

Habitat Use in Heterogeneous Areas:
A Study on the Population Dynamics and
Genetic Structure of the
Florida Marsh Rabbit
(*Sylvilagus palustris paludicola*)

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Jaime L. Warren

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INTRODUCTION

After years of controversy, scientists have reached the conclusion that species occur in habitats of varying quality. Some habitats may contain source populations from which individuals disperse, while others may contain less successful sink populations that persist through continual immigration. Pulliam (1988), Pulliam and Danielson (1991), Morris (1991), and Ostfeld (1992) have modeled source-sink dynamics, but empirical data relating habitat quality and population dynamics are scarce. Morris (1984) has shown that the population dynamics of red-back voles are influenced by habitats that differ in food quality and cover. For rodents, superior habitats generally have been associated with high population density, high survival, and high reproductive activity (Van Horne 1983, Ostfeld et al. 1985, Ostfeld and Klosterman 1986), but the population dynamics may change as environmental conditions decline. For example, in the Florida Everglades, optimal coastal prairie and marl prairie habitats supporting high population densities of small mammals may rapidly become suboptimal with seasonal flooding. If dry downs follow these periods of flooding, the habitat may become optimal again.

The Florida Everglades National Park is 1.4 million acres composed of marine and estuarine, coastal marsh, mangrove, cypress, coastal prairie, freshwater slough, pineland, freshwater marl prairie, and hardwood hammock habitats. It offers an excellent opportunity to investigate how various habitats influence the population dynamics and genetic structuring of the medium-sized mammal *S. p. paludicola*.

Sylvilagus palustris ranges from the swamps of southeastern Virginia southward to Alabama and the lower Florida Keys (Chapman and Willner 1981). Within this range, three subspecies have been identified, *S. p. paludicola*, *S. p. palustris*, and *S. p. hefneri*. *Sylvilagus*

palustris palustris occurs from Virginia to Florida, and *S. p. paludicola* occurs within the state of Florida. *Sylvilagus palustris hefneri* on the other hand is restricted to the lower Florida Keys where it is currently listed as endangered due to habitat fragmentation. Unlike the fragmented and endangered Lower Keys sub-species, both *S. p. paludicola* and *S. p. palustris* are abundant in their geographic areas, but their ecology has not been well studied when compared to other cottontails (Chapman et al., 1982). Based on its large geographical range, it is likely that *S. palustris* is capable of utilizing a variety of habitat types (Blair 1936, Fors 1995).

The Everglades National Park provides a unique opportunity to study the marsh rabbit because it is a Federally protected area composed of a variety of different habitat types that can support this species. *Sylvilagus palustris paludicola* has been sited in three major habitat types in the Everglades: the hardwood hammocks, freshwater marl prairies, and coastal prairies. Each of these habitats may vary in quality for marsh rabbit populations. The hardwood hammocks are found on the highest, driest areas. The hammocks have low tolerance for flooding and salt-water conditions from the coast (Weiner 1981). They are comprised of broad-leaved evergreen species that provide an adequate amount of cover in the form of a dense upper canopy (Gunderson 1994). Previous research indicates that only bracken fern (*Pteridium aquilinum*) and the nonnative citrus plant (*Citrus spp.*) in the hammocks are known to be used by *S. palustris* (Blair 1936, Fors 1995). *Pteridium aquilinum* is a native weed that colonizes fire damaged hammock areas, while *Citrus spp.* is only common in previously cultivated areas. Although these two plant species provide food resources for the marsh rabbit, they do not provide very much ground cover (Gunderson et al. 1988). Despite this lack of ground cover, the hardwood hammocks may be good habitat because they are rarely inundated by flooding, potentially providing a continual supply of food. Individuals may have high survival and reproductive success in conditions like

this, resulting in higher population densities and possibly more genetic diversity if dispersal is occurring.

The freshwater marl prairies are dominated by muhly grass (*Muhlenbergia filipes*) and sawgrass (*Cladium jamaicense*) that occurs over marl substrates, where bedrock elevations are slightly higher and hydro periods are shorter (Gunderson et al. 1988). *Cladium jamaicense* is a highly preferred cover species for *S. palustris hefneri* (Forys 1999). This prairie grass species has managed to adapt to flooding conditions and burning (Davis 1943, Craighead 1971, Forthman 1973, Yates 1974, Hofstetter and Parsons 1979, Wade et al. 1980). The freshwater marl prairie sawgrass near Taylor Slough consists of intermediate sawgrass, which is much smaller in size than the tall, dense marsh sawgrass. The intermediate sawgrass provides less cover than the tall sawgrass, but the lower water levels may provide more abundant food resources. The marl prairie is the driest wetland, where inundation averages 3-7 months/year with mean depths of 10 cm (Olmsted et al., 1980). Marsh rabbits are commonly found near the water, but they must have adequate food resources if the population in that habitat is to persist. Population densities may be more limited in these areas if food is scarce, possibly causing individuals to take greater risks by foraging in roadside clear cuts. This would lead to higher mortality rates, lower population density, and lower genetic diversity.

