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An Evaluation of Movement Patterns and Effects of Habitat Patch Size on the Demography of the Florida Mouse (Podomys floridanus)

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An Evaluation of Movement Patterns and Effects of Habitat Patch Size on the Demography of the Florida Mouse (*Podomys floridanus*)

by

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Dedication

This thesis is dedicated to my husband, Michael Lukanik, without whose constant emotional and financial support I may never have embarked on a college career, much less finished with a Masters degree. His sacrifices did not go unappreciated, especially the many evenings he sat alone while I worked. It was often his pride in my accomplishments that kept me going.

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ABSTRACT

Habitat degradation by humans has been the main reason for the decline in numbers of *P. floridanus*, the only mammal indigenous to the state of Florida, in the past century. The mouse inhabits what remains of scrub and sandhill associations, which are characterized by patches of sandy soils within a more mesic landscape. It has long been accepted that small populations are more prone to decline and extinction than are larger ones as a result of environmental fluctuations. I hypothesized that the demography of a population of *P. floridanus* would be affected by a restriction in numbers through habitat patch size in a deterministic way, even without any environmental effects. I also examined dispersal and looked for evidence of metapopulation dynamics. Mark-recapture data were collected from ten scrub fragments in Lake Wales Ridge State Forest, Polk County, FL, ranging in size from 0.5 to 170 ha. Program MARK was used to model survival, recruitment and population growth rate of *P. floridanus* as a function of habitat patch size and to evaluate temporary migration patterns. Recruitment was positively associated with patch size, but contrary to expectations survival and population growth were negatively associated with patch size. Results suggested that survival was negatively affected by ear tagging, although this effect was temporary. Evidence of migration was found, but

would probably have been greater if trapping had been continued until after peak reproduction, when juveniles tend to disperse in search of resources. The degree of interbreeding among patches can only be determined with the help of genetic analyses. Microsatellites have become useful in analyses at the population level because of their high degree of variability. Future research including genetic analyses is recommended to evaluate the importance of gene flow among subgroups to demography and the viability of the study population.

INTRODUCTION

Habitat fragmentation and destruction have been the main causes for the decline in numbers of the Florida mouse (*Podomys floridanus*) (Layne 1992), as has been the case for many species of flora and fauna worldwide (Burkey 1994, reviewed in Campbell and Reece 2002 and Ricklefs and Miller 1999). *P. floridanus* is the only mammal endemic to the state of Florida (Layne 1992). Its range extends mainly over the northern two thirds of the state's peninsula, but within this area its distribution is patchy and mostly limited to what remains of natural scrub and sandhill associations (Myers 1990). During the Wisconsinan glacial period (approx. 70,000 to 10,000 years ago), when the Florida landmass was much larger and drier, *P. floridanus* may have had a more extensive and continuous distribution; however, as sea level rose during the Holocene and much of the remaining landmass became wetlands, its distribution became more restricted because of its dependence on xeric habitats (Layne 1992). Since the early 1900s, human activities such as phosphate mining, agricultural use and real estate development have further fragmented and reduced upland areas by about 70% (McCoy and Mushinsky 1992, Humphrey 1992). As a result, populations of *P. floridanus* have declined further, and the mouse is currently listed as a species of special concern by the Florida Game and Fresh Water Commission (Layne 1992) and as vulnerable on the IUCN Red List.

Previous studies have shed some light on microhabitat requirements and natural history of this species (Layne 1966, Layne and Jackson 1994, Jones unpublished, Jones

and Franz 1990, Schmutz unpublished). However, although it is generally recognized that, as a result of stochastic events, small populations are more prone to extinction than are larger ones (MacArthur and Wilson 1967, Burkey 1995, Frankham 1997), little is known about the effects of habitat fragmentation on demographic parameters and extinction risk of the Florida mouse. Hokit and Branch (2003) have shown that for populations of the scrub lizard (*Sceloporus woodi)*, which are isolated from each other because of restriction of movement between habitat patches (Clark et al. 1999, Hokit et al. 1999), patch size was positively associated with abundance, survivorship and recruitment. Thus, the size of a fragment not only constrained population size, thereby increasing the risk of extinction as a result of chance environmental fluctuations, but may also have had a direct deterministic effect on population demography. Contrary to the case of groups living in isolation, other studies have shown that some rodents exist in metapopulations, in which individuals migrate between habitat patches by way of landscape corridors. This dispersal provides increased genetic heterogeneity and thus viability of subpopulations (Merriam and Lanoue 1990, Bennett 1990). In metapopulations, therefore, immigration and emigration of individuals among groups would have effects on demographic parameters in addition to those that may result from patch size (Diffendorfer et al. 1995, Fahrig and Merriam 1992). "Source" populations may provide colonists for groups in other fragments, allowing them to persist when otherwise they might become extinct (Pulliam 1988). Genetic flow between patches increases genetic heterogeneity and reduces negative inbreeding effects and thus may contribute to the viability of populations. In the case of a species that exists in metapopulations, conservation efforts would have to encompass all subpopulations and their habitats in order to have a maximum

effect. The current study was conducted in order to determine whether habitat patch size has a deterministic effect on the demography of a population of *P. floridanus* and whether evidence of a metapopulation structure exists.

Taxonomy –

From 1909 until 1980, *P. floridanus* was described as a subgenus of the genus *Peromyscus* (Osgood 1909, Hooper 1968), which is one of the most well represented genera of North American mammals and considered the ecological counterpart of Old World *Apodemus* (Kirkland and Layne 1989). In 1980, Carleton reclassified many groups within *Peromyscus*, elevating *Podomys* to a generic level. The reclassification was based mainly on studies of the male reproductive tract, which indicated a phyletic separation of *P. floridanus* from others in the genus. Carleton found consistent links among *Podomys, Habromys* and *Neotomodon*, the latter two of which are found in southern Mexico and Guatemala. Until the 1970s, taxonomic classification had been based largely on morphological features such as dentition, cranial size and shape and the structure of reproductive organs, but shortly thereafter electrophoretic and karyologic analyses became widely available. Studies based on chromosomal inversions and rearrangements (Yates et al. 1979, Robbins and Baker 1981) confirmed the relationship between *Podomys* and *Neotomodon,* but did not include an examination of *Habromys*. Later, however, *H. lepturus* was proposed as a sister-group to *Neotomodon*. Johnson and Layne (1961) found corroborating evidence for the close relationship among the three genera based on similarities between their most common ectoparasites. According to King (1968), *P. floridanus* is thought to have descended from stock that was at one time

widely distributed in the southern U.S. and possibly in Middle America, lending further support to the idea that it may be closely related to forms currently living in Mexico.

Physical Description –

Podomys floridanus is a relatively large mouse, with adults ranging in total length between 179 and 197 mm and in mass between 25 and 49 g. Mean values vary widely among populations (Layne 1992). Eyes, ears and hind feet are proportionally large. Adult pelage is brownish or tan dorsally, fading to orange along the sides and white ventrally. Juveniles are grayish in overall color with a white venter. One of the most distinguishing features of the Florida mouse is the presence of only five plantar tubercles on the soles of the hind feet as opposed to the six found on other mice within its range. In addition to these characteristics, it has a distinct, skunk-like odor.

Demography –

Means of abundances measured in individuals/100 trapnights vary widely with habitat type and trapping method [3.5-18.1 for Layne and Griffo (1961) and 0.26–7.1 for Humphrey et al. (1985)], and Layne (1990) reported estimates of population densities with a mean and maximum of 5/ha and 28/ha, respectively. In general, scrub systems have been found to support higher densities than have been found in sandhill, presumably because of larger food availability in the form of acorn mast in scrub ecosystems (Layne 1992). Information on home range size for *P. floridanus* is scarce; however, Jones (unpublished) reported home ranges for 20 adults (males and females) ranging between 300 and 1850 m^2. Relative estimates of home range sizes based on mean distances between successive captures of individuals indicated overall larger home ranges in sandhill than in scrub (Layne 1992). Mean survival times were found to be higher for

adults than for younger age classes, with adults surviving 4.2 months and 2.0 months in sandhill and scrub, respectively. Five percent of individuals in a sandhill population survived for more than a year, and one individual survived for more than 7 years in captivity (Layne 1992). Predation by snakes, owls and various mammals is thought to be the main source of mortality. Females become sexually mature by the age of 5 weeks, while males take somewhat longer (Layne 1966). Breeding takes place primarily in late summer and fall with a lesser peak in late winter. Litter sizes can range from 1 to 5, but most often there are two to three young, and females usually produce no more than two litters per season (Layne 1992).

Habitat Requirements –

The Florida mouse occurs mainly in two types of habitats: scrub systems, including sand pine scrub and scrubby flatwoods, and sandhill (Layne 1992). These are xeric, fire-dependent plant communities located on well drained and nutrient-poor, sandy upland soils. Sandhill usually consists of three layers of vegetation. Longleaf pine (*Pinus palustris*) or slash pine (*P. elliottii*) and xeric oaks (mostly turkey oak, *Quercus laevis*) form a scattered overstory, the understory consists of *Serenoa repens, Diospyrus virginiana* and other woody shrubs and the diverse herbaceous ground layer includes *Aristada spp., Asimina angustifolia, Asclepias humistrata, A. tuberosa* and *Chrysopsis scabrella* (Taylor 1998, Hartman 1992). Scrub consists of a sand pine (*P. clausa*) overstory and a shrub layer made up of several scrubby oaks (i.e. *Q. myrtifolia, Q. geminata and Q. chapmanii*) and shrubs such as *Ceratiola ericoides, S. repens, Lyonia ferruginea, Carya floridana and Persia humilis*. Herbaceous ground cover is sparse and interspersed with open, sandy areas. Scrubby flatwoods occur on relatively dry ridges in

typical flatwoods; sand pine is usually replaced by longleaf or slash pine, and *Lyonia lucida* and *Ilex glabra* are common shrubs. Scrub oak species provide a much more abundant acorn mast than that of the turkey oaks in sandhill communities, making scrub the preferred habitat for the Florida mouse (Layne 1992). Other than acorns, the diet of the mouse consists of insects, seeds, fruits, nuts and fungi (Layne 1978, Jones unpublished). In addition to other insects, Florida mice have been observed to feed on engorged soft ticks, *Ornithodoros turicata americanus*, which are known to parasitize the gopher frog (*Rana capito*) and the gopher tortoise (*Gopherus polyphemus*) (Jones unpublished). Predation on this parasite and other insects found in gopher tortoise burrows is presumably one reason why *P. floridanus* is often found living commensally with the tortoise. The mouse is exclusively burrow-dwelling, and although there is some debate as to whether or not it constructs burrows, it is most often found inhabiting tortoise burrows and, to a lesser degree, those of the nine-banded armadillo (*Dasypus novemcinctus*), oldfield mouse (*Peromyscus polionotus*) and cotton rat (*Sigmodon hispidus*) (Layne and Jackson 1994). Excavated gopher tortoise burrows have revealed narrow side tunnels, chimneys and nest chambers constructed by Florida mice (Jones and Franz 1990). Burrows serve as a refuge from extreme temperatures and fire. Burrow temperatures are relatively constant compared with those aboveground, which I recorded to be as high as 44 degrees Celsius during midsummer at my study site in Lake Wales Ridge State Forest. Florida mice are active at night and presumably retreat underground during the day, thereby avoiding high daytime temperatures. Torpor, a physiologically regulated lowering of the body temperature, may also play a role in avoiding heat stress and water loss. Although the phenomenon has not been documented for *P. floridanus*, it has been shown

that torpor may be initiated in *P. polionotus*, which inhabits Florida scrub systems, by a lowering of ambient oxygen concentration such as occurs in burrows. In *Peromyscus eremicus* and *Peromyscus truei,* both of which exist in xeric habitats, torpor seems to be induced by negative water balance (Hill 1983).

