sessions) x 3 (consecutive trapnights)) x 196 (traps) = 75,656 trapnights] using 7.6 x 8.9 x 22.9 cm aluminum Sherman live traps (H.B. Sherman, Tallahassee, FL) sheltered by a plywood cover board and baited with rolled oats. Traps were laid out in an evenly spaced grid with a single trap every 15 m. Trapping grids encompassed the area of each tree island and extended onto the surrounding marsh by a maximum of 15 m. A total of 196 traps were used across 16 islands; 92 traps were placed on large islands (47%), 64 on medium island (33%) and 40 traps (20%) on small islands. At capture animals were identified to species, sexed, weighed to the nearest gram with a Pesola spring scale (www.pesola-scales.com, Ontario, Canada), checked for reproductive condition. New animals were ear-tagged with a uniquely numbered fingerling tag and released at the site of capture. The trap and island where animals were captured were also recorded.

DATA

Tree Island Size States

Limitations in computing power required that I reduce the number of model parameters. We chose to retain the mark-recapture data from 120 trapping periods, while limiting model states to three island size classes, or strata; large, medium and small. Cluster analysis (k-means) of tree island areas was used to assign tree islands into three size classes with significantly different mean areas (ANOVA, $F = 100$; $df = 13$; $P < 0.001$) (Table 2.1): ($\bar{x}$ = mean ± standard error, range) three large ($\bar{x}$ = 938 m^2 ± 163 m^2; 1,110 m^2 – 785m^2); four medium ($\bar{x}$ = 374 m^2 ± 44 m^2; 432 m^2 - 245 m^2), and nine small islands ($\bar{x}$ = 77 m^2 ± 64 m^2; 194 m^2 – 4 m^2).

CAPTURE HISTORIES

Capture histories for adult males and females were constructed using the first 120 months of trapping data, because after June of 2003 the hydrology data were incomplete and trapping was interrupted. Body mass was used to classify *S. hispidus* (> 95 g) (Cameron and Kruchek 2005) and *O. palustris* (> 50 g) (Wolfe 1985) as adults. Because multi-state models have an open-population structure, secondary period (two or three consecutive days) captures were summarized as a single capture per primary period (~monthly). Since animals could be captured on more than one island size class during a single primary period, we assigned size state (island size, Large, Medium or Small) for each primary period to the majority size class (two out three captures) or randomly in cases of two captures in two different tree island size classes.

ANALYSIS METHODS

General Modeling Approach

The goal of capture-recapture modeling is to develop probability models for the biological and sampling processes giving rise to animal capture histories. Capture histories are modeled as a function of parameters associated with both sampling (capture probabilities) and population changes (survival and transition probabilities) (Williams *et al*. 2002). Using a likelihood framework, demographic and sampling parameters of each model are then estimated as a function of covariates (e.g., island size and water level) hypothesized to influence demographic rates (Burnham and Anderson 2002). Each of these models represents a competing ecological hypothesis that is then ranked using an information-theoretic approach that optimizes the tradeoff between model fit, which favors more parameters, and estimator variance, which favors fewer parameters (Williams *et al.* 2002). This approach is based on Akaike's information criterion (AIC) (Akaike 1973), which uses the likelihood for each model ($-2 \ln (L)$) and a penalty term for the number of parameters in the model ($\text{AIC} = -2 \ln (L) + 2q$) where L is the likelihood for a model under consideration and q is the number of parameters in the model. The goal of this approach is to select a model with the fewest parameters necessary to fit the data. The model with lowest AIC value (Burnham and Anderson 1992, 1998) is the model in the candidate set that best represents this tradeoff. Model estimation is based on the number of animals exhibiting each of the observed capture histories. The models in the candidate set with the most support from the data are used to estimate the real parameters (survival and transition probabilities) (Williams *et al.* 2002).

We used multi-state mark-recapture models in program MARK (Version 6.0; White and Burham 1999) to estimate survival rates and transition probabilities of *S. hispidus* and *O. palustris* stratified by island size class and to test hypotheses about tree island use and the influence of hydroperiod variables. Multi-state models employ an extension of the Arnason-Schwarz model (Arnason 1972, 1973, Brownie *et al*. 1993, Schwarz *et al*. 1993), in which state transitions are modeled as Markov transitions; that is, assuming that state transitions from one sampling occasion to the next represent a first-order Markov process in that the probability of making a transition between occasions i and $i + 1$ depends only on the state at time i. The basic parameters for this model are as follows:

S_i^r = the probability that an animal alive in state r at sampling period i survives and remains in the study population (does not permanently emigrate from the study location; *i.e.,* the 16 study islands) until time $i + 1$.

p_i^s = the probability that a marked animal alive in state s at time i is recaptured on that sampling occasion.

$\boldsymbol{\psi_i^{rs}}$ = the probability that an animal is in state s at sampling period $i + 1$, given that the animal was in state r at period i and that it survived until $i + 1$ and remained in the study population. These transitions are assumed to reflect only first-order Markovian processes. Transition probabilities sum to $\sum \psi_i^{rs} = 1$.

Model strata

Model parameters (S_i^r, p_i^s, ψ_i^{rs}) could be stratified by modeling strata separately or by combining strata. For example, parameters could be estimated separately for each tree island size class stratum or collapsed into a single parameter for all three island strata. The strata used were sex (male and female), and island size (Large (L), Medium (M) and Small (S)). Stratification allowed S_i^r, p_i^s, ψ_i^{rs} to be estimated separately for each of the strata.

Hydroperiods and Environmental variables

Daily average water levels, total rainfall, and average air temperature data for the nearest National Park Service gauging stations (Royal Palm Ranger Station) were made available to us by the Everglades National Park, Homestead, FL. Mean water level, accumulated rainfall, and mean air temperature were calculated for each trapping interval starting with the first day of one trapping session and extending to the day before the beginning of the next trapping session. We defined hydroperiods by the presence or absence of standing water at the study site. Once the study site was inundated it tended to remain in the same state until the beginning of the dry season. The durations of wet and dry periods were calculated as the accumulated number of days that the study area was continuously wet or dry. Although the periods when the study site was either dry or inundated (“wet”), generally coincided with the wet and dry seasons, on 31 of the 120 months of data included in this work, water levels at the study site were not consistent with the expected conditions for that month's season. We defined hydroperiods using both the wet and dry conditions at the study site, as well as the calendar periods for the wet (May to October) and dry (November to April) seasons. We allowed model fit to inform us whether *O. palustris* and *S. hispidus* $\hat{S}_i^{\,r}$, $\hat{p}_i^{\,s}$, $\hat{\psi}_i^{\,rs}$ rates differed as a function of hydroperiods and, if so, which of the two hydroperiod definition most likely influenced $\hat{S}_i^{\,r}$, $\hat{p}_i^{\,s}$, $\hat{\psi}_i^{\,rs}$ rates.

Models with hydroperiod-specific S_i^r, p_i^s, ψ_i^{rs} rates were constructed using a binary code ("1" or "0") to differentiate hydroperiods. The specific coding for hydroperiods differed with the model structure. Models with sex-specific rates were similarly constructed using binary coding to differentiate males ("1") from females ("0").

Model covariates

Candidate models were constructed by varying S_i^r, p_i^s, ψ_i^{rs} stratification and by constraining the estimates of S_i^r, p_i^s, ψ_i^{rs} as a function of different covariates or as fixed rates. The following covariates were used to construct the set of candidate models for each species.

Island strata

s_i = Indicates island strata (L, M and S) specific rates.

Environmental and hydrology covariates:

$\mathbf{WL}_i$ = (Water level) The mean daily water level for the interval between two trapping sessions.

WL$_{Pi}$ = (Water level for p_i^s) Mean water level during secondary periods within primary peiod *i*. Because capture probabilities are conditional only on secondary periods, covariates must be time specific to secondary periods.

Rain$_i$ = (Rainfall) Total rainfall during the interval between two trapping sessions.

Rain$_{pi}$ = (Rainfall for p_i^s) Total rainfall during secondary trapping periods within primary period *i*.

DaysDry$_i$ = (Days dry) The number of prior days that the study site was continuously dry up to the day of sampling.

DaysWet$_i$ = (Days wet) The number of prior days that the study site was continuously wet up to the day of sampling.

Temp$_i$ = (Air temperature) The mean daily air temperature for the interval period between two trapping sessions.

Binary covariates:

Wet$_i$**/Dry**$_i$ = Periods when the study site was either dry or inundated (Wet).

Season$_i$ = Wet (May to October) and dry (November to April) season months.

Sex$_i$ = Sex-specific rates were coded by differentiating male rates.

The relationship between covariates and model parameters can also be modeled with an interaction term “*”, meaning that each time- or stratum-specific parameter was modeled as a function of the unique combination the time- or stratum-specific parameter and the covariate. Alternatively, the relationship between parameters and covariates could be modeled as additive “+”, meaning that a parameter was modeled with a covariate that had a constant or fixed effect across the levels of other covariates.

Temporal variation

Model parameters were estimated as time-specific rates when estimated as a function of covariates with ~monthly values (water levels, rain, air temperature), and/or, as season-specific rates, when estimated as a function of seasonal covariates (*seasons*, wet/dry, DaysDry, DaysWet). We did not model S_i^r, p_i^s, ψ_i^{rs} as independent functions of time, because each time-specific rate for each stratum would have added a unique model parameter (119^{48} parameters for full time-dependent model) which would have exceeded the capacity of most personal computers currently available.

Transition probabilities

Inferences about habitat use were based on modeling the transition parameters (ψ_i^{rs}) for large (L), medium (M) and small (S) strata. Because transition probabilities for each state must sum to one ($1 = \hat{\psi}_i^{LS} + \hat{\psi}_i^{LM} + \hat{\psi}_i^{LL}$, $1 = \hat{\psi}_i^{ML} + \hat{\psi}_i^{MS} + \hat{\psi}_i^{MM}$, $1 = \hat{\psi}_i^{SL} + \hat{\psi}_i^{SM} + \hat{\psi}_i^{SS}$), $1 = \sum_{s=1}^{3} \psi_i^{rs}$ the probabilities of individuals remaining within the same state can also be estimated. We report the probability of individuals remaining within the same strata as a simple rate calculated by subtraction. This naïve estimation is suitable for drawing general inferences.

Two-age class survival model

Thirty-three percent (N = 334) of *O. palustris* and 47% (N = 229) of *S. hispidus* were captured once and not seen again. By having been captured on a single occasion, these individuals have an encounter probability of zero and will appear to have 'died'. The presence of individuals captured once and not seen again violates the CJS model assumption that all individuals have the same probability of subsequent encounter and negatively bias survival rate estimates. Following the approach of Brownie and Robson (1983) and Pradel *et al*. (1997), we used a time since marked approach to estimate separate survival rates for individuals in two age-classes. Survival probabilities were estimated for the first interval ($\hat{S}_1$) of every cohort (first age class), which was composed of individuals captured during the first trapping occasion that are not seen again and those individuals that were later recaptured. Survival probabilities were also estimated for all subsequent intervals ($\hat{S}_2$ - $\hat{S}_{119}$) of every cohort (second age class) which was composed solely of individuals that were recaptured after the first primary period. Survival models with two age classes are labeled as "M2," with the parameterization of the first and second age classes separated by a forward slash (*S*(M2 [first age class parameters] / [second age class parameters]).

How ecological covariates influence survival and transition probabilities

We used program MARK to compute S_i^r, p_i^s, ψ_i^{rs} parameter rates as maximum-likelihood estimates of probabilities and to estimate the parameters ($\hat{\beta}$) associated with relationships between S_i^r, p_i^s, ψ_i^{rs} and covariates (White and Burnham 1999). Program MARK uses a general linear model approach, in which parameter rates are estimated as linear constraints of independent covariates. The relationship between $\hat{S}_i^r$, $\hat{p}_i^s$, $\hat{\psi}_i^{rs}$ estimates and model covariates are expressed by the $\hat{\beta}$ coefficient, which indicates whether an independent variable had an effect on a parameter ($|\hat{\beta}| > 0$) or not ($\hat{\beta} = 0$) and whether the effect was positive (+ $\hat{\beta} > 0$) or negative (- $\hat{\beta} < 0$). We interpret the sign ("- "or"+") of $\hat{\beta}$ coefficients as indicating whether states (islands size classes), sex (males), and ecological variables have either a positive or negative effect on survival, capture and transition probabilities. Although the magnitude of the $\hat{\beta}$ coefficients depends on how models are structured and can vary from model to model, we included their numerical values as a reference of the relative strength of a covariate within a model.

To help guide model construction, we developed a priori predictions about how and each ecological covariate, as well as, how sex and island size class stratification, would influence survival and transition probabilities. We consider the basic life-history traits of *O. palustris* and *S. hispidus*, as described earlier, to briefly explain our predictions. In addition, we state our predictions about whether each stratum and ecological covariate would have a positive or negative effect on survival and transition probabilities by specifying the expected sign ("+" or "-") of $\hat{\beta}$ coefficients in table 2.2 and 2.3.

Predictions - O. palustris survival

I expect that the diet of *O. palustris* and its use of the marshes surrounding tree islands to forage, lessens the influence of tree island characteristics on *O. palustris* survival. Results from Chapter One suggested that differences, at least among adult females, were less pronounced for *O. palustris* and they were for *S. hispidus.* I predict that if *O. palustris* survival rates are strata-specific; survival will be lower on small islands where cover can be sparser than on larger islands, possibly increasing the risk of predation on rodents on small islands (Table 2.2). Given that *O. palustris* is semi-aquatic and that much of its diet appears to be composed of aquatic prey, I predict that survival will differ between seasons and that covariates associated with dry seasonal periods (DaysDry, season (dry)) will negatively influence *O. palustris* survival. Conversely, covariates associated with the wet season (DayWet, season(wet), Rain and WL) will positively affect survival rates. As with males of many species, including rodents, I predict that survival will be sex-specific, with *O. palustris* males having lower survival rates than females.