The coastal prairie may provide the most preferred habitat conditions, despite having a long year-round inundation period with mean water depths of 30 cm (Gunderson 1990). The coastal prairie is a graminoid marsh made up of a variety of aquatic plants and succulent shrubs that provide a tightly woven matrix of food, cover, and nest sites. Although this treeless area provides no canopy cover, the dense shrub vegetation does provide ground cover from aerial and land predators. *Sylvilagus palustris paludicola* is more susceptible to predation from avian

predators like the great horned owl (*Bubo virginianus*), turkey vultures (*Cathartes aura*), and red-tail hawks (*Buteo borealis*) in habitats with little cover. In addition to the avian predators, predation by gray foxes (*Urocyon cinereoargenteus*), alligators (*Alligator mississippiensis*) and water moccasins (*Agkistrodon piscivorous*) can also increase mortality rates in habitats with less suitable cover. Saltwort (*Batis maritima*) and glasswort (*Salicornia spp.*) are the most common plants in this habitat, and it is likely that these species serve as food or cover resources for *S. palustris*. This habitat may benefit the marsh rabbit because it provides adequate food and cover. Population density however, may be negatively affected by the long periods of flooding. Due to a decrease in the amount of high land for foraging, den, and nesting sites.

Habitats containing available food resources and cover that provides protection from predators, are essential to *S. palustris*. Therefore, it is possible that resource variation in different habitat types will affect the population dynamics and genetic composition of this species. The objectives of this study are to: 1) to monitor population dynamics in these three different habitat types, and 2) to test whether there is any genetic differentiation among populations in the different habitats.

GENERAL HYPOTHESIS

General Hypothesis 1: Habitat Types Affect Population Dynamics

The first hypothesis I will test is whether habitat types affect population dynamics (i.e. density, mortality, age, sex ratio, breeding activity, and body mass) of *S. p. paludicola* differently. Habitat location and related water levels could cause different patterns of use, which would affect changes in population dynamics. The null hypothesis is that population parameters will be the same for all three habitats. If the null hypothesis is false and habitat type does affect population dynamics, then I can make the following predictions:

1. Across the three habitat types, I would expect lower mortality, higher reproduction, and higher population densities in the hardwood hammocks where there is less standing water, because food, cover, and nest sites would be more available compared to freshwater marl prairie and coastal prairie.
2. Within habitat types, I would expect higher mortality, lower reproduction and lower population densities during the wet season compared to the dry season for the freshwater marl and coastal prairies. The constant flooding in the wet season would reduce the amount of suitable habitat. I would expect no difference in population parameters in the hardwood hammocks between the wet and dry season because there is little seasonal variation in standing ground water in this habitat.

General Hypothesis 2: Populations Among Habitat Types Are Genetically Different

In addition to the influences on population dynamics, habitat patchiness might also affect the genetic structure of *S. p. paludicola* populations. Forsy (1995) found polymorphism among 19 marsh rabbits of the endangered sub-species *S. p. hefneri*, but sample sizes were too small to make any habitat comparisons. Most genetic analyses on the genus *Sylvilagus* have focused on mitochondrial DNA to study phylogenetic relationships among cottontails (Halanych et al. 1996, Casane et al. 1997, Litvaitis et al. 1997), rather than the genetic structure of populations.

The three habitat types in Everglades National Park (hardwood hammocks, freshwater marl prairie and coastal prairie) are beyond the expected dispersal range of an individual marsh rabbits. Thus, there is a low probability that an individual will move from one habitat to another. Based on these conditions, my second hypothesis is that populations among habitat types are

genetically different. The null hypothesis is that there is no genetic difference among populations in the three different habitats. If the null hypothesis is false, then the following predictions can be made:

1. The greater the geographic distances are among habitats, the greater the genetic differences will be. The further two habitats are apart, the less likely the probability of an individual dispersing from one to another.
2. I would expect lower variation within the freshwater marl and coastal prairie habitats because they undergo frequent flooding, reducing density, which can result in population bottlenecks. This is not the case for the hardwood hammocks, which are not susceptible to flooding.