Microsatellites -

The degree of relatedness of organisms is reflected in the degree of similarity in their DNA; two individuals of the same species or population have more similar genomes than do individuals of different species or populations. Nevertheless, high degrees of variability can be found in nuclear as well as organellar DNA in the form of heterogeneity in alleles (Parker et al 1998) even between closely related individuals. Usually, highly variable regions occur in non-coding DNA because mutations are not subject to the same selective pressures that affect coding sections of the genome. The origin of replication in mitochondrial DNA, called the Displacement Loop, is highly variable in most animal species and is therefore useful in studies at the population level. A major drawback, however, is the fact that mitochondrial DNA is inherited in a uniparental fashion, most often as part of the egg's cytoplasm, and thus studies of this DNA type will only reveal matrilines (Parker et al 1998, reviewed in Klug and Cummings 2002). Microsatellites are regions of non-coding nuclear DNA consisting of tandemly repeating units of a core nucleotide sequence of two to six base pairs. Unlike most alleles, those of microsatellites do not vary in their sequences of base pairs, but rather in the number of repeats of the core unit. This variation in number of repeats is common, making microsatellites one of the most variable types of genetic markers in the eukaryotic genome, and because they are found in nuclear rather than mitochondrial DNA they are able to trace

both parental lineages (Parker et al 1998). Once microsatellites have been processed and sequenced, specialized computer software (e.g. Arlequin, POPGENE) may be used to calculate indices of diversity, population structure, genetic distance and clustering in order to determine the relationships of individuals within and among groups (Labate 2000).

METHODS AND MATERIALS

Study Site –

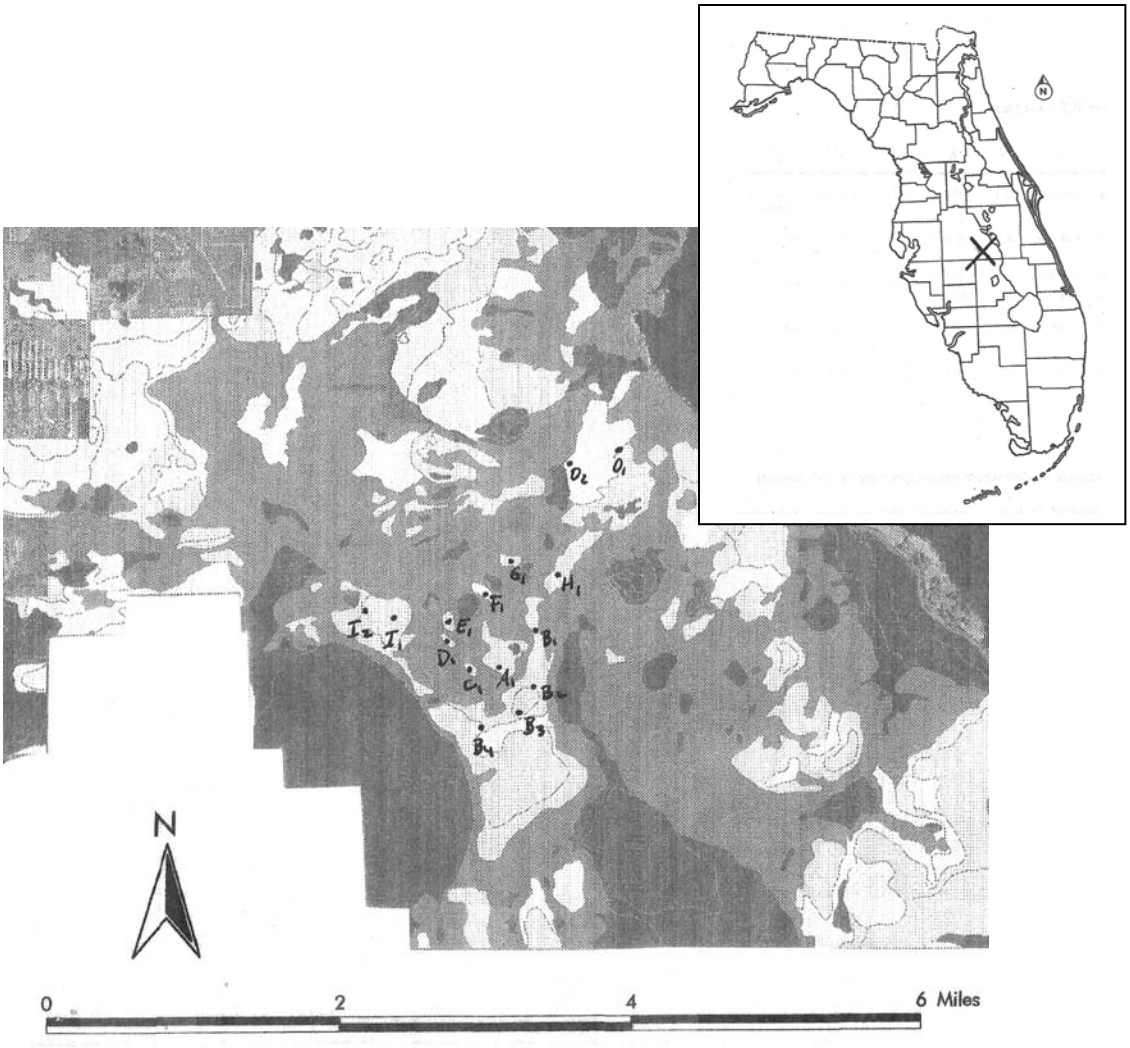
The study was conducted at the Arbuckle Tract in Lake Wales Ridge State Forest (LWRSF), located five miles southeast of the town of Frostproof in Polk County, Florida. This area is part of the Florida Central Ridge, a chain of sand ridges and ancient dunes running north-south from Clay and Putnam Counties to Highlands County (Myers 1990). The range of formerly extensive scrub ecosystems was likely reduced about 5,000 – 7,000 years ago, when climate changes resulted in rising water levels. High water levels in turn led to the present-day mosaic pattern of isolated scrub islands surrounded by low-lying, more mesic habitat. LWRSF represents one of the last remnants of a scrub system which continues to be reduced by Florida's ever-increasing human population.

Data Collection –

Fifteen arrays of 15 Sherman live traps each were installed in ten scrub fragments, which ranged in size from approx. 1.5 to 170 ha. (Figure1). My study proceeded in conjunction with ongoing research conducted by Brian Halstead, a PhD student at the University of South Florida, who was collecting data on prey species of the Eastern coachwhip snake (*Masticophis flagellum flagellum*). Sherman live traps were arranged around trap arrays already installed by Brian for the purpose of capturing reptiles and amphibians. Each of these arrays consisted of four sections of metal drift fence approximately 8 m in length extending in the four cardinal directions with a large, square trap in

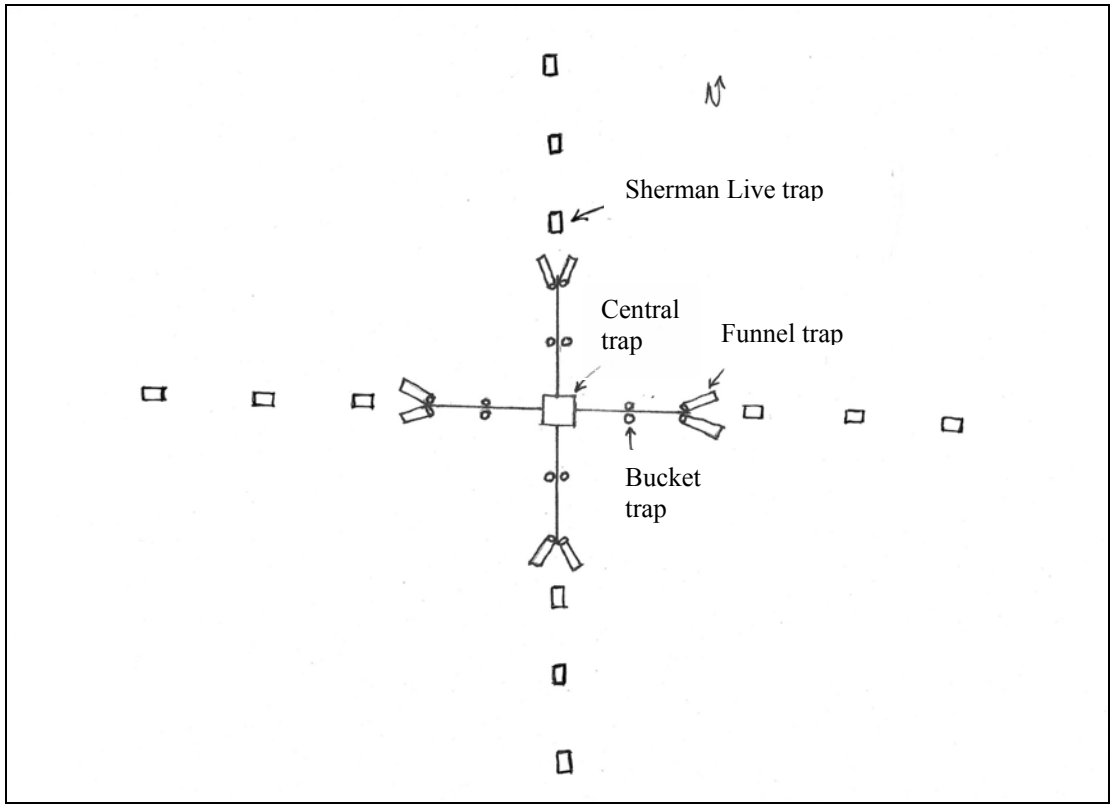
the center and bucket and funnel traps along both sides of each section. My small mammal traps were arranged such that a single row of three traps extended outward from the end of each of the four sections of drift fence, with 10 m intervals between traps (Figure 2). A two-by-four post was also installed at the north arm of each array, to which a rain

Figure 1. Location of Trap Arrays at LWRSF Study Site



gauge and a max/min thermometer were attached. Thermometers were oriented to face north so that they would not be directly inundated with sunlight. Each morning when traps were checked, amount of rainfall and maximum and minimum temperatures were recorded and the instruments were reset.

Figure 2. Arrangement of Trap Arrays



Trapping was conducted for three consecutive nights per month from March to October of 2004 and 2005. Sampling periods of at least five consecutive nights are common for small mammals (Wilson et al. 1996, Swilling and Wooton 2002, Rave and Holler 1992); however, because of the number of researchers already working in LWRSF

and in the interest of limiting human traffic through conservation land, I was only given permission to trap for three nights per month by park management. As a result, the number of models that could be used for analyses was reduced, because models incorporating individual heterogeneity in capture probability (a relaxation of one of the assumptions for closed population capture-recapture models) cannot be used with only three capture occasions per sampling period (Gary C. White, Colorado State University, personal communication). In order to test for heterogeneity in capture probabilities, I trapped for six consecutive nights at eleven of fifteen sites during the month of June 2005 and compared the results with those from other months (see Data Analyses).

Traps were opened at dusk and baited with a small handful of sunflower seeds, then checked and closed after daybreak each morning. Rolled oats with and without peanut butter are also commonly used as bait for small mammal traps; however, anecdotal evidence suggests that fire ants, which are known to prey on live-trapped animals in the southern U.S. and were also observed at the study site, may be less attracted by sunflower seeds (B. Halstead, University of South Florida, personal communication). During colder months, mice caught in traps can develop hypothermia (Jones unpublished). Therefore, traps were insulated with a handful of excelsior (wood shavings used as packing material) when temperatures were forecast to dip below 10 degrees C. Excelsior is superior to Spanish moss (Jones unpublished) and cotton (B. Halstead, personal communication) as an insulation material because it does not absorb moisture.

Captured individuals were identified to species, weighed, sexed, examined with respect to reproductive status and first-time captures were marked with metal ear tags for individual identification using a 1005-1S Monel applicator (Hasco Tag Co.). Initially, I

attempted to mark animals with an ear punch code using a stainless steel ear punch [Fine Science Tools (USA), Inc., 2 mm punch diameter], but because the ears of *P. floridanus* were so fragile, this method resulted in large tears in the ears and I abandoned the technique. Loss of ear tags became a problem in a small percentage of mice. Because site fidelity was high and there were relatively few occasions on which I captured a mouse in more than one array, I felt comfortable in assigning an individual which had obviously lost its tag a number that had belonged to an animal of the same sex and had been recorded in the same array in previous months, but not since then. Small tissue samples were taken from the ears of 86 mice with surgical scissors for DNA analyses. The scissors were swabbed with 70% isopropyl alcohol and flamed with a cigarette lighter between uses to avoid infection. Tissue samples were placed in 1.5 ml Eppendorf tubes containing a salt saturated dimethyl sulfoxide (DMSO) buffer, Ph 7.5, and later frozen to –20C.

Data from *P. floridanus* captured incidentally in B. Halstead's reptile traps during the same time periods were made available to me. I planned to analyze these data as well and compare the results with those obtained from the Sherman Live trap (SLT) arrays. Because recapture rates were very low, however, initial analyses revealed that many parameters would be inestimable and/or estimates would have huge confidence intervals, making these analyses pointless (see Results).