Predictions - O. palustris transitions rates

I anticipate that nest building and rearing of young should favor *O. palustris* female site fidelity on larger tree islands where females presumably can find more resources than on smaller tree islands. Given these expectations, we predict that *O. palustris* transition rates will be sex- and strata-specific, with females having their lowest transition rates on large islands (Table 2.2). I also expect that during dry seasons, when the prairie is dry and offers less cover for animals moving across the prairie between tree islands, *O. palustris* would be less likely to move because between islands. I predict that transition rates will also differ between seasons, with covariates associated with dry seasons negatively affecting *O. palustris* transitions rates and covariates associated with wet seasons positively affecting *O. palustris* transition rates.

Predictions - S. hispidus survival

Given the differences in the body weights of adult females recaptured on different tree island size classes reported in Chapter One, and that plant diversity and resilience to changing conditions are associated with tree island area, I predict that survival for the predominantly herbivorous *S. hispidus,* will be strata-specific with large islands having a positive effect on *S. hispidus* survival rates and small islands having a negative effect on survival (Table 2.3).

S. hispidus captures on the tree islands at Rock Reef Pass were generally higher during the dry seasons and lower during wet seasons. If seasonal differences in captures are influenced by differences in survival rates, we would predict that covariates associated with wet seasons would have a negative effect on survival rates and covariates associated with dry seasons would have a positive effect on *S. hispidus* survival. As with *O. palustris,* we predict that survival will be sex-specific, with *S. hispidus* males having lower survival rates than females.

Predictions - S. hispidus transitions rates

Similar to *O. palustris*, we expect that nest building and rearing of young should also favor greater site fidelity and use of larger tree islands by *S. hispidus* females. Therefore, we also predict that *S. hispidus* transition rates will be sex- and strata-specific, with females having, in comparison to males, lower transition probabilities within each stratum and with large islands having the lowest transition rates (Table 2.3). *S. hispidus* is not semi-aquatic and its fur is not especially water repellent and so we expect that *S. hispidus* movements between islands would be lower during periods when the prairie is inundated. We also expect that *S. hispidus* would also make greater use of larger islands during the dry season where vegetation is greener and offers greater cover than on small tree islands. We predict that transition rates will also differ between seasons, with covariates associated with dry seasonal periods having a positive effect on *S. hispidus* transition rates and covariates associated with wet seasons having a negative effect on transition rates. In addition we predict that transition rates to large islands will be greater during the dry seasons when the vegetation of small islands often becomes dry.

Goodness of fit testing (GOF)

Capture histories were constructed by defining captures by sex and by three island size class strata (large, medium and small). We assessed this modeling of capture histories for violations of the basic assumptions of multi-state analysis, which are state-specific extension of the Cormack-Jolly-Seber live encounters-model (Lebreton *et al.* 1992). Program U-CARE (version 2.3) was used to conduct GOF testing using the combinations of tests under the assumption that transience was present (Choquet *et al.* 2003).

Model selection and Hypothesis testing

Program MARK was used to compute maximum-likelihood estimates of parameters *p*, *S*, and ψ and the parameters associated with covariate relationships. Program MARK conducts model selection based on a modified version of Akaike's Information Criterion that included corrections for small sample size (AICc). Model weights are computed to reflect the relative support of each model by the data (Buckland et al. 1997, Burnham and Anderson 2002). Overall model fit was improved in a step-wise optimization of parameters *p, S* and ψ. We do not report the optimizations of *p* and *S* seperately since the relative fit among *p* and *S* models was mirrored in the overall model selection. We describe the highest ranked capture probability models but omit the optimization details, since the goal for the optimization of *p* was to improve model fit and the estimation of the more biologically relevant $\hat{S}^{rs}{}_t$ and $\hat{\psi}^{rs}{}_t$ rates.

Model averaged rate estimates

Akaike weights computed by program MARK were used to incorporate the uncertainty of model selection into parameter estimation by weighting averaged real parameter estimates by the relative support of each model (Buckland *et al.* 1997). Because of computational limitations, model-averaged parameters were quantified outside of Program MARK using the equation (Burham and Anderson 1998) in program Excel:

$$\widehat{var}(\hat{\theta}) = \sum_{i=1}^{R} \mathrm{w}(i) \left[\sqrt{\widehat{var}\,(\hat{\theta}_i \mid \mathrm{M}_i) + (\hat{\theta}_i - \hat{\theta})^2}\right]^2$$

Model averaged rates are given with ± standard error.

Beta coefficients are structural parameters that can only be averaged among models with the same structure, *i.e;* models with the same time and stratum-specific covariates. Therefore they were not model-averaged.

RESULTS

Goodness of Fit Testing

Capture histories stratified by sex and island strata, were used for GOF testing. The GOF test statistic resulted in a variance inflation factor of < 1. The variance inflation factor (hereafter $\hat{c}$) is a measure of extra binomial variation or overdispersion that generally arises from lack of fit of data to the model assumptions (*i.e.*, violation of the state-specific CJS assumptions). A $\hat{c} = 1$ is an indication of no extra binomial variation. It is generally considered that $\hat{c}$ values ≥ 3 are an indication that the starting model does not adequately fit the data (White and Burnham 1999). There is no generally accepted interpretation of $\hat{c} < 1$, although it is often interpreted as providing no evidence of a need to adjust the overdispersion parameter, c, (which compensates for overdispersion by penalizing more parameterized models) in the model selection process (*e.g*., Breininger *et al*. 2009). Although $\hat{c}$ was < 1 in both species' GOF testing, the overall tests for trap-dependency (test 3G) were significant, indicating that *S. hispidus* males were 'trap-happy'. The overall trap-dependency test for *O. palustris* was not significant but a separate trap dependency test for males was also significant, indicating 'trap-happy' males. Later, after multi-state model selection for both species was completed using $\hat{c} = 1$, we conducted a sensitivity analysis by increasing the overdispersion parameter c in increments of 0.5 and observing changes in the relative ranking of the top models in the set of candidate models. For both species, model selection was robust to increased overdispersion, with changes in the relative ranking of models only occurring as $\hat{c}$ approached 2. We interpreted the robustness of model rankings to increases in the c parameter as an indication that our data met the assumptions of mark-recapture models using $\hat{c} = 1$.

Model Selection - O. palustris

The models in the candidate set that received virtually all support (combined AICc weight ~ 1.0; Burnham and Anderson 1998) were identical or nested (*i.e.*, same starting model but with fewer of the original parameters) in model: *S*(M2 s / Dry [last 2] + sex + WL), *p*(s + WetDry + WL), ψ(s(SM=SL) * WL + sex + rain). The three highest ranked models had substantial support as the best (Δ_i AICc < 2; Burnham and Anderson 1998) approximation models (Table 2.4). These models described *O. palustris* survival rates for first age class as strata-specific constant rates ("M2 s /") ($\hat{S}_1^S = 0.34 \pm 0.33$, $\hat{S}_1^M = 0.38 \pm 0.05$, $\hat{S}_1^S = 0.47 \pm 0.03$). Survival rates for individuals in the second age class were described as differing during the last two ("Dry [last 2]") of 10 periods when the study site was continuously dry. The highest ranked model (Δ_i AICc = 0) also described *O. palustris* survival rates as a + function of monthly water levels ("+ WL") during the sampling period, where "+" refers to an additive model without interactions. The second highest ranked model (Δ_i AICc = 0.64) also described survival rates as a + function of sex, and the third highest ranked model (Δ_i AICc = 1.96) described survival as a function of both sex and water levels during the sampling period ("+ sex + WL"). Capture probabilities were described as strata-specific ("s") rates and as an additive function of either water levels ("s + WL") (Δ_i AICc = 0) or as a combination of both water levels and wet and dry period ("s + WetDry + WL"). *O. palustris* transition rates were best described as an additive function of sex and strata-specific rates that varied as a function of the combination of stratum and water levels ("*WL").

Capture probabilities – O. palustris

Monthly capture probability estimates were model-averaged over the 10 highest ranked models (combined AICc weight = 0.98). Overall, *O. palustris* capture rates (the probability that a marked individual within a given island size class will be recaptured during the same three day sampling period) were high on all strata, especially on small islands were $\hat{p}_t$ was ~1 ($\hat{p}_t^{Large}$ = 0.439, $\hat{p}_t^{Medium}$ = 0.586, $\hat{p}_t^{Small}$ = 0.996).

The highest ranked model described *O. palustris* capture probabilities as strata-specific rates and as + function of water levels during the sampling periods. The coefficient (Table 2.5) for water levels $\hat{\beta}_j^{WL}$ was low in magnitude relative to other coefficients in the same model. The water levels covariate likely improved model fit by allowing capture rates to vary over time. Models describing capture rates with an additional additive covariate for wet and dry periods were similarly ranked as models without this covariate. However, we do not interpret this result as an indication that *O. palustris* recapture rates do not vary seasonally. The water levels covariate included in the description of capture rates, vary seasonally allowing recapture estimates to vary monthly seasonally rates.

Is there evidence of differences in O. palustris survival rates among the three island size classes and do these differ between males and females?

Contrary to our prediction, models where survival for *O. palustris* was stratified by island size were not supported in the data. Survival was not described as sex-specific in the most parsimonious model, but survival differences in sex were included as an additive effect in 8 of the 10 models that received virtually all support (AICc [w] ~ 1.0). Male survivorship was, as predicted, lower than that of females by a constant negative rate (Table 2.6), however, the difference in model averaged survival rates for males and females was minimal (males: $\hat{\bar{S}}_t^{Large} = \hat{\bar{S}}_t^{Medium} = \hat{\bar{S}}_t^{Small} = 0.71$, males: $\hat{\bar{S}}_t^{Large} = \hat{\bar{S}}_t^{Medium} = \hat{\bar{S}}_t^{Small} = 0.75$).

Which environmental variables influence O. palustris survival and does their influence differ with island size?

Overall, only models with little variation in survival received support from the data. As a consequence, survival rates were estimated as a nearly constant rate, except for two prominent decreases in survival during two of 10 dry periods that occurred during this study (Figure 2.4). During these two four month periods, *O. palustris* survival decreased sharply (*e.g.,* $\hat{S}^{Dry}{}_{101} = 0.21$, for males). Environmental conditions do not appear to have been especially severe during these two periods. The duration of these dry periods, as well as the mean air temperature, total rainfall and mean water levels, were not significantly different when compared with the other eight dry periods. *O. palustris* survival rates were also described as an additive function of mean monthly water levels in the most parsimonious model and in three additional models with a combined AICc weight of 0.55. However, contrary to our predictions, the $\widehat{\beta}^{WL}$ coefficient in the most parsimonious model was negative (Table 2.6) and its CI included zero. Although water levels were included in the best fit models, we interpret these results as an indication that the water level data used in these models possibly did not accurately represent conditions at Rock Reef Pass.

Does O. palustris tree island use differ with tree island size class?

Consistent with *a priori* prediction, the most parsimonious model described *O. palustris* transition probabilities as strata-specific, with the exception of transitions from small to medium and from small to large islands. Also as predicted, transition rates were described as sex-specific rates that, as indicated by the positive $\widehat{\beta}_j^{sex\ (males)}$ coefficient (Table 2.7), were higher for males than females. Transition probabilities between tree island size strata, for both *O. palustris* males and females, suggest that overall, *O. palustris* were more likely to remain on larger islands and were more likely to move from smaller islands. The likelihood that *O. palustris* remained on the same islands stratum was higher for *O. palustris* on medium islands ($\widehat{\psi}_i^{MM\ males} = 0.72$, $\widehat{\psi}_i^{MM\ females} = 0.84$) than for *O. palustris* on large ($\widehat{\psi}_i^{LL\ males} = 0.44$, $\widehat{\psi}_i^{LL\ females} = 0.61$) or on small islands ($\widehat{\psi}_i^{SS\ males} = 0.25$, $\widehat{\psi}_i^{SS\ females} = 0.40$) (Figure 2.5).

O. palustris transitions rates were also described by the most parsimonious model as a function of the interaction between water levels and island strata, where as indicated by the $\widehat{\beta}_j^{WL}$ coefficients, water levels had no effect on the transition rates of *O. palustris* between large and medium islands, had a positive effect on transitions from medium to large and from large to small islands and a negative effect on the transition rates of *O.*

palustris from small to both large and medium islands (Table 2.7). Similar to the descriptions of *O. palustris* $\hat{S}_i$ and $\hat{p}_t$, rates, the $\hat{\beta}_j^{WL}$ coefficient was, relative to other transition coefficients, low in magnitude. Because transition rates were described as a function of water levels which vary seasonally, transition rates reflect seasonal changes in water levels where the probability of *O. palustris* remaining within large and medium islands was higher during the dry season and while the probability of *O. palustris* remaining on small islands was greater during the wet season (Figure 2.6). In addition to changes in water levels, *O. palustris* transition rates were also described as a positive function of rainfall but only for transitions from large to small island strata.

Model Selection - S. hispidus

Three highest ranked models received nearly all support in the data (combined AICc weight ~ 1.00) (Table 2.8). These three models also had substantial support from the data as the best approximation models (*i.e.,* Δ_i AICc < 2). These models were nested in model: *S*(M2 . / s * sex, s * rain + WL + seasons), *p*(s * sex + seasons), ψ(s * sex) and differed only in the description of ψ as an additive function of seasonal and monthly water levels. Survival for individuals in the first age class was described as a fixed rate (“M2 . / “) ($\hat{S}_1^{LMS} = 0.51$, ± 0.008). *S. hispidus s*urvival, captures and transition probabilities were described was an additive function of monthly water levels and as strata- and sex-specific rates that differed among strata as a function of sex (“s*sex”). *S. hispidus s*urvival rates were additionally described as an additive function of water levels and total monthly rainfall. Because time is inherent in water levels and rainfall, $\hat{S}^{L,M,S}_{i}$ and $\hat{\psi}_i$ were time-specific rates, while the time-specificity of $\hat{p}$ was described as two seasonal rates (dry and wet seasons).