METHODS AND STATISTICAL ANALYSIS

Study Site and Plots

Marsh rabbit populations will be monitored in the three different habitat types: a coastal prairie habitat of the Flamingo area, the hardwood hammocks near Long Pine Key, and the freshwater marl prairies of Taylor Slough. Habitat areas were selected using resource information from Blair (1935), Forsy (1995), vegetation maps, and ground surveys. Selection was based on the surrounding vegetation type and the presence of rabbit pellets. I will survey two replicate plots within each habitat type to estimate population density, mortality, reproductive rates, age structure, and sex ratios.

Height of cover vegetation in each habitat will be measured at each site using a meter stick. These measurements will be taken every week to help assess which habitat areas possess more suitable cover within and among habitat types. In addition to cover, water level measurements will be taken in each habitat area for every sampling week. Capture-recapture

methods will provide a means of estimating population density. Within each habitat two trapping grids (90 m x 1200 m = 1.08 ha) will be established, consisting of equal numbers of traps.

Approximately twenty collapsible Havahart traps (60.9 cm x 20.3 cm x 20.3 cm) will be set at the two sites within each habitat type (40 total). Trapping stations will be placed 30 meters apart. All traps will be set in the afternoons and checked the following morning, for four consecutive days every four weeks for each habitat site. Traps will be baited with fresh apple slices. I will obtain two months of preliminary trapping data in the summer of 2000. These data will provide a baseline of prospective capture numbers and the trappability of *S. p. paludicola*. Tissue samples taken at this time will allow for a preliminary genetic study.

The following data will be recorded for each study animal captured: trap location, ear tag number (if recapture), sex, reproductive condition (testes scrotal or abdominal for males; nipple size, condition of vagina, pubic symphysis (closed), age status (adult or juvenile determined by weight), and body weight. Individuals will be marked with Monel no. 3 ear tags (National Band and Tag, Newport, KY).

Estimating Population Density

The Jolly-Seber (Jolly 1965, Seber 1965) model will be used to estimate population density and probability of survivorship. This open-population model is valid, if the following assumptions are met: 1) every individual (marked or unmarked) must have the same probability of being captured in a given sampling period; and 2) every individual has the same probability of surviving and remaining in the population until the sampling period is over. Densities, survivorship, and trapping probabilities among habitat types will be statistically compared using

Analysis of Variance (ANOVA). To better understand the effects of habitat on densities, I will consider densities in both the dry and wet seasons, and compare them by using a factorial design.

DNA Isolation, Amplification, and Sequencing

For the genetic portion of the experiment, a plug of tissue ($\sim 1 \text{ cm}^2$) will be taken from each new rabbit's ear and stored in a 1.5 ml centrifuge tube filled with a saline solution discussed in (Seutin et al 1991). Each sample will be labeled and placed on ice for transport back to the University of Miami, where tissue samples will be stored in the laboratory at -80°C . DNA will be extracted from frozen samples using Puregene® DNA (Gentra, Inc.) isolation kits. All extracted DNA will be suspended in Puregene DNA hydration solution and stored at -80°C until further analysis.

Microsatellite loci are highly variable and have proven to be an ideal genetic marker in population studies (Ashley and Dow 1994, Schlötterer and Pemberton 1994, and Storfer 1996). Variation in microsatellite loci will be determined using 10 microsatellite primers designed for the European rabbit (*Oryctolagus cuniculus*). These primers were also successfully amplified using the genus *Sylvilagus* (Rico et al. 1994, Mougél et al. 1996, Surridge et al. 1997). The ten loci are: sol 8, sol 28, sol 30, sol 44, Sat 2, Sat 4, Sat 5, Sat 7, Sat 8 and Sat 16. All microsatellite loci sequences are available on GenBank. The regions of interest will be amplified using polymerase chain reaction (PCR) on a Hybaid Limited Touchdown Thermal Cycler, following the PCR conditions and recipes provided in the literature. Confirmation of polymorphic PCR product will be achieved by running samples on a 6% denaturing polyacrylamide gel and will be analyzed by an ABI 310 DNA sequencer.

Power Analysis

Based on the data obtained from the preliminary study (June 2000 – July 2000), I will perform a power analysis to determine the optimal sample size of marsh rabbits needed to detect statistical significance (Woodward et al. 1988). After determining the appropriate sample size for a sufficient power level, a post hoc analysis will be used to determine if the null hypothesis is true or false. (Keppel 1991).

Statistical Analysis

In order to detect any differences in mean survival rates and population densities among habitat types, I will first test for homogeneity of variances among treatment groups. If the variances are equal, then I will use an ANOVA and, if appropriate, a post hoc test to determine if there are any differences among the variables. Conversely, if the variances are different, I will use the Brown-Forsythe procedure to test for unequal variances (Keppel, 1991). If the Brown-Forsythe F statistic is significant, then the treatment variances are indeed different, and I will use the Welch correction instead of an ANOVA to test the null hypothesis.

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