Data Analyses –

Mark-Recapture Data –

Mark-recapture data from two years (2004 and 2005) were analyzed using the program MARK. Initially, several model types were compared using the 2004 data set.

Those that seemed most appropriate were then selected and also used on the 2005 data. An explanation of MARK and model selection is given in Appendix A.

A factor that could have contributed to an underestimation of population sizes was the low number of secondary sampling occasions to which I had been limited (see Data Collection). I tested for this possibility using the SLT data from June 2005 (the month during which I had sampled for six consecutive nights instead of three) by plotting the cumulative number of first-time captures over time. If the slope of the line reached a horizontal asymptote by the third night, it would indicate that all available animals would have been captured by then and the additional sampling occasions would not have been necessary. Alternatively, a slope that did not level off until after the third sampling occasion would indicate that individuals that had been available for capture in other months had been missed as a result of a lack of sampling, and because population size is estimated individually for each primary sampling period, these estimates would be biased low. Using the same June data, I also ran models with and without heterogeneity in capture probabilities to estimate how much more, if any, variability could have been explained using models with heterogeneity. As previously explained, these types of models cannot be used with as few as three secondary sampling occasions.

DNA Analysis -

A search of GenBank (an open access, annotated collection of publicly available nucleotide sequences produced at the National Center for Biotechnology Information) failed to produce sequences of any known microsatellites for *P. floridanus* or either of the genera thought to be most closely related, *Habromys* or *Neotomodon*. Therefore, primers developed for microsatellites isolated in the oldfield mouse, *Peromyscus polionotus*, and

the deer mouse, *P. maniculatus* (listed below in Table 1) were used. Primers PO-9, PO-26 and PO-68 were obtained from Prince et al. (2002) while the others were among those listed in Mullen et al. (2006). All had previously been used to amplify microsatellite DNA across different species of *Peromyscus*.

DNA was extracted from ear clippings using UltraClean Tissue DNA Isolation kits (Mo Bio Laboratories, Inc.; Catalog No. 12334-S). Touchdown PCR amplifications were performed in a 25µL volume. For all primers, 25ng of template DNA, 1.25 U *Taq* DNA polymerase (ID Labs Biotechnology, Inc.), 2.5µL of 10x ID Proof buffer with 20mM $MgCl_2$ (ID Labs Biotechnology, Inc.), 1.0µL each of 10µM forward and reverse primers (Integrated DNA Technologies, Inc.; see Table 4) and 5.0µL of 1.25mM dNTPs were used. An initial denaturing step at 94 °C for 2 minutes was followed by 10 cycles of 94 °C for 30 s, annealing for 30 s, 72 °C for 45 s, 94 °C for 30 s, annealing for 30 s and 72 °C for 45 s. Initial annealing temperature was set at 62 °C or lower (depending on melting temperatures of primers) and reduced by 1.0 °C each cycle. This procedure was followed by 20 cycles of 94 °C for 30 s, 30 s at 10 °C below the initial annealing temperature and 72 °C for 45 s. The final extension occurred at 72 °C for 90 s. If amplification was unsuccessful, initial annealing temperature was lowered by 1 °C and repeated until DNA amplification could be confirmed using agarose gel electrophoresis.

Table 1. Primers Used to Amplify *P. floridanus* Microsatellites

Primer	**Repeat Motif in Allele**	**Sequence 5'-3'**
PO - 9	$(AC)_{20}N_{14}(AC)_8$ $N_{16}(AC)_{20}$	F: TTTCAGAGGACCAGAGTAGG R: AACTCTGGGTCTTAATACTTT
PO - 26	$(AG)_{13}(ACAGAG)_4$	F: GCTTCAGTGTTGATGTCTGAT R: GCCTCTCTGTCTCTGTCTAT
PO3 - 68	$(TG)_{22+}$	F: GTAGTCTGAGAAGCGAAAGG R: TTTATTTGGGTCAGCTCGAC
PO - 31	$(GA)_{26}$	F: TTTCAGTGGCTCTCATGGTTA R: AGCTTTCTTCTTCCCAACTA
PO - 71	$(AC)_{10}(AG)_{32}$	F:CAGCCAGAACAAAATAGCACT R: AGCTTCATGCCTCCTATATTC
BW4 - 28	$(TCTA)_{15}$	F: TAATCCAGGTGTATCTAATCT R: CCCAGTATTGCTAGTCT
BW4 - 45	$(CTTT)_{19}(CT)_{19}$ $(CCTT)_4$	F: ATGGCCTGCCTACCTCA R: AGGGGAAGTGAAAAGCTACA
BW4 - 93	$(CCTT)_{10}(TTT)_{23}$	F: GACATTTAAAAAGGACTG R: CCCTCTTGATTCCACAC
BW4 - 112	$(AGAT)_{13}$	F: GGCAGTGCATTCATGGTAA R: TGAGTCCCCAGTTGTATGTA
BW4 - 137	$(ATAG)_9$ $(GATA)_{16}$	F: GGCTTGGTGGATTAATG R: ATGCCAGAGCTGTTATAC
BW4 - 178	$(ATAG)_{13}$	F: CCGTTTTTCTTACTCA R: CAAAACAGTGGGTCAA
BW4 - 200	$(ATCT)_5(GTCT)_6$	F: GCACATTTCTCCTTCTAAGC R: GACCACCTGATGAGCATAGAT
BW4 - 234	$(TGAA)_6TAAC$ $(AAAT)_4$	F: ATTCCAACTCAGCAGGTAGA R: GCCCAGAGTGTGTCATGTAG

RESULTS

In total, 419 Florida mice were captured in Sherman Live traps (SLT) during two seasons (207 in 2004 and 212 in 2005) using 7,948 trapnights. Other species encountered were mainly *Peromyscus polionotus* and occasionally *P. gossypinus* and *Sigmodon hispidus*. Densities of *P. floridanus*, calculated as number of individuals per 100 trap-nights, were 0.63 for 2004 and 0.45 for 2005. Only two individuals were captured in both years. A male was captured fifteen times and a female was captured five times, both over ten-month periods. *P. floridanus* trapped incidentally in herp arrays numbered 112 in 2004 (9,672 trapnights) and 99 in 2005 (8,736 trapnights).

Dispersal –

Of the 419 Florida mice captured in SLT arrays, 18 were recaptured in a different habitat patch from the one in which they were originally trapped. For thirteen of those individuals only one-way movement was recorded, while the other five were found to have moved off their original patch and then back again. The longest migration distance recorded was between arrays G_1 and B_4 (Figure 1), approximately 1.7 km.

Mark-Recapture Analyses -

Goodness-of-Fit of Global Models –

Bootstrap tests run on global CJS models [Phi (group*t) p (group*t)] indicated adequate fit for the SLT data sets ($p = 0.22$ for 2004 and $p = 0.15$ for 2005 with 100 simulations each), and no adjustments to $\hat{c}$ were necessary (see Appendix A, Goodness-of-Fit

and Model Selection for an explanation of ĉ). Even the least parameterized models that could have served as global starting models for the herp array data, based on the outcome of the SLT data analyses, did not provide meaningful results in the Bootstrap tests. I interpreted the combination of non-estimable parameters and/or estimates with huge confidence intervals (Appendix B, Tables 15 and 16) and zero ĉ values for the models as well as many of the Bootstrap simulations as meaning that the data were too sparse and excluded the herp array data from the analyses.

Results for 2004 –

Models with two variables connected by a "*", e.g. phi (t * patchsize), denote effects of both variables and an interaction between the two. Variables connected by a "+", e.g. phi (t + patchsize) have additive effects, but there is no interaction term. The notation (all .) in robust design models means that a parameter was held constant between secondary as well as primary sampling occasions (see Appendix A for a description of the robust design model). The notation (.) means the parameter was constant between primary sampling occasions only. Figures showing models with at least 10 % of the total weight based on AIC (Akaike's Information Criterion; see Appendix A) are included in this section, while figures including all models used in the analyses are in Appendix B.

Conventional Robust Design –

Five models all had model weights greater than 10 % (Table 2). Among them, there is significant support for a "time-since-marking" effect (symbolized by "a1"), but only weak (17 %) support for a patch size effect (symbolized "PS") on survival. A time-since-marking effect means that survival was lower in the month following initial capture and marking than in all later months. Three of the top five models incorporated time

since marking, but only the model ranked fourth supported an effect of patch size. All five models included either Markovian migration (where the probability of an individual being available for capture depended on its availability during the previous session) or random migration, with Markovian movement finding greater support overall. "No migration" models found zero support (see Appendix B, Table 17). Capture and recapture rates in the top models were constant over primary as well as secondary sampling periods. An explanation for the zero deviances in these models is provided in the Discussion section. Although γ' and γ" parameters for the last two sampling intervals had been constrained to be equal in Markovian models, which is recommended to improve estimability (Kendall 2007), one of five γ"s and two of four γ's in these models were inestimable. Estimates for the top model are shown in Appendix B, Table 18.

Table 2. 2004 Top Models Using Conventional Robust Design ranked by AIC

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (a1) p,c (all .) N (.) Markov migr}	-351.812	0.00	0.29647	1.0000	11.000	0.000
{Phi (.) p,c (all .) N (.) random migr}	-350.949	0.86	0.19253	0.6494	9.000	0.000
{Phi (a1) p,c (all .) N (.) random migr}	-350.862	0.95	0.18429	0.6216	10.000	0.000
{Phi (a1+PS) p,c (all .) N (.) Markov migr}	-350.717	1.10	0.17147	0.5784	13.000	0.000
{Phi (.) p,c (all .) N (.) Markov migr}	-350.306	1.51	0.13959	0.4708	11.000	0.000

Pradel Robust Design with Individual Covariates –

A single model [Phi, lambda (patchsize*t) p,c (.)] had all the support based on a weight of 0.999 (Appendix B, Table 19). Both survival and population growth rate changed with patch size and over time, and there was an interaction between the two variables. Capture and recapture rates were constant over secondary sampling occasions, but

varied between primary sampling occasions. One lambda parameter could not be estimated. Unlike the results for the conventional robust design type, abundance varied over time in this top model.

Pradel Robust Design with Groups –

As for the previous models using individual covariates, one model [Phi, lambda (gr*t) p,c,N (gr)] had exclusive support with a model weight of 0.997, and it is again the model incorporating effects of patch size (here a group effect based on individuals from large patches versus small patches). Survival and population growth varied between groups and over time with a group-time interaction, and group effects were detected for capture and recapture rates and for abundance N (Appendix B, Table 20). Estimates were higher in small patches than large ones, which was contrary to expectations, at least for survival and population growth. Two lambda parameters were inestimable.

Link-Barker with Individual Covariates –

Two models carried more than 10 % of the total weight (Table 3). Time variation and patch size effect with interaction were indicated for recruitment in both models. Survival varied over time but not with patch size. Recapture rate varied over time in the first model (43 % weight), but first and last recapture parameters were inestimable. In the model ranked second (33 % weight), recapture rate was constant.

Table 3. 2004 Top Models Using Link Barker with Individual Covariates

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (t) f (patchsize*t)}	1346.410	0.00	0.43380	1.0000	23.000	1297.458
{Phi (t) p (.) f (patchsize*t)}	1346.979	0.57	0.32629	0.7522	19.000	1306.969

Link Barker with Groups –

Similar to the Link Barker models with covariates, variation through time and group effect were strongly supported with regard to recruitment. The top model, carrying a weight of 39 %, indicated a group effect only on survival, while models ranked second and third incorporated variation over time but no group effect. Together the second and third models had one third of the model weight (Table 4). Capture rate again varied over time in the top two models but showed no group effect as in the Pradel robust models. Estimates for recruitment were lower in small patches than in large ones, while survival estimates were slightly higher in smaller patches than larger ones.

Table 4. 2004 Top Models Using Link Barker with Groups

Model	Delta AICc	AICc AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (gr) p (t) f (gr*t)}	1351.883	0.00	0.38923	1.0000	19.000	169.329
{Phi (t) p (t) f (gr*t)}	1353.494	1.61	0.17392	0.4468	22.000	164.252
{Phi (t) p (.) f (gr*t)}	1353.805	1.92	0.14891	0.3826	18.000	173.456

Summary of Parameter Estimates for 2004 Data –

Table 5 below shows parameter estimates and standard errors obtained from the five model types. Abundance N is defined in all cases as the total number of animals in the population exposed to sampling efforts (Amstrup et al. 2005). Where best-fit models allowed parameters to vary over time, the estimates represent average values. The two values shown for φ in the conventional Robust Design are estimates for the first month after initial capture and marking (top) and all later sampling intervals combined (bottom).