Capture probabilities – S. hispidus

Overall, *S. hispidus* recapture rates were high, often near 1.0. As indicated by the recaptures $\hat{\beta}_j^{\text{sex}}$ coefficients (Table 2.9) in the most parsimonious model, recapture rates were a negative function of sex, with males having lower recapture rates than females. Although the CI for $\hat{\beta}_j^{\text{sex}}$ included zero, both coefficients for the interaction of sex and medium and small strata, $\hat{\beta}_j^{\text{sex}*M}$ and $\hat{\beta}_j^{\text{sex}*S}$, were negative and their CI's did not bound zero, indicating that male recapture rates on medium and small islands were lower relative to large islands. *S. hispidus* recapture rates were also described as a function of wet and dry seasons, with captures as a positive function of the dry season rate. Male capture probabilities were highest on large islands ($\hat{p}^{L\ male}_{Dry} = 0.89, \pm 0.02$; $\hat{p}^{L\ male}_{Wet} = 0.71, \pm 0.03$), while female capture rates were highest on medium islands ($\hat{p}^{M female}_{Dry} = 0.97, \pm 0.01$; $\hat{p}^{M female}_{Wet} = 0.73, \pm 0.02$). Both male and female recapture rates were lowest on small islands (males: $\hat{p}^{S\ males}_{Dry} = 0.12, \pm 0.04$; $\hat{p}^{S\ males}_{Wet} = 0.04, \pm 0.01$; females: $\hat{p}^{S female}_{Dry} = 0.44, \pm 0.06$; $\hat{p}^{S}_{Wet} = 0.19, \pm 0.03$).

Is there evidence of differences in S. hispidus survival rates among the three island size classes and do these differ between males and females?

The most parsimonious model described *S. hispidus* survival rates as strata-specific and as a function of the interaction between sex and island strata. Contrary to our predictions, large islands had a negative effect on *S. hispidus* survival (Table 2.10). Consistent with our predictions, the medium island stratum had a positive effect on survival rates while small islands had a negative effect on survival rates. The $\hat{\beta}_j$ coefficient for the interaction of males and island strata indicate that large and medium island strata had a negative effect on male survival while small island stratum had a strong positive effect on male survivorship. *S. hispidus* female survival rates were higher than males on large ($\hat{\hat{S}}_t^{L female}$ = 0.68, $\hat{\hat{S}}_t^{L male}$ = 0.66) and medium ($\hat{\hat{S}}_t^{M female}$ = 0.73, $\hat{\hat{S}}_t^{M male}$ = 0.65) islands. On small islands, male survivorship was highest while female survivorship was lowest ($\hat{\hat{S}}_t^{S female}$ = 0.57, $\hat{\hat{S}}_t^{S male}$ = 0.92). Although the coefficient for $\hat{\beta}_j^{sex(male)}$ was negative, because of the high magnitude of the coefficient $\hat{\beta}_j^{S}$, for the interaction of males and small islands, males survival probability on small islands was very high, giving males a higher average survival probability than females ($\hat{\hat{S}}_t^{female}$ = 0.75, $\hat{\hat{S}}_t^{male}$ = 0.66).

Which environmental variables influence S. hispidus survival and does their influence differ with island size?

S. hispidus survival rates were also described by the most parsimonious model as an additive function of rainfall, water levels, and dry seasonal periods. As predicted, $\hat{\beta}_j^{rain}$ was negative, indicating that rainfall had a negative effect on *S. hispidus* survival rates (Table 2.10). The coefficients for the interaction of rain and island strata, $\hat{\beta}_j^{rain*M}$ and $\hat{\beta}_j^{rain*S}$, indicating that relative to large island strata, the negative effect of rainfall on *S. hispidus* survival was greater on medium and small island strata. Contrary to our prediction that water levels would negatively affect *S. hispidus* survivorship, the $\hat{\beta}_j^{WL}$ coefficient for water levels was positive, although, relative to the other $\hat{\beta}_j$ coefficients in the model, low in magnitude. Consistent with our prediction, *S. hispidus* survival in the most parsimonious model is described as a positive function of dry seasons. The $\hat{\beta}_j^{season}$ coefficient for dry seasons was positive and, relative to other $\hat{\beta}_j$ coefficients, the effect of dry seasons was also higher in magnitude. Seasonal differences in *S. hispidus* survival probability are visible in figures 2.7 and 2.8, where survival probability is most often the highest between October and December (dry season) and most often lowest between May and August (wet season).

Does S. hispidus tree island use differ with tree island size class?

The three highest ranked models (combined AICc weight ~ 1.00) received similar support in the data with the most parsimonious model describing *S. hispidus* transition probabilities as strata- and sex-specific (Table 2.8). The second and third best fit models additionally described transitions rates as additive functions of seasons and water levels, and, although these models received identical support in the data, the $\hat{\beta}_j$ coefficient CI's for the seasons and water level effects included zero. Contrary to our expectations, the $\hat{\beta}_j$ coefficient for the interaction of sex (males) and large strata indicating that males on large islands were more likely to move, while males on small islands were more likely to remain within the same strata (Table 2.11). Comparisons of monthly transition rates for *S. hispidus* within each stratum, indicate that males on small islands were more likely to remain within the same stratum ($\hat{\hat{\psi}}_i^{SS} = 0.9$) than males on either medium ($\hat{\hat{\psi}}_i^{MM} = 0.74$) or large islands ($\hat{\hat{\psi}}_i^{LL} = 0.81$). Males on large and medium strata that moved to another stratum, were also more likely to move to small islands than to other strata (Figure 2.9). While these transition rates were contrary to our predictions and appear to suggest that *S. hispidus* males make greater use of small islands, only 16% (N = 141) of *S. hispidus* males were captured on small islands while 61% (N = 508) of *S. hispidus* were captured on large islands. Transition probabilities for *S. hispidus* females were more consistent with our prediction that females would make greater use of large tree islands. Females on large islands were more likely to remain within the same strata ($\hat{\hat{\psi}}_i^{LL} = 0.9$) than females on medium ($\hat{\hat{\psi}}_i^{MM} = 0.77$) or small island strata ($\hat{\hat{\psi}}_i^{SS} = 0.69$). Of the *S. hispidus* females that moved between strata, females were most likely to move between small and medium islands (Figure 2.9).

DISCUSSION

The goal of the work presented here was to draw inferences about the relationship between two of the Everglades most abundant animal species, *O. palustris* and *S. hispidus*, and two of the Everglades most salient habitat features, the tree islands that provide most of the permanently dry ground available to terrestrial species, and the hydroperiods that shape the life-histories of the flora and fauna in this ecosystem. Mark-recapture data for *O. palustris* and *S. hispidus,* collected between February of 1994 and June of 2003 on 16 tree islands at Rock Reef Pass, Everglades National Park, were used in a multi-state analysis approach to draw inferences about the influences of tree island size and environmental covariates associated with hydroperiods on the survivorship of *O. palustris* and *S. hispidus*. This approach also allowed us to simultaneously draw inferences about tree island size and their use by *O. palustris* and *S. hispidus*.

O. palustris survival

The descriptions of *O. palustris* survival by the best fit models were not consistent with our predictions. The best fit models did not describe *O. palustris* monthly survival rates as having differed among large, medium and small island size classes, or as having differed between seasons, as we had predicted. With the exception of two brief declines in survival, *O. palustris* monthly survival rates were nearly constant. Survival was described by the most parsimonious model as a function of water levels, however, contrary to our prediction, the $\hat{\beta}_j^{\,WL}$ coefficient was negative and its CI overlapped zero. The numbers of *O. palustris* individuals captured each month were correlated with monthly water levels ($\rho = 0.34$, $P < 0.001$, N = 118), suggesting that water levels would influence *O. palustris* survival rates. The water levels covariate, which we expected to have a strong affect on parameter estimates, was included in models with support in the data for both species, however, its effect was weak and/or its CI included zero. It is possible that we did not describe time- and strata-specific differences in *O. palustris* survival rates for three possible reasons.

First, it is possible that the covariates used in the survival analysis were not representative of conditions at the study site. The water level data from the Royal Palm Ranger Station may not have been the best description of conditions at Rock Reef Pass, but they improved model fit by allowing parameter estimates to vary over time. It is also possible that other factors that have a greater influence on *O. palustris* survival were not included in this analysis. Not included in this analysis was animal density, since abundance estimates from the capture histories used in model fitting would have produced autocorrelated estimates of the effects of density on survival. However, we visually explored the possibility of a relationship between the two prominent declines in *O. palustris* survival (Figure 2.4) and animal density, by superimposing the number of *O. palustris* present at the study site each month over the $\hat{S}_i^{\,rs}$ time-series (Figure 2.10). The two declines in survival were preceded by peaks in the number of *O. palustris* during the previous month, suggesting the potential existence of density effects on survival. However, in 1997 there was a similar increase in the number of *O. palustris* that was not followed by a decline in survival.

Second, it is also possible that because water levels, and the values of the other environmental covariates, were consistent from season to season, that relative to other factors, these covariates had little influence on survival rates. *O. palustris* and *S. hispidus* successfully colonized the Everglades because their life-history strategies buffer these species from changing seasonal conditions. It is unlikely that *O. palustris* and *S. hispidus* survival rates would be strongly affected by average environmental conditions, making it more difficult to detect the influence of environmental variables under normal conditions.

Third, animal movements likely affected our ability to detect time- and strata-specific differences in *O. palustris* survival rates. $\hat{S}_i^{rs}$, or apparent survival, is the complement of both death and permanent emigration. If individuals permanently emigrate from the study site they will appear to have died, thus decreasing survival probability estimates. The two–age class survival model allowed us to address the negative biasing of survival estimates by individuals not reencountered after their first capture. Permanent emigration by individuals recaptured at least once, is indistinguishable from death and decreases survival estimates for individuals in the second age class. Given *O. palustris'* high survival probability estimates, it is unlikely that permanent immigration after the first interval biased overall *O. palustris* survival estimates.

Estimates of survival from the two-age classes also allowed us to derive an estimate $(1 - (\hat{S}_i^{\text{age } 1} / \hat{S}_i^{\text{age } 2}))$ of the proportion of transients in the ‘newly marked’ sample of individuals for a given interval (Pradel *et al.* 1997). Individuals not seen again after being marked are often referred to as “transients”. In using this term we do not assume that all individuals not reencountered after the first capture have permanently emigrated from the study site. We model averaged $\hat{S}_i$ estimates for both age classes and because $\hat{S}_1^{L}$, $\hat{S}_1^{M}$, $\hat{S}_1^{S}$ were described as constant rates by the best fit model, we estimated average $\hat{S}_i^{age2}$ and $\hat{\hat{S}}^{age2}$ rates for males and females. The derived proportions of transients for males and females differed by < 3% and, for convenience we averaged them into a single value for each stratum. On average, 52 %, 48% and 33% of *O. palustris* captured each period on large, medium and small strata, respectively, were transients. The high proportion of transients suggests that *O. palustris'* habitat use is highly dynamic, with large proportions of individuals moving among islands. The greater the spatial scale of habitat use by a species, relative to spatial scale over which individuals are sampled, the less representative capture histories are of the overall 'population' dynamics and the more difficult it becomes to identify the factors influencing survival rates. The increased movement of *O. palustris* may also have contributed to an averaging effect of survival rates estimates among strata by decreasing the influence that any one stratum has on survival rates.

O. palustris transition rates

Consistent with our predictions, transition rates were sex-specific, with the best fit models describing *O. palustris* male transition rates between strata as greater than those of females. Also consistent with our predictions, transition rates were strata-specific with *O. palustris* males and females on medium and large islands having higher probabilities remaining within the same stratum than *O. palustris* on small islands (Figure 2.5). Transition rates were described as a function of water levels that vary seasonally and, therefore, transition rates also varied seasonally (figure 2.6). *O. palustris* on large and medium island strata were more likely to remain within the same stratum during the dry season than during the wet season. Conversely, *O. palustris* on small islands were more likely to remain on small islands during the wet season than in the dry season. *O. palustris* transition rates between large and small strata were also described as a positive function of rain, although it is unclear to us why. We interpret these results as an indication that *O. palustris* makes greater use of larger islands than smaller islands, especially during the dry season, when large islands provide cover, cooler temperatures, and green foliage on which *O. palustris* might also find more insect prey. In contrast, the small islands in this study did not support mature trees whose roots can reach the water table and in the dry season the vegetation on small islands was often sparse and dry.

S. hispidus survival

The description of *S. hispidus* survival rates as a negative function of large tree islands (Table 2.10) was contrary to our expectation that large islands would provide more favorable conditions for *S. hispidus*. Nonetheless, both males and females have similar survival rates on both large and medium island strata and although males have their highest survival rates on small islands, females have, as expected, their lowest survival rates on small islands. In addition, only 16% (N = 141) of *S. hispidus* males were captured on small islands, while 61% (N = 508) of *S. hispidus* were captured on large islands. Even if males do actually have higher survival rates on small islands, fewer males seem to use smaller than large and medium islands and their recapture rates are much lower on small islands than on either medium or large islands. The description of survival as a positive function of dry seasons, and as a negative function of rain were consistent with our prediction that dry season conditions are more favorable for *S. hispidus*. However, contrary to our prediction, survival was a positive function of water levels (Table 2.10), which could be attributed to the growth of the vegetation and *S. hispidus'* herbivorous diet.

S. hispidus transition rates

The most parsimonious model described transition rates only as a function of sex and stratum (Table 2.8). The second and third most supported models also described *S. hispidus* transitions rates as additive functions of seasons and water levels, but since the CI's for the seasons and water level $\hat{\beta}_j$ coefficients included zero, there was no support for the influence of these covariates on survival rates. Similar to the description of *S. hispidus* survival rates, the description of female transition rates was more consistent with our prediction that *S. hispidus* would be more likely to remain on large islands than on small islands (Figure 2.11). Contrary to our expectation, males on small islands were most likely to remain within the same stratum; however, the probabilities of males remaining on large and medium island strata were also high.

CONCLUSIONS

The strongest evidence of the significance of different size tree islands for *O. palustris* is given by the transition probability analysis that provide evidence that, overall, *O. palustris* were more likely to remain on larger islands than on smaller islands, and were more likely to move from smaller islands than from large islands. The average proportions of *O. palustris* transients calculated using the two-age classes and the higher proportion of transition rates between strata by *O. palustris* in comparison to *S. hispidus,* suggest that the use of tree islands in the Everglades by *O. palustris* is highly dynamic. Nonetheless, the seasonal differences in the likelihood that *O. palustris* remain within the same stratum suggests that large and medium islands could possibly provide resources not found on smaller islands during dry seasons. The *O. palustris* survival analysis was less informative, possibly because *O. palustris* survival is more likely to be influenced by the overall properties of tree islands over a given area rather than by the properties of individual islands, such as the size of study islands within the area of the study site.