In all other cells containing two estimates, the upper and lower values stand for large and small patches, respectively.

Table 5. Parameter Estimates for 2004 Data

Model Type	φ	p	c	N	λ	f	γ''	γ'
Conventional Robust Design	0.64; 0.05 0.69; 0.04	0.60; 0.03	0.69; 0.02	72; 1	N/A	N/A	0.22; 0.09	not estimated
Pradel Robust with Individ. Covariates	0.74; 0.06	0.53; 0.07	0.68; 0.05	68; 6	0.98; 0.15	N/A	N/A	N/A
Pradel Robust with Two Groups	0.60; 0.08 0.84; 0.04	0.52; 0.04 0.75; 0.03	0.68; 0.03 0.69; 0.03	32; 1 40; 0	0.96; 0.15 1.33; 0.18	N/A	N/A	N/A
Link Barker with Individ. Covariates	0.67; 0.08	0.79; 0.08	N/A	N/A	N/A	0.20; 0.08	N/A	N/A
Link Barker with Two Groups	0.69; 0.08 0.70; 0.08	0.80; 0.07	N/A	N/A	N/A	0.29; 0.12 0.15; 0.08	N/A	N/A

Several trends became evident in models where parameters were time-dependent. Abundance varied with time in the Pradel robust design model with covariates. Estimates peaked at 87 individuals in April, the second month of trapping, and decreased continually to 36 in September (Figure 3). Survival was time-dependent in top models of all types except the conventional robust design, where it showed a time-since-marking effect instead. Similar patterns of an overall increase from April through July or August followed by a sharp decline to September were evident in all time-variant models (Figure 4). An exception in the last sampling interval was the estimate for small patches using the Pradel robust design; it was higher than the estimate for the previous interval. In the Pradel robust design model with covariates, survival rate peaked at 0.94 in July and fell

to 0.44 in September. In the Pradel robust design with two groups, survival for large patches peaked at 0.77 in July and decreased to 0.31, while for small patches it was about 1 until July and decreased to 0.61 by September. Link Barker models showed August peaks of 0.82 with individual covariates and 0.75 and 0.76 for large and small groups, respectively, followed by September lows of 0.40 with covariates and 0.57 and 0.58 for large and small groups, respectively. Trends in population growth rate were somewhat difficult to assess because several parameters were inestimable, but estimated values of λ fluctuated slightly between March and August and fell sharply in September. Recruitment parameters for the first and last intervals were not estimable as a result of confounding with other parameters in fully time-variant models. For the intervening months, values were at a maximum in the April-May interval, followed by lows in the next two intervals and a second peak in July-August (Figure 5).

Figure 3. Abundance Estimates for March - September, 2004

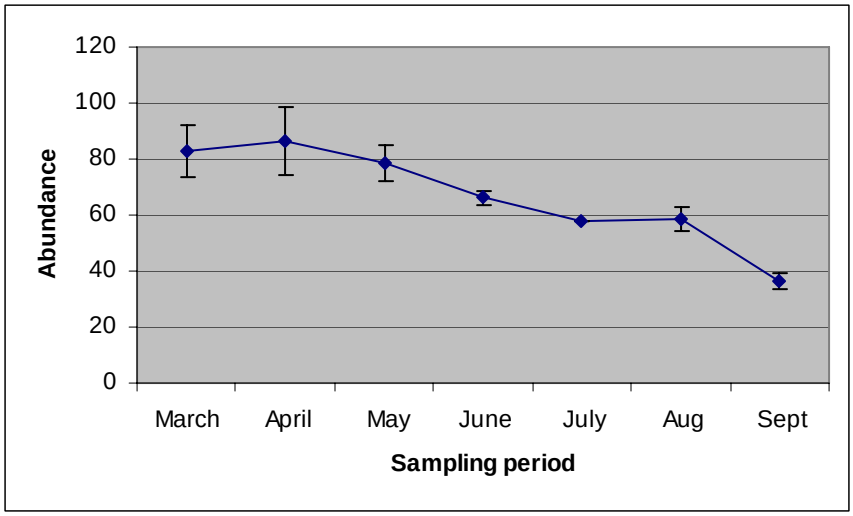


Figure 4. Survival Estimates for March-September 2004 Using Different Model Types

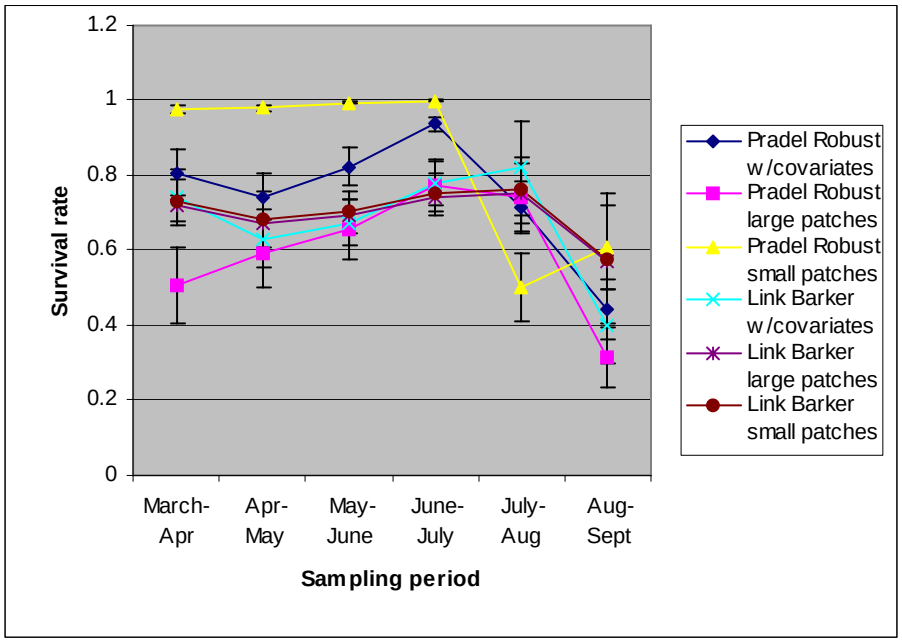
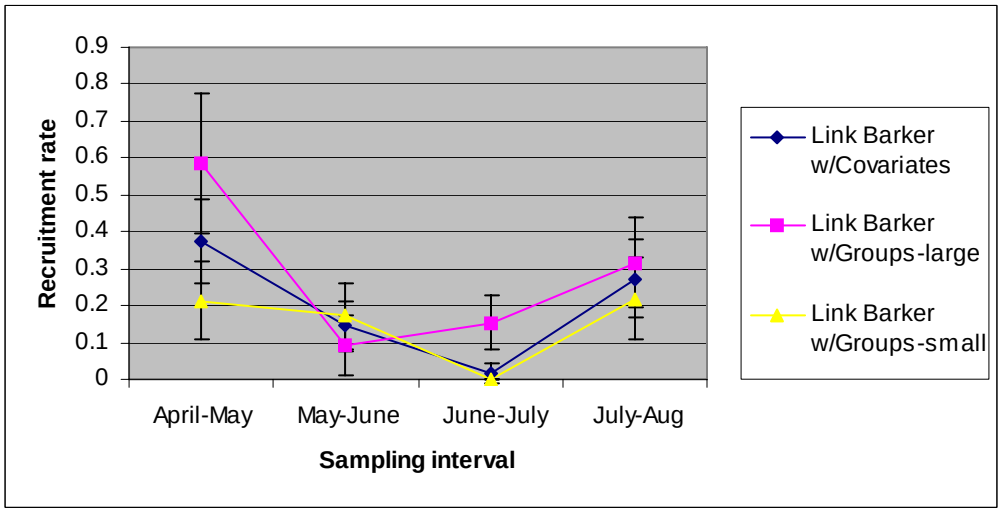


Figure 5. Recruitment Rates Using Link Barker Models



Results for 2005 Data -

Conventional Robust Design –

Similar to the results for the previous year, all best-fit models included a time-since-marking effect on survival (Table 6). Support for a patch size effect was marginal (Appendix B, Table 23). Markovian migration was again strongly supported in the top models (69 % model weight), but a "no migration" model also received some support, while random movement had zero support in this year. Capture and recapture parameters were constant over secondary sampling periods but varied between primary periods, and abundance was constant over time. Two out of three γ' parameters were inestimable in the top model.

Table 6. 2005 Top Models Using Conventional Robust Design

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (a1) p,c (.) N (.) Markov migr}	-169.681	0.00	0.52935	1.0000	20.000	0.000
{Phi (a1) gammas (.) p,c (.) N (.) Markov migr}	-167.341	2.34	0.16436	0.3105	17.000	0.000
{Phi (a1) p,c (.) N (.) no migr}	-166.620	3.06	0.11457	0.2164	15.000	0.000

Pradel Robust Design with Individual Covariates –

Models ranked first and second showed only time variation in survival and population growth rate λ. Only the model ranked third (10 % model weight) supported a patch size effect on λ (Table 7). Capture and recapture rates varied between sampling periods but were constant within them. The top model held N constant, but the second and third models (41 % combined model weight) showed variation over time in abundance.

Table 7. 2005 Top Models Using Pradel Robust with Individual Covariates

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) lambda (t) p,c (.) N (.)}	263.740	0.00	0.50239	1.0000	23.000	215.600
{Phi (t) lambda (t) p,c (.) N (t)}	264.720	0.98	0.30768	0.6124	27.000	207.767
{Phi (t) lambda (PS+t) p,c (.) N (t)}	266.875	3.14	0.10477	0.2085	28.000	207.697

Pradel Robust Design with Groups –

The top two models had almost equal weights (Table 8). Both showed variation over time in survival and population growth, but there was no support for a group effect. The top model showed time variation in abundance while the second one held N constant.

Table 8. 2005 Top Models Using Pradel Robust with Groups

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) lambda (t) p,c (.) N (t)}	670.382	0.00	0.46722	1.0000	27.000	613.429
{Phi (t) lambda (t) p,c (.) N (.)}	670.440	0.06	0.45405	0.9718	23.000	622.300

Link-Barker with Individual Covariates –

Only weak support (16 %) existed for a patch size effect on recruitment in best-fit models of this type, although the two top models held parameters constant. No patch size effect was indicated for survival, but time variation had support. Recapture rate was constant over time (Table 9).

Table 9. 2005 Top Models Using Link Barker with Individual Covariates

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (.) f (.)}	918.824	0.00	0.46775	1.0000	7.000	904.453
{Phi (.) p (.) f (.)}	920.705	1.88	0.18267	0.3905	3.000	914.626
{Phi (t) p (.) f (PS)}	920.920	2.10	0.16401	0.3506	8.000	904.442

Link Barker with Groups –

The top five models all had support, with the first one being more than twice as likely as the second and the remaining four all having similar weights (Table 10). The top model did not support a group effect in either survival or recruitment, but models ranked second through fourth showed 31 % support for a group effect on survival and 31 % support for a group effect on recruitment. Recapture rates were constant in all models and survival varied over time in the first and third models. Similar to results in 2004, models indicating group effects showed higher estimates for survival in small versus large patches and lower estimates for recruitment in small versus large patches.

Table 10. 2005 Top Models Using Link Barker with Groups

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (.) f (.)}	918.824	0.00	0.36181	1.0000	7.000	94.339
{Phi (gr) p (.) f (.)}	920.431	1.61	0.16199	0.4477	4.000	102.186
{Phi (t) p (.) f (gr)}	920.515	1.69	0.15540	0.4295	8.000	93.922
{Phi (gr) p (.) f (gr)}	920.636	1.81	0.14626	0.4042	5.000	100.324
{Phi (.) p (.) f (.)}	920.705	1.88	0.14130	0.3905	3.000	104.512

Summary of Parameter Estimates for 2005 Data –

Table 11 shows parameter estimates and standard errors for the 2005 data. As for the 2004 data set, abundance is the total number of animals exposed to sampling efforts, estimates are mean values where parameters varied over time, and two values in a cell are estimates either for time-since-marking cohorts (Conventional Robust Design) or for large vs. small patches (group effect models).

Table 11. Parameter Estimates for 2005 Data

Model Type	φ	p	c	N	λ	f	γ''	γ'
Conventional Robust Design	0.65; 0.12 0.92; 0.17	0.49; 0.06	0.50; 0.06	72; 3	N/A	N/A	0.20; 0.17	not estimated
Pradel Robust with Individ. Covariates	0.64; 0.07	0.47; 0.07	0.50; 0.06	71; 5	0.84; 0.11	N/A	N/A	N/A
Pradel Robust with Two Groups	0.63; 0.07 0.63; 0.07	0.49; 0.06 0.49; 0.06	0.50; 0.06 0.50; 0.06	40; 2	0.84; 0.11 0.84; 0.11	N/A	N/A	N/A
Link Barker with Individ. Covariates	0.65; 0.08	0.80; 0.04	N/A	N/A	N/A	0.19; 0.04	N/A	N/A
Link Barker with Two Groups	0.64; 0.08 0.67; 0.08	0.80; 0.04 0.80; 0.04	N/A	N/A	N/A	0.20; 0.03 0.18; 0.04	N/A	N/A

Abundance varied over time in several best-fit models of the Pradel robust types, although parameters for September, the last sampling period, were inestimable. In the models using covariates, model-averaged estimates were highest in April with 77 individuals and fell to 64 by August (Figure 6). The decrease in numbers was not as dramatic as in 2004, but it showed a similar trend. Pradel robust models using groups resulted in

much lower estimates than those obtained using covariates (see Table 11 and Figure 6). The values decreased from 44 individuals in April to 35 in August and are probably faulty. Models that incorporated no group effect on abundance obtained the greatest support, but apparently program MARK calculated abundance for one group for these models rather than for the entire population. Two models in the set that incorporated a group effect on abundance but received no support based on AIC values showed estimates of 42 and 40 for large groups and 30 and 26 for small groups, totaling 72 and 69, respectively, and approximating the estimates from models using covariates. As in 2004, time variation in survival was found in all models except the conventional robust design (Figure 7). Only one set of survival estimates was obtained for the Pradel robust design using groups because only models without a group effect on survival received support. Estimates peaked in the May-June interval, whereas in the previous year maximum values were found one to two months later. Overall, however, similar trends of increasing survival from spring into summer followed by a decline into early fall could be observed in both years. Survival estimates were slightly higher in small patches than in large patches in the Link Barker models, but there was considerable overlap of confidence intervals. Estimates for population growth rate were virtually identical in all Pradel robust models. They peaked at 0.97 in the May-June interval and decreased to 0.57 and 0.56 in models with covariates and models with groups, respectively (Figure 8). Recruitment did not vary with time in best-fit models for 2005, so that no trends could be observed in this parameter.

Figure 6. Abundance Estimates for April - August, 2005

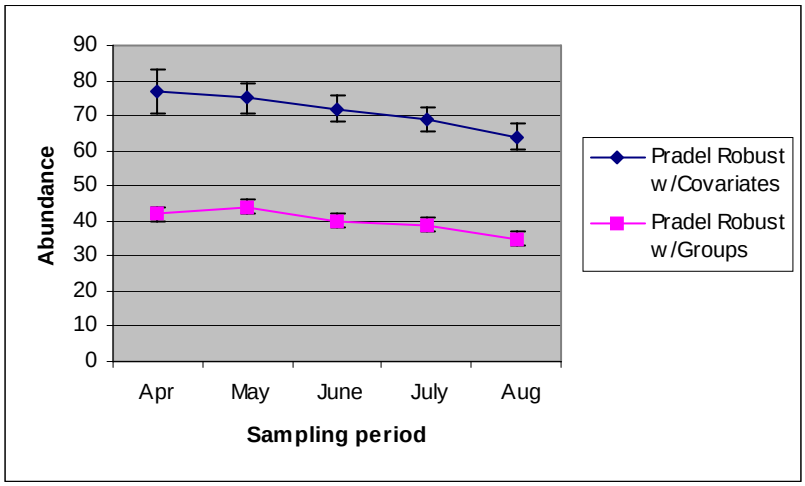


Figure 7. Survival Estimates for April - September 2005 Using Different Model Types

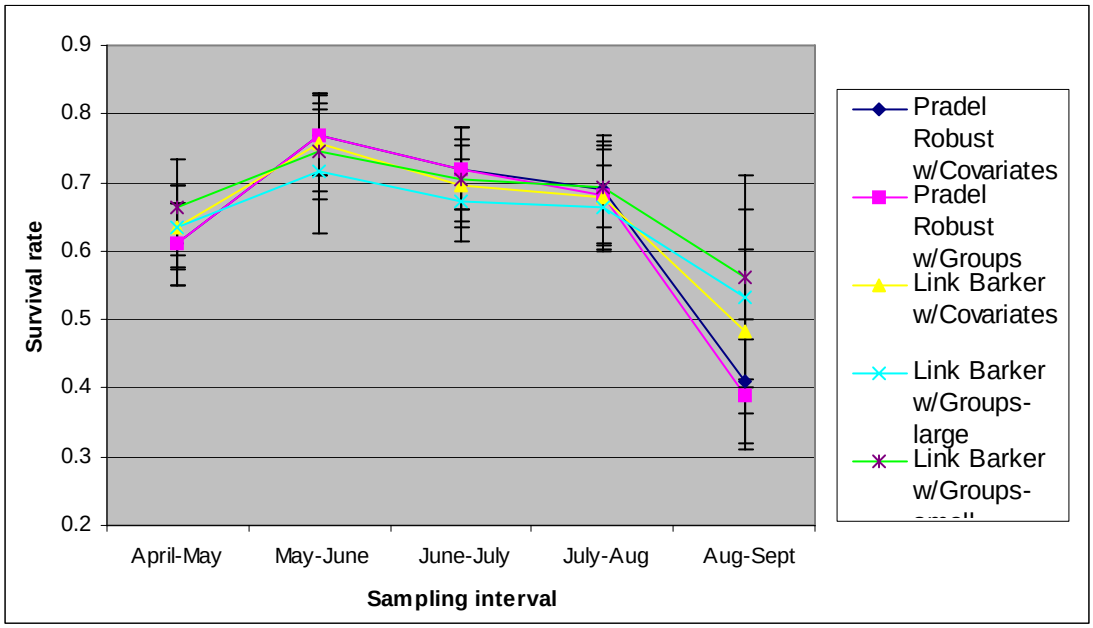
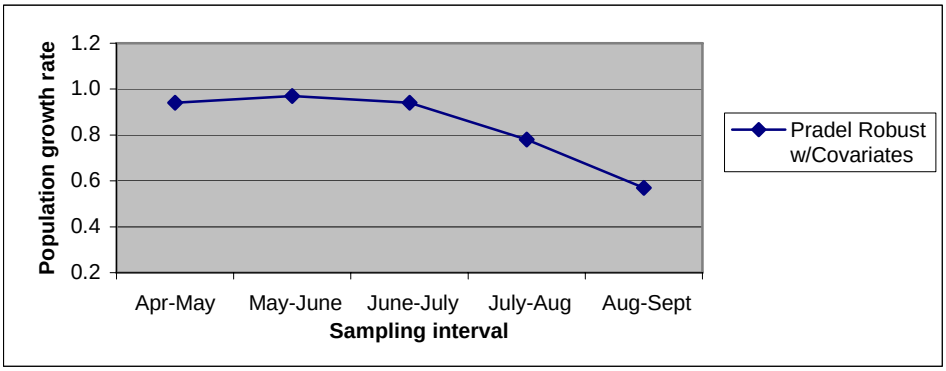


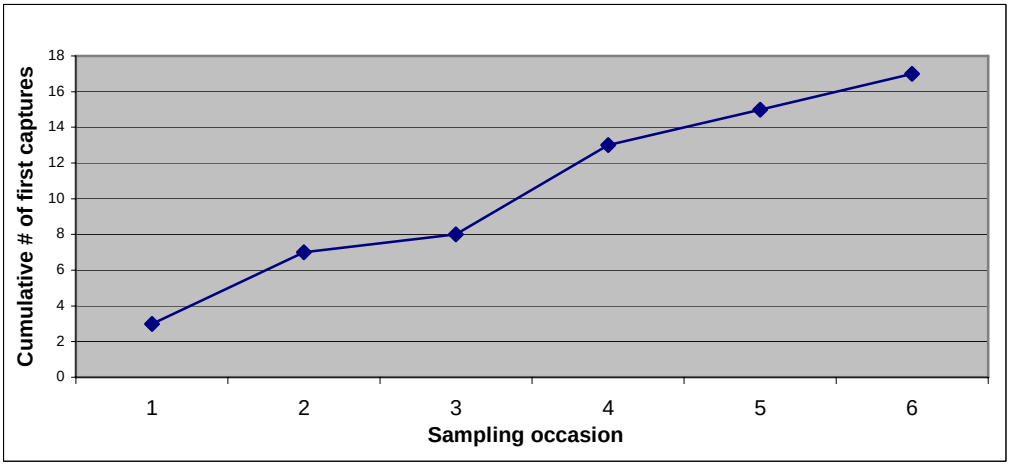
Figure 8. Estimates for Population Growth Rate in 2005



Effect of Limiting Number of Capture Occasions –

Figure 9 shows a plot of the number of cumulative first-time captures over the only six-day trapping session conducted in June of 2005. The capture rate clearly did not level off by the third sampling occasion, lending strong support to the idea that not all available individuals were trapped in other months when only three consecutive sampling occasions were used. As a result, abundance estimates are most likely biased low.

Figure 9. Cumulative First Captures Over A Six-Day Sampling Period



Modeling Heterogeneity in Capture Probabilities -

Using the same six days of data from June 2005, a comparison between models using "closed captures" and "full closed captures with heterogeneity" data types revealed that incorporating heterogeneity in capture probabilities into a model resulted in significantly better fit than the model without heterogeneity (Table 12). The model ranked second is the best supported one for the closed captures data type, but the same model using the closed captures with heterogeneity data type carries more than 1500 times as much weight. This model type relaxes the assumption of equal catchability among individuals, but it requires more than three secondary sampling occasions and could not be used in this study.

Table 12. June 2005 Models for Six Day Sampling Period

Model	Delta AICc	AICc AICc	Model Weight	Likelihood	#Par	Deviance
{P,c (t) pt=ct full closed caps w/het}	88.794	0.00	0.99920	1.0000	20.000	52.291
{P,c (t) pt=ct closed caps}	103.468	14.67	0.00065	0.0007	11.000	86.654
{P,c (t) p(t)=p(t-1) closed caps}	106.441	17.65	0.00015	0.0000	11.000	89.627
{P,c (.) closed caps}	117.129	28.33	0.00000	0.0000	3.000	116.994

Molecular Analyses –

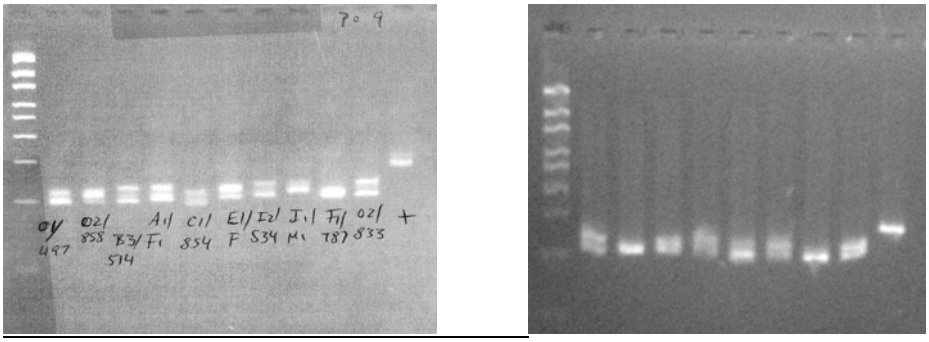
Twenty-four of the 86 tissue samples collected from Florida mice were used in PCR amplifications. Of those, 16 samples were successfully amplified at least once and some as many as five times. With the exception of PO-26, all primer pairs successfully amplified *P. floridanus* DNA at least once. Table 13 shows the initial annealing temperatures (T_a) used in successful trials. PCR products were run on agarose gels along with a

positive control (DNA from *Peromyscus polionotus* obtained from the Peromyscus Genetic Stock Center, University of South Carolina). This procedure confirmed that the fragments that had been obtained were in the correct size range (Figure 10), but could not identify them as the desired microsatellites. A sequencing step would have been necessary to determine nucleotide base sequences and thereby allow identification of the fragments, but because of time constraints this step was never reached. After several months of running PCR under various conditions without repeatable results, DNA analyses were abandoned.