S. hispidus survival and transition probabilities differed with island size and, although island size class influenced male and female survival and transition rates differently, overall, *S. hispidus* were more likely to survive and remain on larger islands than on smaller islands. These results provide evidence that large islands may indeed be of greater relative value to both *O. palustris* and *S. hispidus.*

The work presented here represents an initial step towards describing the ecology of two of the Everglades most abundant and widely distributed animals, *O. palustris* and *S. hispidus.* I hope that research on the ecology of Everglades rodents and on their role in the Everglades ecosystem will be conducted in the near future. The potential impact of the introduction of Burmese pythons (*Python molurus bivittatus*) on Everglades rodents emphasizes the need for baseline measures of rodent populations and demographic rates to determine the impact of pythons on rodent populations.

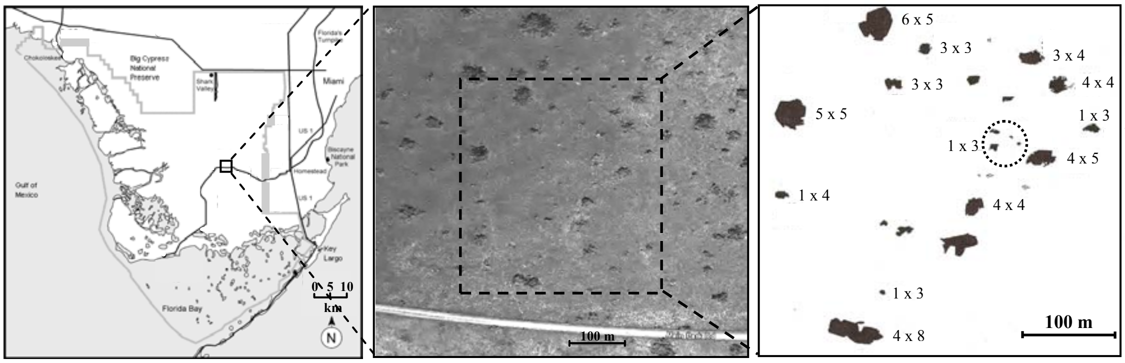


Figure 2.1 (a) Study was conducted in the Everglades National Park, Homestead, FL, in an area commonly known as Rock Reef Pass. (b) The study site located just north of the main Park road, 17 kilometers from the main National Park entrance. (c) The 16 tree islands of varying sizes were selected for small mammal live-trapping and are indicated by the trapping grid size shown adjacent to each tree island.

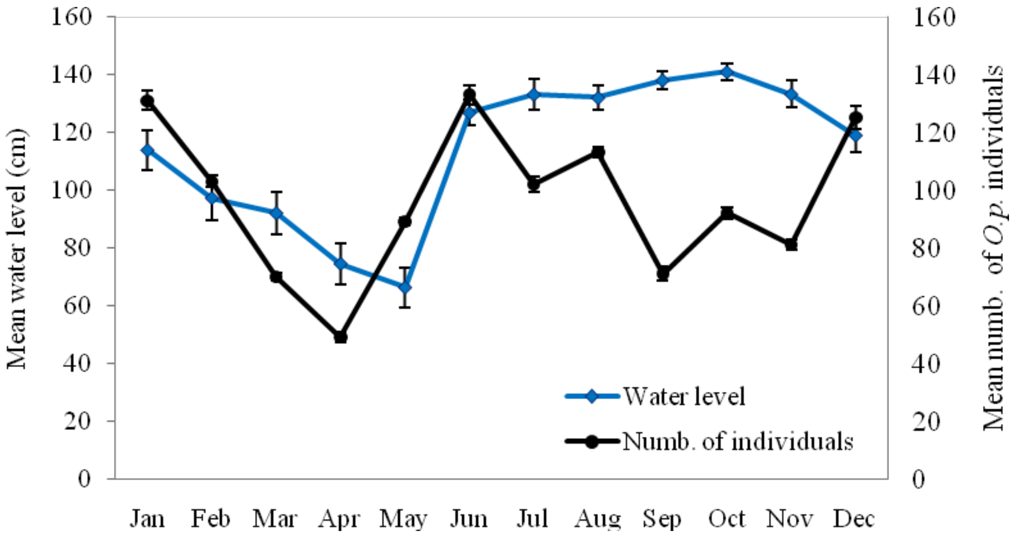


Figure 2.2. Comparison of monthly water levels and the number of *O. palustris* individuals known to be present during monthly 3 day trapping periods at the Rock Reef Pass study site, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. The left side y-axis is the mean monthly water level and on the the right side y-axis are the total number of *O. palustris* individuals known to be in the study site during the 3 day trapping periods of each calendar month. Error bars indicate standard error.

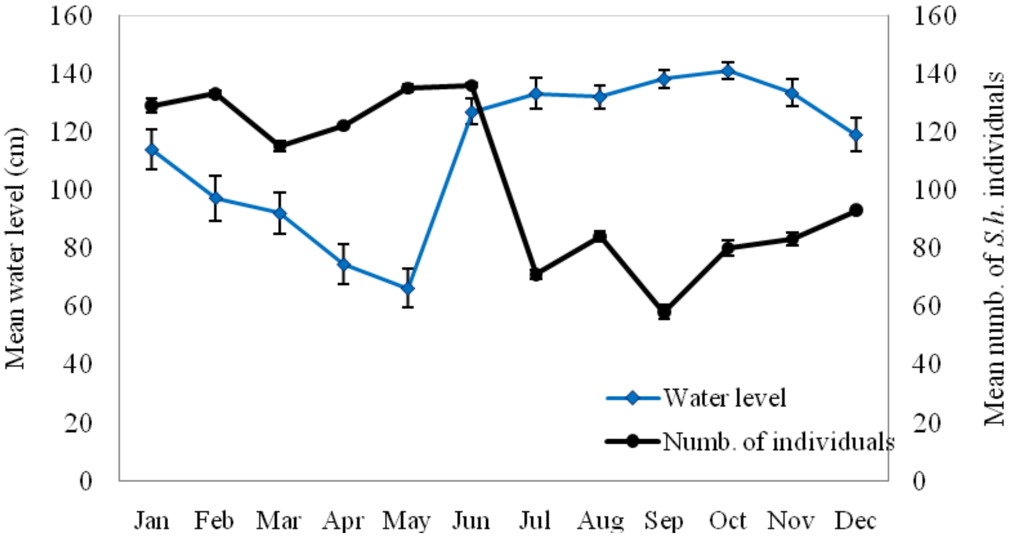


Figure 2.3. Comparison of monthly water levels and the number of *S. hispidus* individuals known to be present during monthly 3 day trapping periods at the Rock Reef Pass study site, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. The left side y-axis is the mean monthly water level and on the the right side y-axis are the total number of *S. hispidus* individuals known to be in the study site during the 3 day trapping periods of each calendar month. Error bars indicate standard error.

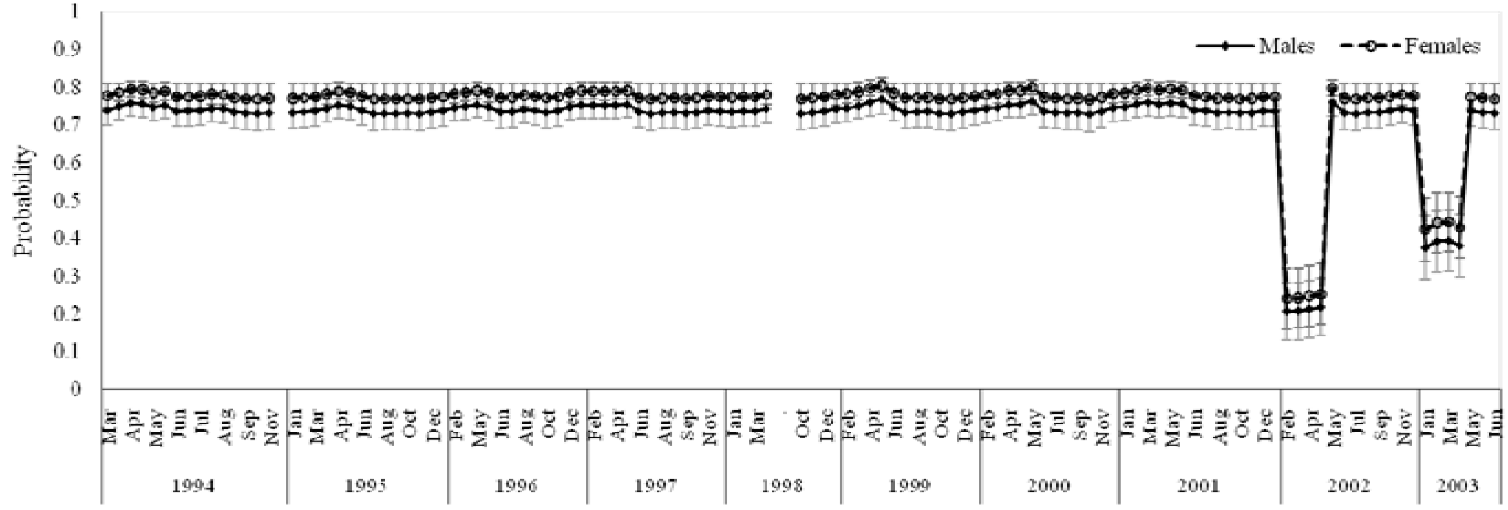


Figure 2.4. Model-averaged monthly survival probability estimates for *O. palustris* males and females at Rock Reef Pass, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. Survival probability estimates were model-averaged using the 10 best fit models that combined received nearly all support in the data (AICc weight ~ 1.0). Bars indicate model-averaged standard errors.

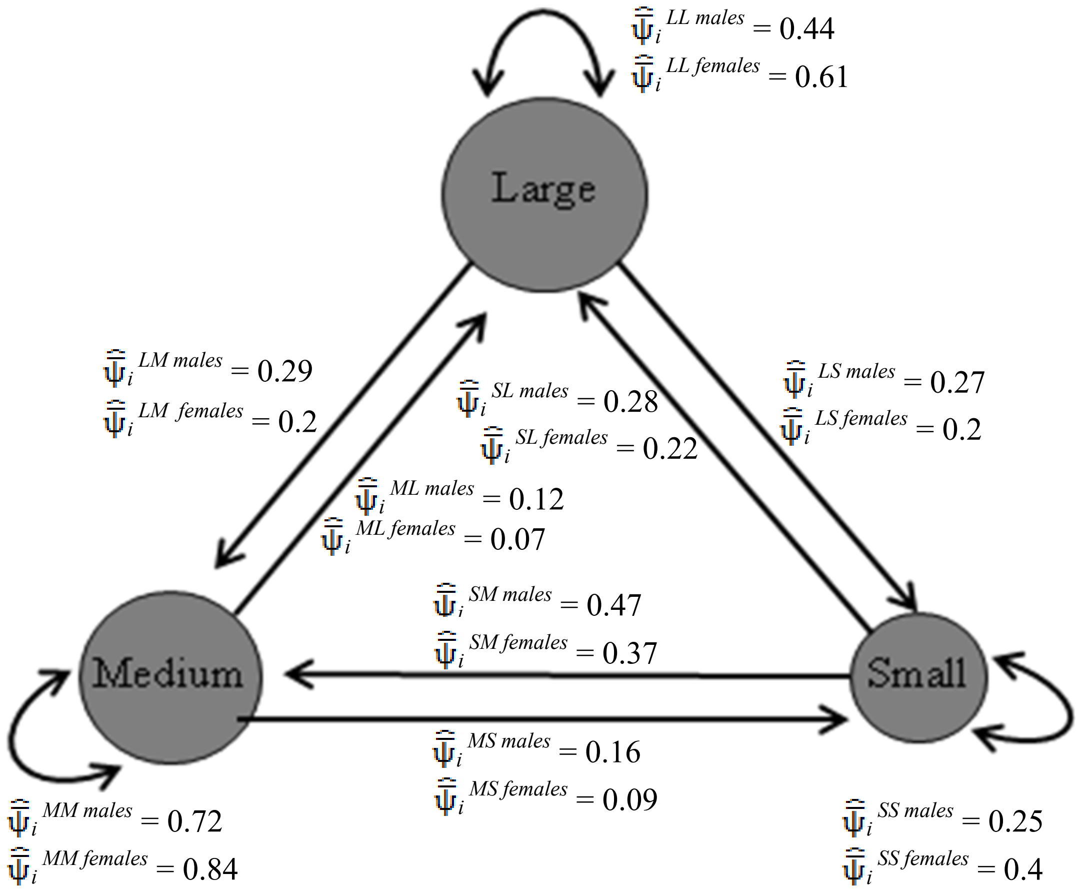


Figure 2.5. Average monthly transition probabilities ($\psi_i^{Sex\ tratum}$) for male and female *O. palustris* on large (L), medium (M) and small (S) tree island size strata. Transition probabilities sum to $\sum(\ \psi_i^{rs} = 1)$ within each stratum for males and females. Transition rates were first model-averaged using the 10 multi-state models that combined received nearly all support in the data (AICc weight ~ 1.0), then averaged as a single rate for each state transition. *O. palustris* transition rates were described by the most parsimonious model was a strata-specific rates, expect for transitions from small to medium and small island strata.