Table 13. Primer-Specific Annealing Temperatures Used in PCR Amplifications

Primer	Initial T_a (°C)
PO - 9	62
PO - 26	none found to work
PO3 - 68	62
PO - 31	58
PO - 71	60
BW4 - 28	57
BW4 - 45	60
BW4 - 93	55
BW4 - 112	60
BW4 - 137	57
BW4 - 178	50
BW4 - 200	61
BW4 - 234	62

Figure 10. Bands of PCR Products Obtained with Primers PO-9 and BW4-28



DISCUSSION

Zero Model Deviances –

Deviances for all models run under the conventional robust design data type were reported as zero (Tables 2 and 6). According to a response posted by G. White on the Analysis Forum, an online discussion forum for the MARK program, this is because a saturated model likelihood has not yet been computed for the robust design model and a negative constant is left out of the likelihood to speed up computation. Leaving out the constant leads to positive likelihoods, which in turn result in negative deviances. The lack of a saturated model combined with negative deviances causes deviances to be reported as zero. The AIC values, however, do scale appropriately and can be used to assess the fit of models.

Temporary Effect of Marking on Survival -

Models run under the robust design with a time-since-marking effect ("a1") on survival received strong support for 2004 and sole support for 2005 (Tables 2 and 6). Probabilities of survival were 0.64 (+/- 0.05) for the month immediately following initial capture and tagging versus 0.69 (+/- 0.04) for all later months combined in 2004 (Table 5) and 0.65 (+/- 0.12) and 0.92 (+/- 0.17), respectively, in 2005 (Table 11). These differences could mean that the process of ear tagging caused a temporary reduction in survival, but there could also be another explanation. Because survival in juveniles is often lower than in adults (Schwarz and Seber 1999, Dinsmore et al. 2003, Layne 1992,

Gardali et al. 2003), I examined the possibility that first-time captures may have been concentrated at a time of year when juveniles may have been abundant relative to other times and the difference in survival could therefore be between age classes and not a result of marking. The majority of first-time captures took place in March and April of both years, when trapping was initiated. Results of the 2004 data analyses showed a peak in abundance in April (Figure 3) and a peak in recruitment in the April-May interval (Figure 4), indicating that lower juvenile survival may have been a factor during that time period. In 2005, however, recruitment was constant in best-fit models and abundance did not vary as much as in the previous year (Figure 5), but the difference in survival estimates between time-since-marking cohorts in conventional robust design models was greater than in 2004 (Tables 5 and 11). This result indicates that the process of ear tagging temporarily affected survival in 2005, but the cause for the difference in survival in 2004 cannot be determined. Infections were observed in a few individuals over the course of the study, and possibly mice could be distracted by the tags and could therefore be more susceptible to predators. I chose this method of identification because it seemed less invasive than toe clipping and my initial attempts at using an ear punching code resulted in severe damage to the ears of mice (albeit my inexperience with the technique may have played a role).

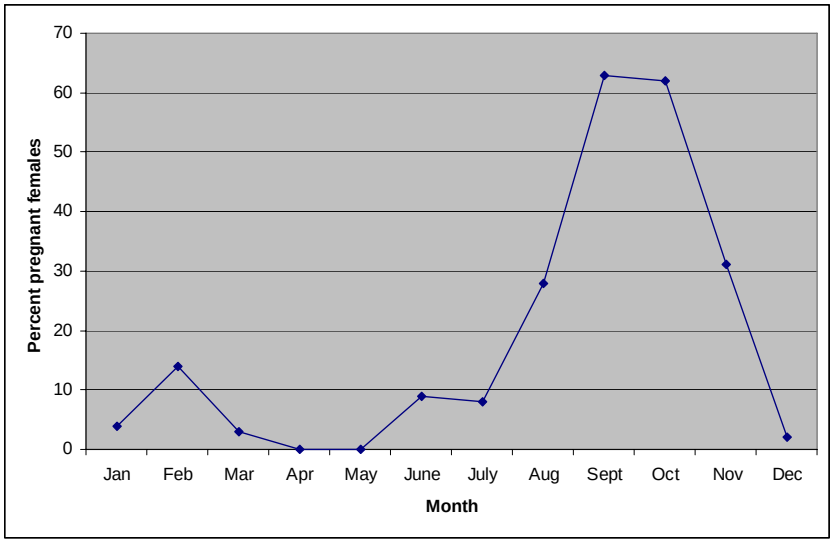
Migration -

Results of conventional robust design models showed strong support for temporary migration of individuals into and out of sampling areas. Best-fit models in 2004 incorporated both Markovian and random movement while in 2005 only Markovian migration was supported. The difference in interpretation between the two is that Markovian

models assume the probability of being available for capture depends on an individual's availability in the previous session, while in random models it does not (Kendall 2007). In other words, the Markovian model assumes that an animal "remembers" whether or not it was in the trapping area in the previous session. When modeling Markovian migration, no constraints are placed on migration parameters (γ' and γ'') if survival is time-invariant. For random migration, γ's are set equal to γ''s, the interpretation being that the probability of being out of the study area is the same whether an animal was in or out of the study area during the previous occasion. The greater parameterization of Markovian models (probably combined with sparseness of data) led to inestimability of several migration parameters and unusually large confidence intervals. The probability of temporary emigration (γ'') calculated for the 2004 data from five out of six parameters was 0.22 (+/- 0.09), but four out of five immigration parameters were inestimable. Deriving the probability of immigration ($1- \gamma'$) from a single γ' was deemed unreliable and therefore no value was reported. For 2005, γ'' was estimated as 0.20 (+/- 0.17), and two out of three γ's were again inestimable. Although obtaining values for migration parameters was problematic, AIC ranking strongly indicated that temporary migration existed in this population. Whether it can be interpreted as movement out of habitat patches or simply as movement out of the trapping area to another part of the same patch is not clear, but the previously reported dispersal of 18 individuals between patches (see Results) strengthens the argument that metapopulation dynamics may exist. Although 18 individuals is only a small portion of the animals encountered, I suspect that a higher number of dispersing mice would have been observed had trapping been continued into the winter. This suspicion is based on the fact that juveniles and subadults usually disperse

from their natal areas in search of mates and other resources (Swilling and Wooton 2002, Zug et al. 2001). According to Layne (1966), the vast majority of pregnancies in a population of *P. floridanus* he studied in Alachua County occurred during September and October (see Figure 11). Assuming reproduction also occurs mainly during those months in the population studied here, offspring would not be weaned until late fall or early winter, at which time they would begin to disperse. Because trapping was only conducted from March through September, I was not able to observe whether or not this occurred. However, even a small number of dispersing animals may be sufficient to augment the gene pools of subpopulations and increase fitness. Dispersal itself does not provide insight into whether or not the individuals involved are interbreeding with other subpopulations. Genetic analyses, on the other hand, can determine the degree of gene flow among subpopulations and the relatedness of individuals from neighboring patches.

Figure 11. Seasonal Variation in Pregnancies in Alachua County



(Adapted from Layne 1966)

Parameter Estimates –

With the exception of abundance estimates obtained for 2005 using the Pradel robust design with groups, which must be viewed with caution (see Results), estimates from all model types and for both years indicated that approximately 70 individuals on average were exposed to sampling efforts in each month (Tables 5 and 11). In mark-recapture studies, traps are usually arranged on rectangular grids and the sampling area can be calculated relatively easily, but because of the unusual arrangement of traps around herp arrays in the current study, the area sampled was more difficult to determine. A rough estimate of the area per trap array is 200 m^2, and with 15 arrays the total sampling area would have been approximately 3000 m^2. Overall, abundance estimates are likely biased low as a result of the limited number of secondary sampling occasions (see Results). In addition, low estimates of abundances as well as recruitment and population growth rates are likely a result of not having included the peak reproductive period in the overall sampling period. Finally, it has been shown that heterogeneity in capture probabilities is strongly indicated for this population, and heterogeneity has been known to produce unreliable abundance estimates (Pollock and Alpizar-Jara 2005, Conn 2006). In both 2004 and 2005, time-variant models indicated that the number of mice was high in April and decreased into the fall (Figures 3 and 6), which probably reflects a minor peak in reproduction around February (see Figure 11).

Average monthly survival estimates were between 0.67 (+/- 0.08) and 0.74 (+/- 0.06) in 2004 and between 0.63 (+/- 0.07) and 0.66 (+/- 0.08) in 2005 (see Tables 5 and 11). In conventional robust design models, averages of survival per cohort were 0.67 (+/- 0.05) in 2004 and 0.79 (+/- 0.15) in 2005. The outlier in 2005 was the value for the

second cohort (0.92 +/- 0.17), but estimates for both cohorts in this year showed very large confidence intervals because best-fit models incorporated Markovian movement with numerous parameters. Values were similar when comparing survival estimates between models using covariates and those using groups. In terms of trends over time, survival rate estimates in both years were low between April and May, increased during the summer and declined substantially by September (Figures 4 and 7). Low survival in the April-May interval is probably the result of a relatively high ratio of juveniles born around March (see minor peak in February pregnancies in Figure 11) and weaned by April. The drop in survival rates in September might be explained by females retreating underground in preparation for the peak reproductive period and being unavailable for capture.

Recruitment rates averaged 0.21 (+/- 0.09) in 2004 and 0.19 (+/- 0.04) in 2005. All Link Barker models for 2004 showed peaks in the April-May interval (Figure 5), correlating with the peak in abundance in April of that year. The trend in recruitment rates for 2004 approximates the trend in pregnancies in the Alachua County population shown in Figure 11, but with a one-to-two month lag. Gestation time for *P. floridanus* is thought to be 23-24 days (Layne 1968b), followed by another three weeks before newborns would be weaned and begin to be encountered in traps. Top models for 2005 held recruitment constant over time, which is consistent with the smaller decrease in abundances over time for this year compared with the previous one (Figure 6). Only models ranked fourth (with 7 % model weight) and lower showed a decrease in recruitment similar to the trend seen in 2004. Link Barker models with covariates resulted in somewhat lower survival estimates than those using groups in 2004 (Table 5), but in 2005 estimates were

very similar (Table 11). Population growth rates were lower in models using covariates versus groups for 2004, but were identical between model types for 2005. Estimates indicated that the population was increasing on a whole in 2004, but decreasing in 2005. However, because population growth is partly a function of recruitment and recruitment rates obtained during the study did not include peak reproduction, yearly population growth rates are likely higher.

The greatest differences observed among model types were in estimates of recapture probabilities between Link Barker and robust design models. Link Barker models estimate recapture probabilities although the parameter is symbolized as p (which in robust design models is the probability of first-time capture) and the resulting estimates should therefore be compared with recapture probability c in robust design models (Tables 5 and 11). Link Barker estimates are much higher than those obtained with the robust design type (0.80 in both years for Link Barker vs. 0.69 in 2004 and 0.50 in 2005 using robust design) because estimates are derived from pooled data in the case of Link Barker models. Link Barker estimates the probability of being captured at least once during several consecutive sampling occasions (three in the current study) as opposed to the robust design, which estimates recapture probabilities between two consecutive occasions.

Using models with group effects proved valuable in understanding the direction of observed differences. Based on Hokit and Branch (2003), it was expected that survival, population growth rate and recruitment would all be lower in smaller habitat patches than larger ones, but in both years only recruitment followed this trend while the opposite was true where differences in survival and population growth were indicated (Figures 12-14).

Figure 12. Estimates of Recruitment Rates in Large vs. Small Patches

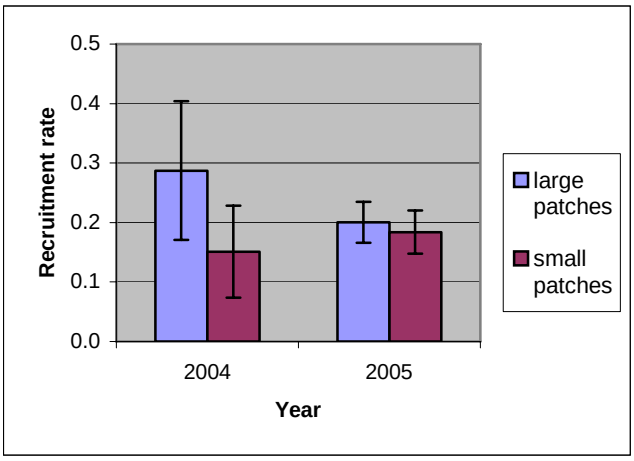


Figure 13. Estimates of Population Growth Rates in Large vs. Small Patches

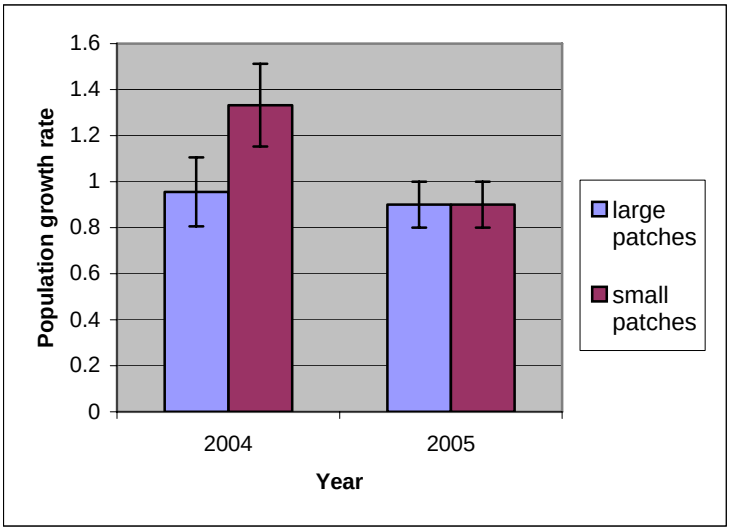
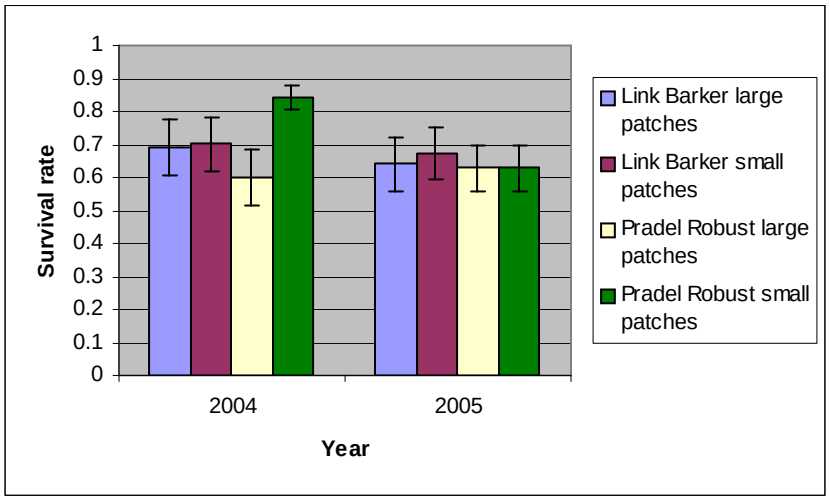


Figure 14. Estimates of Survival Rates in Large vs. Small Patches



An explanation for these unexpected findings might be that for some reason predation is higher in large scrub patches than in small ones. It is conceivable that predators that can easily move between patches may spend more time in large ones, where there is greater selection and/or overall abundance of prey. Coachwhip snakes, for example, tended to be found more often in larger patches than smaller ones (B. Halstead, personal communication). If this theory is true, recruitment rate at the study site might not have been noticeably affected because it was already quite low (~ 0.2) during the months when the study took place. Survival rate, however, was about 0.7 and differences between groups would have been more easily discernable. Because population growth rate is the sum of survival and recruitment rates and recruitment was relatively low during the entire study, population growth would have been high where survival was high and low where survival was low.

Future Direction -

The mark-recapture analyses discussed here have shown that habitat patch size was associated either positively or negatively with different demographic parameters of *P. floridanus*. They also indicated a temporary effect of ear tagging on survival and showed support for migration between habitat patches. However, the analyses fell short of determining whether or not a metapopulation structure exists in the study population. I had originally planned to address this question using genetic analyses of microsatellites, but because of time constraints and the need to use non-specific primers that proved to be of limited utility, I was forced to abandon this portion of my study. PCR annealing temperatures given in the original literature from which the primers were obtained did not always lead to successful or consistent amplification, so that numerous attempts were necessary in order to find the conditions under which the study organism's DNA could be amplified. Eventually, however, all primers except one were successfully used in PCR, and primer PO-26 may possibly have worked with continued persistence.

The analyses of mark-recapture data showed that habitat area was associated with demographic parameters of the study population. However, had no associations been evident, it would not have been clear whether they did not in fact exist or whether source-sink dynamics (Pulliam 1988) might be counteracting the relationships. Even with the current results, metapopulation dynamics may still be at play and may lessen or increase effects of habitat patch size. The rate and direction of movement of individuals among subpopulations can strongly affect variation in abundances and population viability (Diffendorfer et. al. 1995). For example, one scenario might be that large patches serve as sources for small patches, animals migrate to the small patches and because predation

is lower in small patches survival is higher there, but without new arrivals from the large patches, the smaller ones could not persist. Future research employing genetic analyses should be conducted on the study population in order to determine the degree and kinds of interactions among subgroups. The primers discussed here may serve as a starting point from which customized primers could be designed that would ensure more consistent results in PCR amplification.

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APPENDICES

Appendix A: Program MARK

Program MARK is based on maximum likelihood estimation of the probabilities defining the occurrence of one or more events (Cooch and White 2007). A likelihood function containing the parameter(s) in question is constructed and the value that maximizes the likelihood function, given the set of data, is then chosen as the best estimator for the parameter. The input data consist of a set of encounter histories, one for each individual, in the form of a row of dummy variables (0 and 1). Each dummy variable represents a sampling occasion, whereby a 0 indicates that the individual was not captured at that occasion and a 1 indicates that it was captured. For example, based on a three-year study during which animals are marked and released on the first occasion and sampling is conducted once per year after that, an encounter history of 101 would mean that the individual associated with that encounter history was captured and marked in the first year, not seen in the second year and recaptured in the third year. In all, four encounter histories are possible for the individuals in this hypothetical study: 111, 110, 101 and 100. Each of these encounter histories is associated with a certain probability of occurrence, which in turn is based on two parameters: phi_t (φ_t, the probability of an individual surviving from occasion t to occasion t + 1) and p_t (catchability, i.e. the probability that, if alive and in the sample at time t, an individual will be captured). In practice, the death of an individual cannot be distinguished from permanent emigration, so that φ is more correctly defined as "apparent survival". In our example, the encounter history 101 would be defined by the probability $\varphi_1 (1-p_2) \varphi_2 p_3$, meaning that the individual survived to the second occasion (we know this because it was seen alive at the third occasion), was not captured at the second occasion (with probability $1 – p_2$), survived to the third occa-

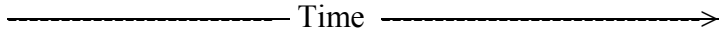
sion and was seen alive at the third occasion. Depending on how many individuals were found to have a particular encounter history, each history would occur with a certain frequency. The problem addressed in MARK, then, is to estimate for which values of φ and p the probability of finding this set of encounter histories with the given frequencies would be maximized.

Many models can be run using the MARK program, and different models derive estimates for different parameters. Cormack-Jolly-Seber (CJS) models estimate survival and catchability as in the above example. Jolly Seber (JS) models also estimate φ and p, but make the assumption of equal survival and catchability for all animals in the population, whether marked or unmarked, while CJS models make no assumptions about the unmarked population and assume these parameters to be equal only for marked individuals (Schwarz and Arnason 2007). The main difference between these models, then, is that estimates pertain only to the marked population in CJS models, while they apply to the entire population in JS models. The overall assumption of equal catchability in the JS models allows for the estimation of additional parameters such as recruitment and population growth and size. The assumptions of equal catchability and survival among individuals are necessary for the estimation of parameters, but are often unrealistic, and methods have been developed that can relax one or both of these assumptions (Lebreton et al. 1992, Schwarz and Seber 1999). JS and CJS models are referred to as open population models because they allow changes in population size over time in the form of births, deaths, immigration and emigration of individuals. Closed population models, on the other hand, assume a constant population size throughout the study. They estimate p (the

probability that an animal in the population will be captured for the first time), c (the probability of recapture given that an animal was captured at least once before) and population size or abundance N (Lukacs 2007). Because of the closure assumption it is appropriate to use these models only for data sets that were collected in a short time period, during which it can be assumed that there was virtually no change in population size. MARK supports a number of closed population data types. They can be grouped broadly into those of Otis et al. (1978), which have the abundance estimates in the likelihood function, and those of Huggins (1989), which are conditioned on the number of animals captured, and N must be estimated as a derived parameter. Within these broad groups, models become increasingly complex as the equal catchability assumption is relaxed and/or uncertainty in identification (usually a result of genotyping errors) is incorporated. MARK allows parameters to vary over time for all model types and between cohorts for some types (a cohort can refer to an age class or to a group of individuals first captured and marked at a particular occasion). In the case of fully time-dependent models, where all parameters may change over time, several parameters are usually confounded (especially for first and last sampling occasions) and constraints must be placed on some of them (Cooch and White 2007). Group effects (effects resulting from individuals being categorized in some way, e.g. by size or sex) and individual covariates can be incorporated into some models, while others can handle data from multiple sources or strata (discrete locations or conditions, e.g. breeding vs. non-breeding, in which the marked individual may potentially be encountered).

The current study was designed to use models of the robust design type, which is a combination of open and closed population models (Kendall et. al. 1995, Kendall 2007). The main difference between an open model and the robust design model is that, instead of only one capture occasion between sampling intervals, there are multiple (k) occasions sufficiently close in time so that the population can be assumed to be closed for that time period (Figure 15). These consecutive capture occasions allow estimation of population size for each primary sampling period, while survival is estimated between sampling periods when the population is assumed to be open to births, deaths, immigration and emigration. In addition, the classical robust design models allow estimation of the probabilities of temporary emigration of individuals from the trapping area and immigration of marked animals back to the trapping area (Kendall 2007). These calculations are possible because a distinction is made in the robust design model between the capture probabilities estimated in closed and open population models. Capture probability p was previously defined as the probability that, if alive and in the sample at time t, an individual will be captured. However, just as the "apparent survival" φ estimated in open popu-

Figure 15. Basic Structure of the Robust Design Model



Primary sampling periods	1	2	3
Secondary sampling periods	1,2,… k_1	1,2,… k_2	1,2, … k_3

(Adapted from Cooch and White 2007)

lation models is actually a product of true survival and the probability of not permanently emigrating, capture probability in these models is also a product of two other probabilities: that of being captured, conditional on being alive and in the sample, and that of *being available* for capture. Animals may be alive and in the sample, but may not be available for capture and will thus not be captured (e.g. if sampling of birds were conducted at a nesting site, only breeding birds would be available for encounter and non-breeding individuals would not be observed). In closed population models, on the other hand, p is the true probability of capture because by definition N is constant in these models and individuals can neither enter nor exit the sample. With estimates for both "apparent" and "true" capture probabilities available from the combined use of open and closed models in the robust design, gamma (γ), the probability of being available for capture during a particular primary sampling period, can also be obtained. In fact, two gamma parameters are used in assessing temporary migration: γ' and γ''. γ' is the probability of being off the study area during a particular primary sampling period t given that the individual was also off the study area during the sampling period t – 1. It follows then that $1-\gamma'$ is the probability that an individual enters the study area between t – 1 and t, given that it was off the study area at time t – 1, which is a measure of temporary immigration. γ'' is the probability that an individual is off the study area and unavailable for capture during sampling period t given that it was *in* the study area at sampling period t – 1, a measure of temporary emigration. Temporary migration can be modeled to be random or Markovian. In the case of random movement, the probability of an individual being available for capture during a primary sampling period does not depend on whether

or not it was available in the previous sampling period, whereas for Markovian movement it does.