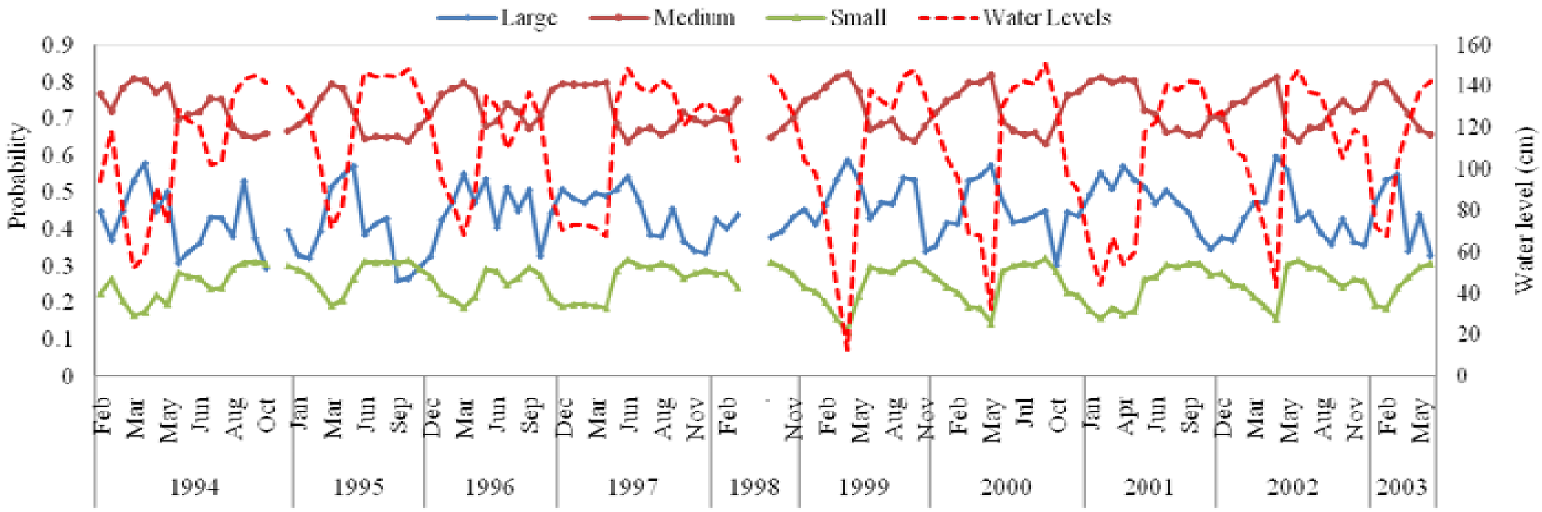


Figure 2.6. Model-averaged monthly estimates of the probability *O. palustris* males remaining within the same tree island size class at Rock Reef Pass, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. Transition probability estimates were model-averaged using the 10 best fit models that combined received nearly all support in the data (AICc weight ~ 1.0). The left y-axis represents the probability of *O. palustris* remaining within large, medium and small tree island size classes from one monthly sampling period to the next. The right y-axis shows mean monthly water levels. The figure suggests that the probability of *O. palustris* remaining of within large and medium island strata is greater during dry periods and the probability of *O. palustris* of remaining within small island stratum is greater during wet or inundated periods. For simplicity only the transition rates for *O. palustris* males are shown. Male and female *O. palustris* transition probabilities differ only a small constant rate and therefore their lines are parallel.

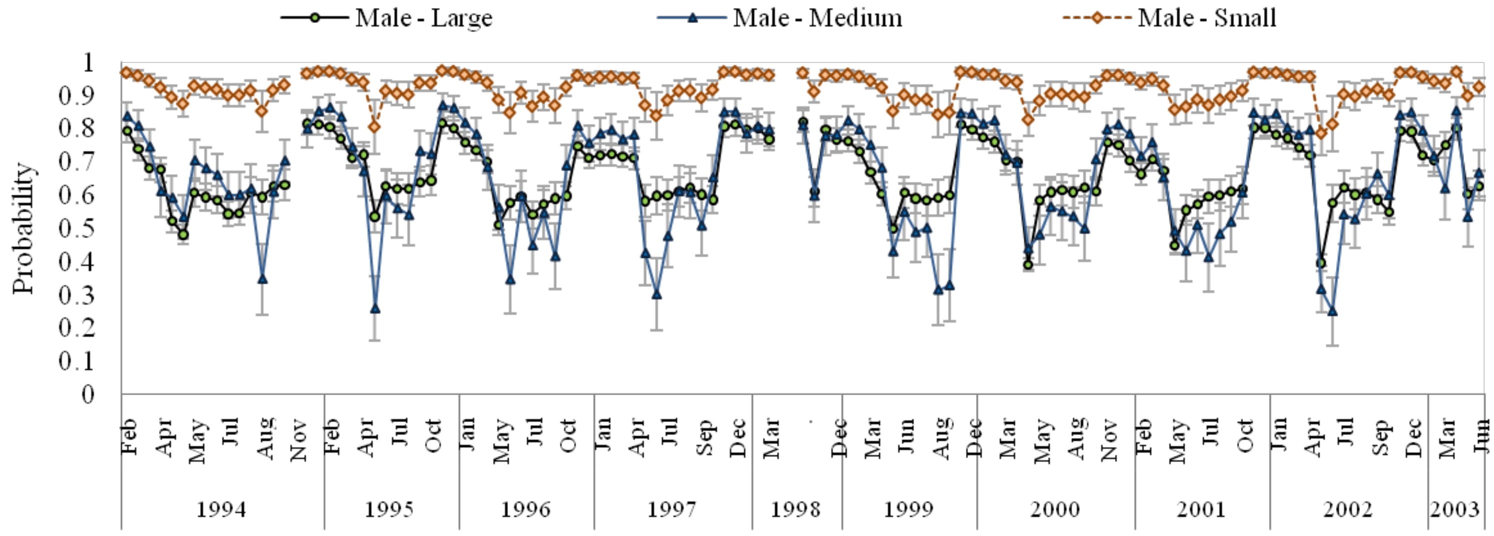


Figure 2.7. Model-averaged monthly survival probability estimates for *S. hispidus* males at Rock Reef Pass, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. Survival probability estimates were model-averaged using the 3 best fit models that combined received nearly all support in the data (AICc weight ~ 1.0). Bars indicate model-averaged standard errors.

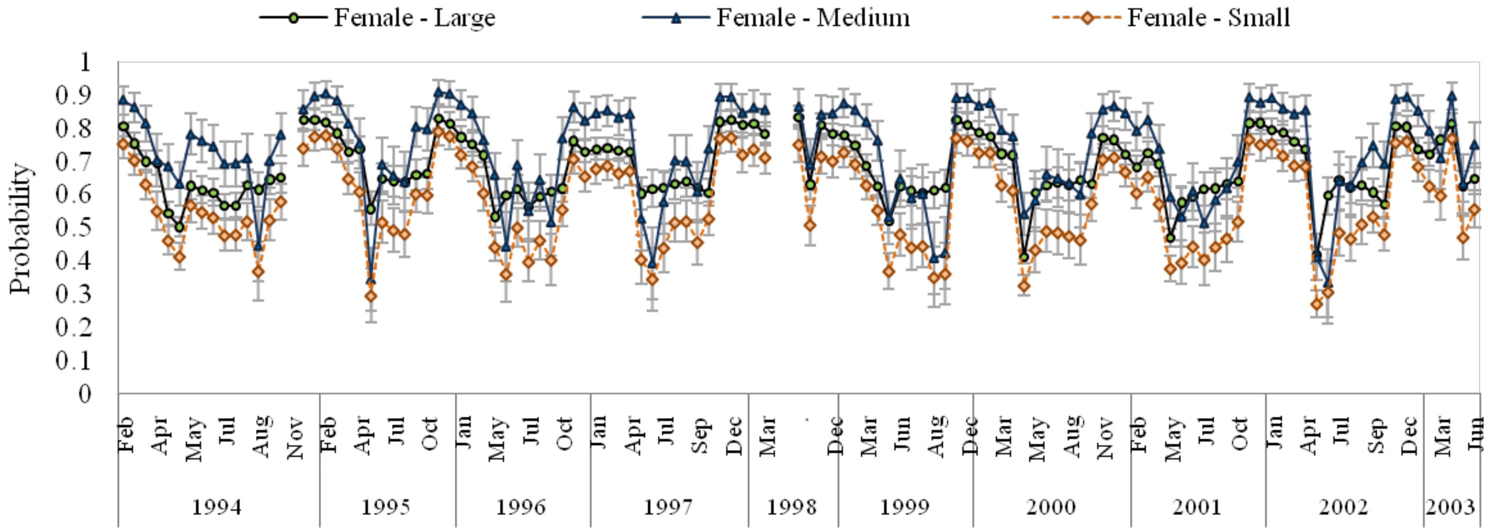


Figure 2.8. Model-averaged monthly survival probability estimates for *S. hispidus* females at Rock Reef Pass, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. Survival probability estimates were model-averaged using the 3 best fit models that combined received nearly all support in the data (AICc weight ~ 1.0). Bars indicate model-averaged standard errors.

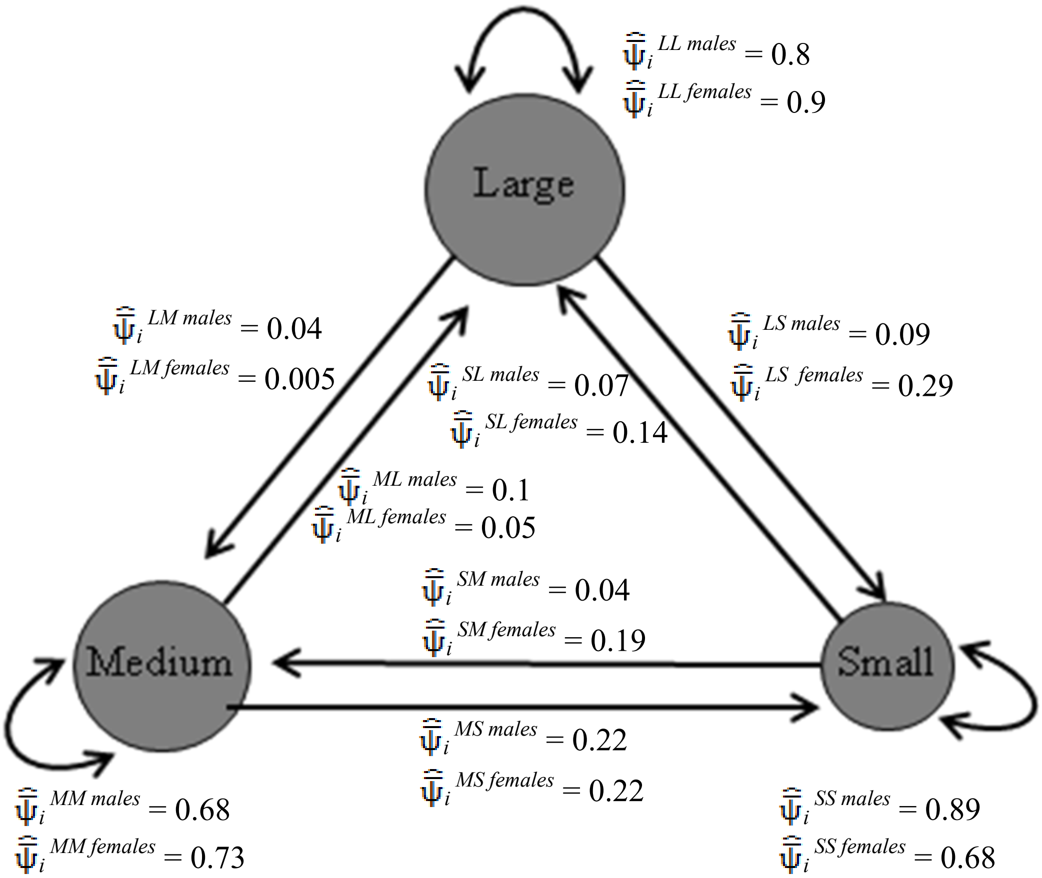


Figure 2.9. Model-averaged transition probabilities ($\psi_i^{Stratum\ sex}$) for male and female *S. hispidus* on large (L), medium (M) and small (S) tree island size strata. Transition probabilities sum to 1$\sum(\ \psi_i^{rs} = 1)$ within each stratum for males and females. Transition rates were model-averaged using the 3 best fit models that combined received nearly all support in the data (AICc weight ~ 1.0), then averaged as a single rate for each state transition.

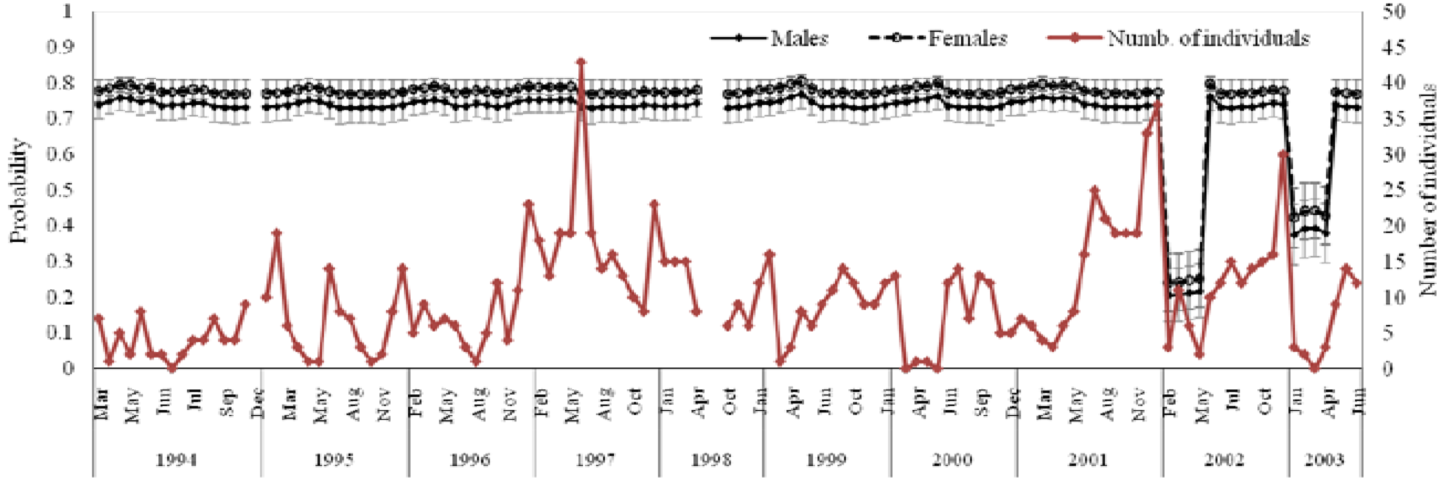


Figure 2.10. Model-averaged monthly survival probability estimates for *O. palustris* males and females at Rock Reef Pass, Everglades National Park, Homestead, Florida, between February 1994 and June 2003. Represented in the left y-axis are monthly survival probabilities for *O. palustris* males and females and in the right y-axis the total number of *O. palustris* individuals known to be in the study site during monthly 3 day trapping periods. The November 2001 and October 2002 peaks in the number of *O. palustris* individuals are followed by decline in survival probability. These declines in apparent survival reflect the complement of potential increases in permanent emigration and declines in survival probability.

Tree Island Size Classes

Tree island areas (m^2)		
Large	Medium	Small
1,110	432	194
920	431	149
785	386	118
	245	76
		52
		51
		45
		8
		4
$\bar{x} = 938\ m^2 \pm 94\ m^2$	$\bar{x} = 374\ m^2 \pm 44\ m^2$	$\bar{x} = 77\ m^2 \pm 21\ m^2$

Table 2.1. Sixteen study tree islands were classified into large, medium and small island size classes. Cluster analysis (k-means) of tree island areas was used to assign tree islands into size classes with significantly different mean areas (ANOVA, $F = 100$; $df = 13$; $P < 0.001$): three large, four medium and nine small islands.

O. palustris

$\hat{S}_i^{\,r}$ covariates	A priori prediction
Sex-specific (males)	$-\ \hat{\beta}_j^{\,sex(male)}$
Tree island strata-specific	$+\ \hat{\beta}_j^{\,L} \approx +\ \hat{\beta}_j^{\,M} > +\ \hat{\beta}_j^{\,S}$
Seasons *or* Dry/Wet periods	$-\ \hat{\beta}_j^{\,Dry}$ *or* $-\ \hat{\beta}_j^{\,season}$
Water levels	$+\ \hat{\beta}_j^{\,WL}$
Rainfall	$+\ \hat{\beta}_j^{\,rain}$
Days continuously dry	$-\ \hat{\beta}_j^{\,DaysDry}$
Days continuously wet	$+\ \hat{\beta}_j^{\,DaysWet}$
Air temperature	$-\ \hat{\beta}_j^{\,temp.}$

$\hat{\psi}_i^{\,sr}$ covariates	A priori prediction
Sex-specific	$-\ \hat{\beta}_j^{\,sex(male)}$
Tree island strata-specific	$-\ \hat{\beta}_j^{\,L} \approx -\ \hat{\beta}_j^{\,M} < +\ \hat{\beta}_j^{\,S}$
Seasons *or* Dry/Wet periods	$-\ \hat{\beta}_j^{\,Dry}$ *or* $-\ \hat{\beta}_j^{\,season}$
Water levels	$+\ \hat{\beta}_j^{\,WL}$

Table 2.2. Predicted negative or positive ($\hat{\beta}_j$) effect of strata, sex and environmental covariates on *S. hispidus* apparent survival probability ($\hat{S}_i^{\,r}$) and ($\hat{\psi}_i^{\,sr}$) strata transition probabilities.

S. hispidus

$\hat{S}_i^{\,r}$ covariates	A priori prediction
Sex-specific	$- \hat{\beta}_j^{\,sex(male)}$
Tree island strata-specific	$+ \hat{\beta}_j^{\,L} > + \hat{\beta}_j^{\,M} > + \hat{\beta}_j^{\,S}$
Seasons *or* Dry/Wet periods	$+ \hat{\beta}_j^{\,Dry}$ *or* $+ \hat{\beta}_j^{\,season}$
Water levels	$- \hat{\beta}_j^{\,WL}$
Rainfall	$- \hat{\beta}_j^{\,rain}$
Days continuously dry	$+ \hat{\beta}_j^{\,DaysDry}$
Days continuously wet	$- \hat{\beta}_j^{\,DaysWet}$
Air temperature	$- \hat{\beta}_j^{\,temp.}$

$\hat{\psi}_i^{\,sr}$ covariates	A priori prediction
Sex-specific	$- \hat{\beta}_j^{\,sex(male)}$
Tree island strata-specific	$- \hat{\beta}_j^{\,L} \approx - \hat{\beta}_j^{\,M} < \hat{\beta}_j^{\,S}$
Seasons *or* Dry/Wet periods	$+ \hat{\beta}_j^{\,Dry}$ *or* $+ \hat{\beta}_j^{\,season(dry)}$
Water levels	$- \hat{\beta}_j^{\,WL}$

Table 2.3. Predicted negative or positive ($\hat{\beta}_j$) effect of strata, sex and environmental covariates on *S. hispidus* apparent survival probability ($\hat{S}_i^{\,r}$) and strata transition probabilities ($\hat{\psi}_i^{\,sr}$).

S	*p*	ψ	Delta-AICc	AICc Weights	No. parameters
M2 s . / Dry [last 2] + WL	s + WL	s(SM=SL) * WL + sex + rain (LS)	0	0.32	24
M2 s . / Dry [last 2] + sex	s + WetDry + WL	s(SM=SL) * WL + sex + rain (LS)	0.64	0.23	25
M2 s . / Dry [last 2] + sex + WL	s + WetDry + WL	s(SM=SL) * WL + sex + rain (LS)	1.96	0.12	26
M2 s . / Dry [last 2] + sex	s + WL	s(SM=SL) * WL + sex + rain (LS)	2.65	0.08	24
M2 s . / Dry [last 2] + sex + WL	s + WL	s(SM=SL) * WL + sex + rain (LS)	3.54	0.05	25
M2 s . / Dry [last 2] + WL	s + WetDry + WL	s(SM=SL) * WL + sex + rain (LS)	3.54	0.05	25
M2 s . / Dry [last 2] + sex	s + WetDry + WL	s * WL + sex + rain	3.72	0.05	26
M2 s . / Dry [last 2] + sex	s + WetDry + WL	s * WL + sex	4.25	0.04	25
M2 s . / Dry [last 2] + sex	s + WL	s * WL + sex + rain	5.94	0.02	25
M2 s . / Dry [last 2] + sex	s + WL	s * WL + sex	6.65	0.01	24

Table 2.4. Model selection rankings for *O. palustris* captured and marked at Rock Reef Pass, Everglades National Park, Florida, USA, 1994 – 2003. Shown are the models that received nearly all support in the data (combined AICc weight ~ 1.0). Survival (*S*) was described as a "M2" to a two-age class model whit state-specific fixed survival rates "s ." for the first age-class. Survival rates for the second age-class were described as a function of the last two dry periods "Dry [last 2]" that occurred during this study and as sex-specific rates where survival differs between sexes by a fixed additive term. Capture probabilities (*p*) were described as strata-specific and as an additive function "+" of water levels "WL". Transition probabilities (ψ) were described as strata-specific "s" except in models where transitions from small to other strata are equal "s(SM=SL), and with the best fit models, as a function of the interaction "*" of strata and water levels. Transition rates were also described as additive functions of sex, or in this case the effect of being male and of rain, where in the best fit six models, rain effects only transitions from large to small island size classes "rain(LS)".

O. palustris

Model delta-AICc: 0

S(M2 s . / Dry [last 2] + WL) ***p*(s + WL)** ψ(s(SM=SL) * WL + sex + rain (LS))

	$\hat{p}_i$	
β_j Description	$\hat{\beta}_j$	95 % Confidence interval
Large islands strata	-1.07	-1.51 to -0.63
Medium islands strata	-3.22	-3.48 to -2.96
Small islands strata	2.56	2.56 to 2.56
Water levels	0.02	0.01 to 0.02

Model delta-AICc: 0.64

S(M2 s . / Dry [last 2] + sex) ***p*(s + WetDry + WL)** ψ(s(SM=SL) * WL + sex + rain (LS))

	$\hat{p}_i$	
β_j Description	$\hat{\beta}_j$	95 % Confidence interval
Large islands strata	- 1.36	- 1.56 to - 1.15
Medium islands strata	0.54	0.17 to 0.91
Small islands strata	13.21	13.21 to 13.21
Dry periods	- 0.54	- 0.86 to - 0.21
Water levels	0.007	- 0.001 to 0.02

Table 2.5. $\hat{\beta}$ coefficients for capture probability ($\hat{p}$) model covariates from the two highest overall ranked *O. palustris* models. $\hat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and capture probability (p).

O. palustris

Model delta-AICc: 0

***S*(M2 s . / Dry [last 2] + WL)** *p*(s + WL) ψ(s(SM=SL) * WL + sex + rain (LS))

$\hat{S}_{2\text{-}119}$			
β_j Description	$\hat{\beta}_j$	95 % Confidence interval	A priori prediction
Second to last dry period	- 2.41	- 3.46 to - 1.37	- $\hat{\beta}_j$
Last dry period	- 1.58	- 2.46 to - 0.70	- $\hat{\beta}_j$
Water level	- 0.003	- 0.008 to 0.002	+ $\hat{\beta}_j$

Model delta-AICc: 0.64

***S*(M2 s . / Dry [last 2] + sex)** *p*(s + Dry + WL) *p*(s + WetDry + WL) ψ(s(SM=SL) * WL + sex + rain (LS))

$\hat{S}_i$			
β_j Description	$\hat{\beta}_j$	95 % Confidence interval	A priori prediction
Second to last dry period	- 0.329	- 0.62 to - 0.04	- $\hat{\beta}_j$
Last dry period	- 2.381	- 3.32 to - 1.44	- $\hat{\beta}_j$
Sex (male)	- 1.514	- 1.79 to - 1.24	- $\hat{\beta}_j$

Table 2.6. $\hat{\beta}_j$ coefficients for survival probability parameter ($\hat{S}_i$) model covariates from the two highest ranked *O. palustris* models. $\hat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and survival probability (*S*).

O. palustris

Model delta-AICc: 0

S(M2 s . / Dry [last 2] + WL) *p*(s + WL) **ψ(s(SM=SL) * WL + sex + rain (LS))**

$\widehat{\psi}_i^{L,M,S}$

β_j Description	$\hat{\beta}_j$	95 % Confidence interval	A priori prediction
$\widehat{\psi}^{LM}$	- 1.44	- 1.86 to - 1.02	+ $\hat{\beta}_j$
$\widehat{\psi}^{LS}$	- 2.85	- 3.23 to - 2.46	- $\hat{\beta}_j$
$\widehat{\psi}^{ML}$	- 2.20	- 2.64 to - 1.77	+ $\hat{\beta}_j$
$\widehat{\psi}^{MS}$	- 4.69	- 5.07 to - 4.32	- $\hat{\beta}_j$
$\widehat{\psi}^{SL} = \widehat{\psi}^{SM}$	0.83	0.51 to 1.15	+ $\hat{\beta}_j$
Water Level $^{\textit{Large to Medium}}$	0.002	- 0.01 to 0.015	- $\hat{\beta}_j$
Water Level $^{\textit{Large to Small}}$	0.02	0.01 to 0.03	+ $\hat{\beta}_j$
Water Level $^{\textit{Medium}\text{ to Large}}$	- 0.003	- 0.02 to 0.01	- $\hat{\beta}_j$
Water Level $^{\textit{Medium to Large}}$	0.02	0.02 to 0.02	- $\hat{\beta}_j$
Water Level $^{\textit{Small to Large+ Medium}}$	- 0.013	- 0.015 to - 0.01	+ $\hat{\beta}_j$
Sex $_{\text{males}}$	0.008	0.008 to 0.008	+ $\hat{\beta}_j$
Rainfall $^{\textit{Large to Small}}$	0.71	0.71 to 0.71	*No prediction*

Table 2.7. $\hat{\beta}_j$ coefficients for transition probability parameter ($\widehat{\psi}$) model covariates from the two highest overall ranked *O. palustris* models. $\hat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and transition probability ($\widehat{\psi}_i$).

S	*p*	ψ	Delta-AICc	AICc Weights	No. parameters
M2 (.) / s * rain + WL + seasons	s * sex + seasons	s * sex	0	0.394	31
M2 (.) / s * rain + WL + seasons	s * sex + seasons	s * sex + season + WL	0.2260	0.352	33
M2 (.) / s * rain + WL + seasons	s * sex + seasons	s * sex + season	0.8900	0.253	32
M2 (.) / s * rain + WL + seasons	s + sex + seasons	s * sex + season	11.1519	0.002	26

Table 2.8. The four highest ranked models for *S. hispidus* captured and marked at Rock Reef Pass, Everglades National Park, Florida, USA, 1994 – 2003. The four models shown are the models that received nearly all support in the data (combined AICc weight ~ 1.0).

S. hispidus

Model delta-AICc: 0

S(M2 (.) / s * rain, s*sex, + WL + seasons), ***p*(s * sex + season),** ψ (s * sex)

	$\hat{p}_i$	
β_j Description	$\hat{\beta}_j$	95 % Confidence interval
Large islands strata	1.04	0.86 to 1.23
Medium islands strata	1.30	0.97 to 1.62
Small islands strata	-2.49	-2.85 to -2.13
Sex (male)	-0.14	-0.35 to 0.07
Seasons	1.19	0.93 to 1.46
Medium*Sex(male)	-2.15	-2.74 to -1.56
Small*Sex(male)	-1.61	-2.09 to -1.13

Table 2.9. $\hat{\beta}_j$ coefficients for capture probability ($\hat{p}$) model covariates from the most parsimonious *S. hispidus* model. $\hat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and capture probability (p).

S. hispidus

Model delta-AICc: 0

S(M2 (.) / s * rain, s*sex, + WL + seasons), p(s * sex + season), ψ (s * sex)

$\hat{S}_i$			
β_j Description	$\hat{\beta}_j$	95 % Confidence interval	A priori prediction
Transient	0.05	0.03 to 0.08	*No prediction*
Large	-0.64	-0.74 to -0.54	+ $\hat{\beta}_j$
Medium	0.73	0.56 to 0.91	+ $\hat{\beta}_j$
Small	-0.24	-0.33 to -0.15	- $\hat{\beta}_j$
+ Sex (male)	-0.08	-0.15 to -0.01	- $\hat{\beta}_j$
+ rain	-0.01	-0.01 to 0.00	- $\hat{\beta}_j$
+ Calendar season (dry)	1.01	0.85 to 1.18	+ $\hat{\beta}_j$
+ water levels	0.01	0.01 to 0.01	- $\hat{\beta}_j$
Rain * Medium	-0.04	-0.05 to -0.03	- $\hat{\beta}_j$
Rain * Small	-0.02	-0.03 to -0.01	- $\hat{\beta}_j$
Male * Medium	-0.31	-0.52 to -0.10	- $\hat{\beta}_j$
Male * Small	2.36	1.90 to 2.81	*No prediction*

Table 2.10. $\hat{\beta}$ coefficients for survival probability ($\hat{S}$) model covariates from the most parsimonious *S. hispidus* model. The a priori column shows the predicted sign for each $\hat{\beta}_j$. $\hat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and survival probability (S).

S. hispidus

Model delta-AICc: 0

S(M2 (.) / s * rain, s*sex, + WL + seasons), p(s * sex + season), **ψ (s * sex)**

$\widehat{\psi}_i^{L,M,S}$			
β_j Description	$\widehat{\beta}_j$	95 % Confidence interval	A priori prediction
$\widehat{\psi}^{LM}$	-5.157	-5.59 to -4.72	+ $\widehat{\beta}_j$
$\widehat{\psi}^{LS}$	-2.293	-2.6 to -1.99	- $\widehat{\beta}_j$
$\widehat{\psi}^{ML}$	-2.733	-3.23 to -2.24	+ $\widehat{\beta}_j$
$\widehat{\psi}^{MS}$	-1.199	-1.55 to -0.85	- $\widehat{\beta}_j$
$\widehat{\psi}^{SL}$	-1.602	-1.93 to -1.27	+ $\widehat{\beta}_j$
$\widehat{\psi}^{SM}$	-1.280	-1.68 to -0.88	+ $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{LM}$	2.109	1.37 to 2.84	- $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{LS}$	0.684	0.22 to 1.15	- $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{ML}$	0.833	0.07 to 1.59	- $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{MS}$	0.070	-0.21 to 0.35	- $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{SL}$	-0.927	-1.64 to -0.21	- $\widehat{\beta}_j$
Sex (male) * $\widehat{\psi}^{SM}$	-1.861	-2.57 to -1.15	- $\widehat{\beta}_j$

Table 2.11. $\widehat{\beta}$ coefficients for transition probability parameter ($\widehat{\psi}$) model covariates from the most parsimonious *S. hispidus* model. $\widehat{\beta}_j$ is the estimated slope parameter of the linear-logistic relationship between a specified habitat covariate and transition probability ($\widehat{\psi}_i$).

CONCLUSIONS

This work was motivated by concerns that the loss of tree islands in the Everglades, with a disproportionate greater loss of larger tree islands (Wetzel *et al.* 2005), could negatively affect the rodent community. Given the lack of information on the ecology of rodent species in the Everglades, the primary goal the work presented here was to contribute to the limited information on the ecology of Everglades rodents by examining the relationship between the two most abundant rodent species throughout the Everglades, *O. palustris* and *S. hispidus,* and the most salient features of the Everglades ecosystems, its tree islands and hydroperiods.

Habitat patch size has been shown to directly influence animal fitness and fecundity (Morrison *et al.* 1992). Patch size-related differences in animal fitness and fecundity can be observed as patch-specific quantitative changes in life history traits, such as movement and reproductive condition, and as quantitative changes in patch size-specific demographic rates, such as reproduction and survival. If patch-specific demographic rates differ sufficiently among patches, the relative availability and use of those patches that positively influence demographic success become of greater conservation value, and the loss or degradation of such patches is likely to have a disproportionately greater effect on animal populations. This is especially true for animal populations on islands systems, since the negative consequences of patch loss are greater because the loss of islands results in both the permanent loss of habitat and an alteration in how habitat is distributed. Therefore, understanding the relationship between habitat patches and animal populations is of special interest in ecosystems where islands are being degraded and lost, such as in the Everglades. In particular, the disproportionate loss of larger tree islands in the Everglades (Wetzel *et al.* 2005), which are thought to provide a more favorable habitat to rodents, could magnify the effects of the loss of tree islands, resulting in decreased demographic performance of the rodent community in the Everglades.

If tree island area influences the relative quality or suitability of the habitat that tree islands provide for rodents, it would be expected that individual fitness traits and demographic rates should differ with tree island area. In Chapter One, island size-related differences in rodent fitness and demographic rates were investigated by correlating the values for traits associated with adult female fitness and reproduction with tree island area and by comparing the tree island size class-specific values for these traits for individuals on islands of different sizes. In Chapter Two, I described the use of a multi-state mark-recapture approach, where states were defined as three tree island size classes. This approach allowed for the modeling of the probabilities for survival, animal transition between states, and recaptures as a function of island strata, sex and environment covariates. A model selection approach was used to order models from least likely to most likely to explain estimated survival rates, recapture and transition probabilities (Nichols *et al*. 1994, Nichols and Kendall 1995).

These analyses were conducted using rodent capture histories and data on animal weights and reproductive condition data (collected at the time of capture on 16 tree islands at Rock Reef Pass, Everglades National Park, Homestead, FL, between February 1994 and December 2005) were used to quantify traits associated with adult female fitness and reproductive state for the two most common rodent species on tree islands of the Everglades, the hispid cotton rat (*Sigmodon hispidus*) and the marsh rice rat

(*Oryzomys palustris*). Animal body weights, which have been shown to be a fitness component in rodents (*e.g.*, Krackow 1992), were used as an indicator of adult female fitness. The proportions of captured females that were reproductively active, the proportions of captured individuals that were juveniles and the number of juvenile individuals per adult female were used as indirect indicators of rodent reproduction.

S. hispidus – body weight

The relationship between adult female *S. hispidus* body weight was consistent with the prediction that larger tree islands provide a more suitable habitat for *S. hispidus*, and where, relative to smaller tree island size classes, adult female fitness would be higher on large size class islands.

The body weights of *S. hispidus* adult females were positively correlated (ρ = 0.184; P = 0.002) to tree island area (Figure 1.6), suggesting that there is a positive relationship between fitness and island area. If this relationship arises because large islands provide a more favorable habitat, it might be expected that heavier, more dominant females would make greater use of large islands while subordinate, lighter females would be displaced more often, thus contributing to lower body weights among adult females recaptured on different islands. Consistent with this possible interpretation, the weights of adult *S. hispidus* females recaptured on the same tree island were positively correlated (ρ = 0.174, P = 0.001) with tree island area (Figure 1.7a) and differed among island size classes – females recaptured on the same large or medium island weighed more than females recaptured on the same small island. The weight of *S. hispidus* females recaptured on the same island were also higher than the weights of adult females recaptured on a different tree island and whose body weight was not correlated with the area of the tree island on which females were previously captured (Figure 1.7b).

S. hispidus – traits associated with reproduction

The relationship between tree island size and the proportions of *S. hispidus* adult females that were reproductively active, as well as the proportions of juveniles in *S. hispidus* captures, were mostly consistent with the prediction that *S. hispidus* reproductive rates would be higher on larger islands than on smaller islands. Although the monthly proportions of reproductively active *S. hispidus* females captured on each tree island were not correlated to the area of the tree islands on which they were captured (Figure 1.12), the proportions of females that were reproductively active on large tree islands were greater ($t = 3.126$; $df = 159$; $P = 0.0019$) than on medium islands but did not differ between large and small tree islands (Figure 1.13). The results also suggest that reproductively active females make greater use of larger islands than non-reproductively active *S. hispidus* females. The proportion of reproductively active *S. hispidus* females captured on large islands was greater than the proportions of non-reproductively active females captured on large islands (Figure 1.14).

Both the monthly proportions of *S. hispidus* individuals captured within each tree island that were in the juvenile age class and the number of juveniles per female were positively correlated ($\rho = 0.084$; $P = 0.037$; $\rho = 0.096$, $P = 0.038$) with tree island area (Figures 1.18 and 1.20). The proportions of individuals captured that were juveniles were also greater on large islands than on small islands, while the number of *S. hispidus* juveniles per females did not differ among tree island size classes.

S. hispidus fitness, as indicated by body weight, and reproduction, as indicated by the proportions of juvenile and of reproductive active females within tree islands, provide indirect evidence that relative to smaller tree islands, larger tree islands provide *S. hispidus* with a more suitable habitat where females have higher fitness and possibly have higher reproductive success. If larger tree islands do provide a more suitable habitat for *S. hispidus,* then it would be predicted that survival probabilities should differ among tree island size classes and survival rates should be higher on larger islands than on smaller tree islands (see Table 2.3 for detailed a priori predictions).

S. hispidus – survival probability

The most parsimonious model (Table 2.8) described *S. hispidus* monthly survival rates as strata-specific as predicted, however, contrary to a priory predictions, the $\hat{\beta}_j$ coefficient for the large island strata effect on survival indicated that large islands had a negative effect on *S. hispidus* survival (Table 2.10). Despite this, the estimated female survival rates on large and medium islands were similar and higher than on small islands ($\hat{S}_t^{L\,female} = 0.68$, $\hat{S}_t^{M\,female} = 0.73$, $\hat{S}_t^{S\,female} = 0.57$) as expected.

Male survival rates on large and medium islands were ($\hat{S}_t^{L\,male} = 0.66$, $\hat{S}_t^{M\,male} = 0.65$) nearly identical and just slightly lower than those of females. Surprisingly, male survival rates on small islands were very high ($\hat{S}_t^{S\,male} = 0.92$). However, only 15% (N = 224) of *S. hispidus* male captures occurred on small islands, while 62% (N = 927) of *S. hispidus* male captures occurred on large islands, meaning that even if males do experience much higher survival rates on small islands, the overall affect on the population is relatively minor, given the small number of males captured on small islands.

Despite the negative effect of large islands on *S. hispidus* survival rates, the estimated monthly survival probabilities were, with the exception of (a few) males with high survival rates on small islands, consistent with the prediction that large islands provide a more suitable habitat for *S. hispidus* and that individuals on larger islands have higher survival rates than on small islands.

In addition to describing *S. hispidus* survival rates as a function of sex and island strata, the most parsimonious model also described survival rates of *S. hispidus* as an additive function of rainfall, water levels, and dry seasonal periods. Rainfall, as expected, had a negative effect (Table 2.10) on *S. hispidus* survival rates – as it often does on rodents. The coefficients for the interaction of rain and island strata, $\hat{\beta}_j^{\,rain*M}$ and $\hat{\beta}_j^{\,rain*S}$, indicated that relative to large island strata, the negative effect of rainfall on *S. hispidus* survival was greater on medium and small island strata, providing additional support for the greater suitability of large islands as habitat for *S. hispidus*. Water levels, contrary to what was predicted, had a positive effect on survival, although relative to the other $\hat{\beta}_j$ coefficients in the model, the effect of water levels on survival rates was low in magnitude. As predicted, the survival rates of *S. hispidus* were described as a positive function of dry periods. Of the environmental covariates in the most parsimonious model, dry seasonal periods (November to April) had the highest magnitude effect on *S. hispidus* survival rates (Table 2.10). Seasonal variations in survival rates are readily visible in the *S. hispidus* male (Figure 2.7) and female (Figure 2.8) monthly survival probability time-series, as periods of higher survival rates that primarily occur during dry season months.

The descriptions of *S. hispidus* survival by the most parsimonious model as a function of environmental covariates were consistent with the expectation that *S. hispidus* survival rates are higher during the dry season than during the wet season. Contrary to my expectations however, the influence of water levels on *S. hispidus* survival was weaker than expected and the covariates for the duration of wet (Days Wet) and dry periods (Days Dry) were not supported in the data as affecting survival rates.

S. hispidus – transition probabilities

The most parsimonious model described *S. hispidus* transition probabilities among tree the three island size classes as strata- and sex-specific (Table 2.8). Transition probabilities for *S. hispidus* females were consistent with the prediction that females would make greater use of large tree islands. Females on large islands were more likely to remain within the same strata ($\hat{\bar{\psi}}_i^{LL} = 0.9$) than females on medium ($\hat{\bar{\psi}}_i^{MM} = 0.77$) or small island strata ($\hat{\bar{\psi}}_i^{SS} = 0.69$) (Figure 2.9). Male transition rates mirrored male strata-specific survival rates. Males on small islands were more likely to remain within the same stratum ($\hat{\bar{\psi}}_i^{SS} = 0.9$) than males on either medium ($\hat{\bar{\psi}}_i^{MM} = 0.74$) or large islands ($\hat{\bar{\psi}}_i^{LL} = 0.81$) (Figure 2.9). Contrary to my prediction, *S. hispidus* transition rates were not described as a function of seasonal periods, suggesting that periods of inundation do not impede the movement of *S. hispidus* at Rock Reef Pass.

Conclusions - S. hispidus

Overall, the results reported in this work were consistent with an interpretation that, relative to smaller tree islands, larger tree islands provide a more favorable habitat for *S. hispidus*. Given these findings, it would be expected that in areas where larger tree islands have been lost it is likely that *S. hispidus* populations experienced declines.

S. hispidus survival rates differed seasonally; however, since survival rates represent the complement of death and permanent emigration, it is possibly that seasonal differences in survival are the result of seasonal permanent emigration. However, it has been my experience, and those of other working in the field, that *S. hispidus* individuals generally have high site fidelity and when moved a significant distance, they tend to return to the same area.

State-transition rates and the number of *S. hispidus* captured on different island strata, suggest that overall, *S. hispidus* are more likely to make greater use of large islands.

O. palustris – body weight

In contrast to the results for *S. hispidus* females, *O. palustris* adult female fitness, as indicated by body weight, was not as strongly associated with island size. The body weights of adult *O. palustris* females were not correlated to tree island area and did not differ between females recaptured on the same tree island and those recaptured on a different tree island from where they were last captured. The only significant differences in *O. palustris* adult female body weights were among *O. palustris* females recaptured on the same tree island, where females recaptured on the same large island weighed more than adult females recaptured on the same medium or small tree island (Figure 1.11). These results suggest that, overall, *O. palustris* adult female fitness, as indicated by body weight, does not differ greatly with the area or size class of the tree island where females were captured. Unlike *S. hispidus* adult females, the body weights of *O. palustris* females captured on different size tree islands do not suggest that larger tree islands offer a more suitable habitat for *O. palustris* females than smaller tree islands. It is possible however, that *O. palustris* adult female fitness is influenced by the overall distribution and availability of larger islands rather than by the specific island females are captured on. These results would also predict that *O. palustris* adult female survival rates are not strata-specific.

O. palustris– traits associated with reproduction

Contrary to *S. hispidus* and my predictions, the results reported in Chapter One suggest that *O. palustris* reproductive rates are higher on small tree islands. The monthly proportions of *O. palustris* females captured on each tree island that were reproductively active were negatively correlated (ρ = - 0.134; P = 0.009) to tree island area (Figure 1.15). The proportions of reproductively active *O. palustris* females on small tree islands were also greater than on large islands (Figure 1.16). On small tree islands the proportions of reproductively active female captures were greater than the proportions of non-reproductive female captures that occurred on small islands. This suggests that reproductively active females make more use of smaller islands than non-reproductive females do. Although the monthly proportions of *O. palustris* individuals captured within each tree island that were in the juvenile age class were not correlated with the area of the tree island where individuals were captured, greater proportions of *O. palustris* captured on small tree islands were in the juvenile age class than those captured on large tree islands (Figure 1.23). The number of juveniles per adult female was not correlated with tree island area and did not differ among tree island size classes.

O. palustris – survival rates

Contrary to my initial prediction, but consistent with the analysis of *O. palustris* adult female traits associated with fitness and reproduction, *O. palustris* survival probabilities were not described by the most parsimonious model as strata-specific (Table 2.4). Survival was also not described as sex-specific in the most parsimonious model, but sex was included in 8 of the 10 models that received virtually all support (AICc [w] ~ 1.0). Male survivorship was, as predicted, lower than that of females (Table 2.6), however, the difference in model averaged survival rates for males and females was minimal (males: $\hat{\hat{S}}_t^{Large} = \hat{\hat{S}}_t^{Medium} = \hat{\hat{S}}_t^{Small} = 0.71$, males: $\hat{\hat{S}}_t^{Large} = \hat{\hat{S}}_t^{Medium} = \hat{\hat{S}}_t^{Small} =$ 0.75). Only models with little variation in survival received support in the data. As a consequence, survival was estimated as a nearly constant rate, except for two prominent decreases in survival during two of 10 dry periods (Figure 2.4). Although water levels were included in the best fit models, the $\widehat{\beta}^{WL}$ coefficient in the most parsimonious model was negative (Table 2.6) and its CI included zero.

O. palustris – transition probabilities

Unlike the survival probability analysis that did not provide many insights on the ecology of *O. palustris* in the Everglades, the analysis *O. palustris* transition rates among tree island size classes, was more informative and provided insights in to the use of tree islands by *O. palustris.* Consistent with a priori predictions (Table 2.2), the most parsimonious model described *O. palustris* transition probabilities as strata-specific, with the exception of transitions from small to medium and from small to large islands (Table 2.4). Also as predicted, transition rates were described as sex-specific with males having higher transition rates than females (Table 2.7). Overall, *O. palustris* were more likely to remain on larger islands and to move from smaller islands (figure 2.5). Although seasonal covariates were not included in the most parsimonious model, transition rates were described as a function of monthly water levels, allowing survival rates to vary as monthly-specific rates that also varied as a function of seasonal differences in water levels. The $\hat{\beta}_j^{WL}$ coefficient for the interaction of water levels and strata-specific transition rates (Table 2.7) indicated during the dry season, when water levels are lower, *O. palustris* on large and medium islands were more likely to remain within the same strata, while *O. palustris* on small islands were more likely to remain within the same stratum during the wet season (Figure 2.6). *O. palustris* transition rates were also described as a positive function of rainfall for transitions from large to small islands (Table 2.7). Relative to other model coefficients, the $\hat{\beta}_j^{rain}$ coefficient suggests that rain has a moderate to strong effect on *O. palustris* transitions from large to small islands, possibly as a result of an increased *O. palustris* densities on tree islands, especially after the first heavy rains of the wet season, that displaces individuals from larger to smaller islands. In comparison to *S. hispidus, O. palustris* transition rates among islands were greater was expected

Conclusions - O. palustris

O. palustris are generally thought of as moving more frequently and greater distances than *S. hispidus*. This greater movement among islands may have contributed to the less distinct differences in *O. palustris* adult female traits among tree island size classes and to the lack of support in the data for strata-specific survival rates. State-transition rates indicate that, in comparison to *S. hispidus*, *O. palustris* are more likely to move among tree islands. The higher proportions of reproductive active females and of the higher number of juveniles per females on small islands was not consistent with my expectations that large islands provided a more suitable habitat, especially for females during the rearing of young. It is possible that a study sampling *O. palustris* at greater spatial scales may find relationships between *O. palustris* and tree islands that were not identifiable at the spatial scale of this study.

WORKS CITED

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In* B. N. Petran and F. Csdki, (eds.). International symposium on information theory. Second edition. Akad&miai Kiadi, Bu-dapest, Hungary.

Armentano, T. V., D. T. Jones, M. J. Ross, and B. W. Gamble. 2002. Vegetation pattern and process. *In* F. H. Sklar and A. van der Valk (eds.). Tree islands of the Everglades. Kluwer Academic Publishers, Boston, Massachusetts.

Arnason, A. N. 1972. Parameter estimates from mark recapture experiments on two populations subject to migration and death. Researches on Population Ecology 13:97–113.

Arnason, A. N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Researches in Population Ecology 15:1–8.

Beck, Harald. 2008. Linking Amazon forest dynamics with mammalian diversity: forest dynamics and mammal diversity. VDM Verlag. Saarbrücken, Germany.

Brandt, L. A., K. M. Portier and W. M. Kitchens. 2000. Patterns of change in tree islands in Arthur R. Marshall Loxahatchee National Wildlife Refuge from 1950 to 1991. Wetlands 20(1):1-14.

Breininger, D. R., J. D. Nichols, G. C. Carter, and D. M. Oddy. 2009. Habitat-specific breeder survival of Florida Scrub-Jays: inferences from multistate models. Ecology 90:3180–3189.

Birkenholz, D. E. 1963. Movement and displacement in the rice rat. Quarterly Journal of Florida Academy of Sciences 26:269 -274.

Brownie, C. and D. S. Robson. 1983. Estimation of time-specific survival rates from tag–resighting samples: a generalization of the Jolly–Seber model," Biometrics 39: 437–453.

Brownie, C., J. E. Hines, and J. D. Nichols. 1993. Capture recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49: 1173–1187.

Buckland, S. T., K. P. Burnham, and N. H. Augustin. 1997. Model selection: an integral part of inference. Biometrics 53: 603–618.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., and D. R. Anderson. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. *In* McCullough, D. R., and R. H. Barrett (eds.). Wildlife 2001: Populations, Elsevier Applied Science, New York, New York, USA.

Cameron, G., and S. Spencer. 1981. Sigmodon hispidus. Mammalian Species 158: 1-9.

Cameraon, G. N., and B. L. Krucher. 2005. Use of coastal wetlands by hispid cotton rats (*Sigmodon hispidus*). The Southwestern Naturalist 50(3):397-401.

Caswell, H., R. M. Nisbet, A. M. de Roos, and S. Tuljapurkar. 1997. Structured population models: many methods, a few basic concepts. *In* S. Tuljapurkar and H. Caswell (eds.). Structured-Population models in marine, terrestrial, and freshwater systems. Chapman and Hall, New York.

Choquet, R., A. M. Reboulet, R. Pradel, O. Gimenez, and J. D. Lebreton. 2003. User's manual for U-CARE. Imeographed document, CEFE/CNRS, Montpellier, France. hhttp://ftp. cefe.cnrs.fr/biom/Soft-CR/Last_Update)

DeAngelis, D. L., and L. J. Gross (eds.). 1992. Individual-Based models and approaches in ecology. Routledge, Chapman and Hall, New York.

DeAngelis, D. L., L. J. Gross, M. A. Huston, W. F. Wolff, D. M. Fleming, E. J. Comiskey, and S. Sylvester. 1998. Landscape modeling for Everglades ecosystem restoration. Ecosystems 1:64-75.

Duever, M. J., J. F. Meeder, L. C. Meeder, and J. M. McCollom. 1994. The climate of South Florida and its role in shaping the Everglades ecosystem. *In* S. M. Davis and J. C. Ogden (eds.). Everglades: the Ecosystem and its Restoration. St. Lucie Press, Delray Beach, Florida.

Esher, R. J., J. L. Wolfe, and J. N. Layne. 1978. Swimming behavior of rice rats and cotton rats. Journal of Mammalogy 59: 551 – 558.

Fleming, T. H., 1979. Life-History Strategies. *In* D. M. Stoddart (ed.). Ecology of small mammals. Chapman and Hall, London.

Gaines, M. S., G. R. Sasso, J. E. Diffendorfer, and H. Beck. 2003. Effects of tree island size and water on the populations of small mammals in the Everglades. *In* F. H. Sklar and A. van der Valk (eds.). Tree islands of the Everglades. Kluwer Academic Publishers, Boston, Massachusetts.

Gentile, J. H., M. A. Harwell, W. Cropper, Jr., C. C. Harwell, D. DeAngelis, S. Davis, J. C. Ogden, and D. Lirman. 2001. Ecological conceptual models: a framework and case study on ecosystem management for South Florida sustainability. The Science of the Total Environment 274:231-253.

Golley, F. B., Petrusewicz, K. and L. Ryszkowski (eds.). 1975. Small mammals: their productivity and population dynamics. Cambridge University Press. Cambridge

Harris, V. T. 1953. Ecological relationships of meadow voles and rice rats in tidal marshes. Journal of Mammalogy 34: 479 – 487.

Hayward, G. F., and J. Phillipson. 1979. Community structure and functional role of small mammals in ecosystems. *In* D. M. Stoddart (ed.). Ecology of small mammals. Chapman and Hall, London.

Hofmockel, K. 1999. Effects of hydrological management decisions an marsh structure in Water Conservation Area 2A of the Everglades, Florida. Duke University. Masters Thesis.

Huston, M. A., D. L. DeAngelis, and W. M. Post. 1988. New computer models unify ecological theory. BioScience 38:682-691.

Jayachandran, K., S. K. Sah, J. P. Sah, and M. S. Ross. 2004. Characterization, biogeochemistry, pore water nutrient chemistry, and other aspects of soils in tree islands of Shark Slough. *In* M. S. Ross and D. T. Jones (eds.). Tree islands in the Shark Slough landscape: interactions of vegetation, hydrology, and soils. Miami, FL: Florida International University. Study No. EVER 00075.

Joule, J., and D. L. Jameson. 1972. Experimental manipulation of density in three sympatric rodents. Ecology 53:653 - 660.

Krackow, S. 1992. The effect of weaning weight on offspring fitness in wild house mice (*Mus musculus domesticus*): A preliminary study. Ethology 95:76-82.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson, 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62: 67–118.

Lodge, T. E. 2004. The Everglades Handbook: understanding the ecosystem. 2nd ed. CRC Press, Boca Raton, Florida.

Loope, L. L., and N. H. Urban. 1980. A survey of fire history and impact in tropical hardwood hammocks in the East Everglades and adjacent portions of Everglades National Park. South Florida Research Center Report T-592. Homestead, FL: National Park Service.

Michener, W. K., E. R. Blood, K. L. Bildstein, M. M. Brinson, and L. R. Gardner. 1997. Climate change, hurricanes, and tropical storms, and rising sea level in coastal wetlands. Ecological Applications 7:770–801.

Nichols, J. D., J. E. Hines, K. H. Pollock, R. L. Hinz, and W. A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. Ecology 75:2052–2065.

Nichols, J. D., and W. L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835–846.

Olmsted, I. C., L. L. Loope, and R. E. Ritz. 1980. A survey and baseline analysis of aspects of vegetation of Taylor Slough, Everglades National Park. *In* Everglades National Park South Florida Research Center Report T-586. Homestead, Florida.

Orem, W. H., D. A. Willard, H. E. Lerch, A. L. Boylan and M. Comm. 2002. Nutrient geochemistry of sediments from two tree islands in Water Conservation Area 3B, the Everglades, Florida. *In* F. H. Sklar and A. van der Valk (eds.). Tree Islands of the Everglades. Kluwer Academic Publishers, Boston, Massachusetts.

Patterson, K., and R. Fink. 1999. Tree Islands of WCA3 Aerial Photointerpretation and Trend Analysis Project Summary Report. St. Petersburg, FL: Geonex Corp. Report to The South Florida Water Management District.

Pradel, R., J. E. Hines, J.-D. Lebreton and J. D. Nichols.1997. Capture-recapture survival models taking account of transients. Biometrics 53: 60-72.

Schwarz, C. J., J. Schweigert, and A. N. Arnason. 1993. Using tag-recovery data to estimate migration rates. Biometrics 49: 177–194.

Sklar, F. H., and A. van der Valk. 2002. Tree Islands of the Everglades: An Overview. . *In* F. H. Sklar and A. van der Valk (eds.). Tree Islands of the Everglades. Kluwer Academic Publishers, Boston, Massachusetts.

Smith, A. T., J. M. Vrieze. 1979. Population structure of Everglades rodents: responses to a patchy environment. Journal of Mammalogy 60(4):778-794.

Smith, A. T. 1980. Lack of interspecific interactions of Everglades rodents on two spatial scales. Acta Theriologica 25(6):61-70.

Turchin, P., 2003. Complex Population Dynamics: a theoretical/empirical synthesis (Monographs in population biology). Princeton University Press, Princeton, New Jersey.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management 47:813–901.

Wetzel, P. R., A. G. van der Valk, S. Newman, D. E. Gawlik, T. T. Gann, C. A. Coronado-Molina, D. L. Childers and F. H. Sklar. 2005. Maintaining tree islands in the Florida Everglades: nutrient redistribution is the key. Frontiers in Ecology and the Environment 3(7): 370-376.

White, G. C., and K. P. Burnham. 1999. Program MARK for survival estimation. Bird Study 46:S120–S139.

Williams, B., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press. San Diego. CA.

Wolfe, J. L. 1985. Population ecology of the rice rat (*Oryzomys palustris*) in a coastal marsh. The Zoological Society of London 205:235-244.