A comparison between robust design models using regular closed captures (after Otis et. al.) and Huggins closed captures data types showed similar results in terms of selection of the top model and parameter estimates, although standard errors for population size estimates were slightly larger for the Huggins models. I chose to use regular closed capture models in my analyses. Next, I compared models with a group effect (comparing data obtained from mice captured in large habitat patches versus in small patches) to models that used patch size as an individual covariate. In several cases, I adjusted the patch size covariate to reflect where the trap array was located within the patch. For example, arrays B_1, B_2, B_3 and B_4 were all located in a patch approximately 170 ha. in size (Figure 1), but B_1 lay on a fingerlike projection of scrub away from the main portion of the patch and surrounded by flatwoods. This relative isolation presumably reduced access to resources and conspecifics (for mating purposes) for *P. floridanus* located in B_1 relative to mice in other parts of the patch. B_2 was located closer to the main portion, but separated from it by Tram Road (a sand road approximately 9 m in width), while arrays B_3 and B_4 lay nearer to the center of the patch. The adjustments I made were subjective, but I kept them small in order to err on the side of caution (see Table 14). Patch sizes were adjusted down for arrays located at the edge of a habitat patch and up when patches lay close to one another, effectively enlarging the sizes of

Table 14. Actual and Adjusted Habitat Patch Sizes

Array	Actual size of patch (ha.)	Adjusted size of patch (ha.)
O_1	80	80
O_2	80	70
H_1	10	10
G_1	2	2
B_1	170	100
B_2	170	150
B_3	170	170
B_4	170	170
A_1	12	20
C_1	1.5	1.5
F_1	3	3
E_1	2	2
D_1	1.5	1.5
I_1	40	40
I_2	40	40

both fragments. A comparison of the two model sets again showed that the models with greatest support based on AIC values (see Goodness-of-Fit and Model Selection) were virtually identical, but estimates for abundance were lower in the two-group models. There were several disadvantages to using two-group models. One was that they required a greater number of parameters and some of them were inestimable because of small sample sizes. Another was that the cut-off between large and small patch sizes was rather arbitrary. On the other hand, Cooch and White (2007) point out that individual covariates are difficult to interpret in models estimating population growth (λ) and recruitment (f) because $\lambda_t = \varphi_t + f_t$, and "while individual covariates could apply to survival rates, the recruitment parameter is not tied to any individual – it is a population-based, average

recruitment per individual in the population". I decided to use both model types and compare estimates between them. Next, a comparison between Pradel robust models and simple Pradel models (e.g. Pradel Robust Survival and Lambda and Pradel Survival and Lambda) showed that top models were again identical and estimates were very similar, so that there was no added benefit in also running the simpler models. The set of model types I decided on was as follows:

- The classical robust design model, because it allows modeling of temporary migration and age/cohort effects to test for differences in survival
- The Pradel Robust Survival and Lambda for estimation of population growth (models with group effect and with individual covariates)
- Link-Barker models with group effect and individual covariates for estimation of recruitment rate f

The Link-Barker model, like the Pradel models, is based on the original JS model and estimates the per capita recruitment rate f. It uses pooled capture histories, where secondary sampling occasions (see Figure 15) are pooled and an individual is either captured at least once during a primary sampling period or it is not captured.

Goodness-of-Fit and Model Selection –

Much of data analysis relies on the correct choice of a model; in other words, a model must be chosen which most adequately fits the data at hand (Lebreton et al. 1992, Cooch and White 2007). When using MARK, a set of models that seem biologically reasonable is chosen a priori. The next step that should be performed is to test the most global model of the set (i.e. the most parameterized one) for goodness-of-fit. If the most

global model adequately fits the data, it can be assumed that the others in the set do as well. All models can then be run and compared as to which one is most parsimonious, meaning which model represents the given data adequately and with the fewest possible parameters. If more than one model has significant support, estimates from the top models can be averaged. Unfortunately, none of the goodness-of-fit tests that have been developed to date (e.g. Bootstrap, Chi Square, Release) can be used for robust design models (G. White, personal communication, W.R. Clark, Iowa State University, personal communication). Cooch and White (2007) recommend using Program RELEASE or the Parametric Bootstrap method on the fully parameterized CJS model that corresponds to the more complicated model being used, and if the CJS model is sup-ported by the test, one can proceed with the more complex model. Program RELEASE could not be used because of insufficient data; therefore I applied the Bootstrap method. Bootstrapping estimates the variance inflation factor, ĉ, which is a measure of the lack of fit of the model to the underlying data. If ĉ equals 1, the model fits the data well, but a ĉ greater than 1 indicates overdispersion (extra variation) in the data. This means that "the arrangement of the data do not meet the expectations determined by the assumptions underlying the model" (Cooch and White 2007), most importantly the assumptions of equal catchability and survival. If overdispersion of data is indicated, the value of ĉ can be adjusted to account for the lack of fit by calculating the ratio of the model deviance and the mean deviance (or the ratio of model ĉ to mean ĉ) from the bootstrap simulations. Once a set of models had been run, the most parsimonious model was identified with the help of Akaike's Information Criterion (AIC). AIC is defined as AIC = -2 ln (L) + 2 K,

where L is the model likelihood and K is the number of parameters. The most parameterized model in a set will always fit the data best; however, the more parameters a model includes, the lower the precision becomes for the individual estimates. The AIC strikes a balance between the best possible fit of a model (reflected by a low log likelihood) and the number of parameters, choosing the model that is most parsimonious overall. Results browsers in MARK list models in order of lowest to highest AIC values, and the model with the lowest AIC value has the greatest support. Where there was significant support (which I chose to be an AIC weight of at least 0.1) for more than one model, I used model averaging.

Appendix B: Additional Figures

Table 15. 2004 CJS Model for Herp Array Data

Real Function Parameters of {Phi (gr*t) p (gr)}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.9528634	0.4980721	0.7350119E-08	1.0000000
2:Phi	0.2657063	0.2106244	0.0417901	0.7501424
3:Phi	1.0000000	0.2290427E-07	1.0000000	1.0000000
4:Phi	1.0000000	0.3366622E-06	0.9999993	1.0000007
5:Phi	0.8364372	0.2876243	0.0766558	0.9968355
6:Phi	1.0000000	0.6238900E-07	0.9999999	1.0000001
7:Phi	1.0000000	0.5633052E-07	0.9999999	1.0000001
8:Phi	0.9621496	0.5417493	0.3530284E-09	1.0000000
9:Phi	0.2013092E-15	0.1003268E-07	-0.1966405E-07	0.1966405E-07
10:Phi	0.2404760E-15	0.9807671E-08	-0.1922304E-07	0.1922304E-07
11:Phi	0.5737598E-15	0.3387505E-07	-0.6639511E-07	0.6639511E-07
12:Phi	0.3408025	0.6322205E-15	0.3408025	0.3408025
13:Phi	0.2000000	0.1788854	0.0271820	0.6910541
14:Phi	0.2500000	0.2165063	0.0335100	0.7621677
15:Phi	0.1919038E-15	0.7997995E-08	-0.1567607E-07	0.1567607E-07
16:Phi	0.2000000	0.1264911	0.0504114	0.5407151
17:p	0.3041469	0.0996881	0.1479421	0.5238764
18:p	1.0000000	0.4897021E-06	0.9999990	1.0000010

Table 16. 2005 CJS Model for Herp Array Data

Real Function Parameters of {Phi (gr*t) p (t)}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.5556494	0.2392547	0.1576577	0.8931003
2:Phi	0.2318002	0.1593927	0.0496135	0.6355863
3:Phi	1.0000000	0.2465402E-06	0.9999995	1.0000005
4:Phi	0.5852174	0.3601328	0.0715127	0.9627499
5:Phi	0.5153360	0.3192536	0.0798827	0.9286854
6:Phi	0.4840061	0.2001161	0.1632128	0.8185449
7:Phi	0.5708425	270.39279	0.1847300E-10	1.0000000
8:Phi	0.4979545	0.1704301	0.2067913	0.7905116
9:Phi	1.0000000	0.3611931E-07	0.9999999	1.0000001
10:Phi	0.6165312	0.3737527	0.0676301	0.9727050
11:Phi	0.7617800	0.5250086	0.0109009	0.9989234
12:Phi	0.7246216	0.4216839	0.0401398	0.9939967
13:Phi	0.6143448	0.2089097	0.2205224	0.8996959
14:Phi	0.8086938	383.05697	0.5870741E-10	1.0000000
15:p	0.7634795	0.1983777	0.2726260	0.9652780
16:p	0.4140473	0.1378648	0.1883095	0.6827665
17:p	0.1396365	0.1036179	0.0290631	0.4680853
18:p	0.3234532	0.1815741	0.0859400	0.7085501
19:p	0.4253910	0.1983320	0.1311289	0.7840884
20:p	1.0000000	0.1249396E-06	0.9999998	1.0000002
21:p	0.6182810	292.86328	0.2249470E-10	1.0000000

Table 17. 2004 Models Using Conventional Robust Design Ranked by AIC

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (a1) p,c (all .) N (.) Markov migr}	-351.812	0.00	0.29647	1.0000	11.000	0.000
{Phi (.) p,c (all .) N (.) random migr}	-350.949	0.86	0.19253	0.6494	9.000	0.000
{Phi (a1) p,c (all .) N (.) random migr}	-350.862	0.95	0.18429	0.6216	10.000	0.000
{Phi (a1+PS) p,c (all .) N (.) Markov migr}	-350.717	1.10	0.17147	0.5784	13.000	0.000
{Phi (.) p,c (all .) N (.) Markov migr}	-350.306	1.51	0.13959	0.4708	11.000	0.000
{Phi (t) p,c (all .) N (.) Markov migr}	-344.750	7.06	0.00868	0.0293	27.000	0.000
{Phi (PS) p,c (all .) Markov migr}	-341.799	10.01	0.00198	0.0067	16.000	0.000
{Phi (a1+PS) p,c (.) Markov migr}	-341.270	10.54	0.00152	0.0051	32.000	0.000
{Phi (.) p,c (all .) N (t) Markov migr}	-341.063	10.75	0.00137	0.0046	16.000	0.000
{Phi (a1) p,c (all .) Markov migr}	-340.484	11.33	0.00103	0.0035	17.000	0.000
{Phi (a1) gammas (.) p,c (all .) N (.) Markov migr	-338.747	13.07	0.00043	0.0015	7.000	0.000
{Phi (t+PS) p,c (.) Markov migr}	-338.625	13.19	0.00041	0.0014	34.000	0.000
{Phi (a1+PS) gammas (.) p,c (all .) N (.) Markov migr}	-337.172	14.64	0.00020	0.0007	9.000	0.000
{Phi (t*PS) p,c (.) Markov migr}	-332.841	18.97	0.00002	0.0001	39.000	0.000
{Phi (a1) p,c (all .) N (.) no migr}	-325.151	26.66	0.00000	0.0000	5.000	0.000
{Phi (.) p,c (all .) N (.) no migration}	-324.109	27.70	0.00000	0.0000	4.000	0.000

Table 18. 2004 Parameter Estimates for the Conventional Robust Design

Real Function Parameters of {Phi (a1) p,c (all .) N (.) Markov migr}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:S	0.6202346	0.0432286	0.5326612	0.7006210
2:S	0.6970948	0.0405358	0.6123580	0.7702579
3:Gamma''	0.2699954	0.0825089	0.1400182	0.4565716
4:Gamma''	0.3693414	0.1023471	0.1984113	0.5808265
5:Gamma''	0.0410575	0.0586186	0.0023081	0.4420833
6:Gamma''	0.5195290E-06	0.3588293E-03	0.7215194E-17	0.9999733
7:Gamma''	0.2490882	0.0829622	0.1220852	0.4417329
8:Gamma'	0.1361717E-07	0.2937626E-04	0.1891145E-18	0.9989812
9:Gamma'	0.4471174	0.2289154	0.1163638	0.8323919
10:Gamma'	0.5685376E-08	0.0000000	0.5685376E-08	0.5685376E-08
11:Gamma'	0.2073623	0.4470773	0.0012640	0.9818437
12:p Session 1	0.6026984	0.0270800	0.5486117	0.6543871
13:c Session 1	0.6870859	0.0188669	0.6489745	0.7228268
14:N Session 1	72.253391	1.1212247	70.687215	75.273387

Table 19. 2004 Models Using Pradel Robust Design with Individual Covariates

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi, lambda (patchsize*t) p,c (.)}	223.360	0.00	0.99856	1.0000	44.000	130.231
{Phi, lambda (patchsize*t) p,c,N (.)}	236.454	13.09	0.00143	0.0014	39.000	154.438
{Phi, lambda (patchsize*t) p,c,N (all t) pt=ct}	247.306	23.95	0.00001	0.0000	58.000	122.277
{Phi, lambda (patchsize*t) p,c (all t) pt=ct N (.)}	252.292	28.93	0.00000	0.0000	54.000	136.496
{Phi(t) lambda(patchsize*t) p,c(.)}	282.995	59.64	0.00000	0.0000	39.000	200.980
{Phi, lambda (patchsize+t) p,c (.)}	315.683	92.32	0.00000	0.0000	35.000	242.456
{Phi(patchsize*t) lambda(t) p,c(.)}	322.567	99.21	0.00000	0.0000	39.000	240.551
{Phi, lambda(com inter-patchsize*t) p,c(.)}	327.130	103.77	0.00000	0.0000	35.000	253.903
{Phi, lambda (t) p,c(.)}	333.733	110.37	0.00000	0.0000	33.000	264.867
{Phi, lambda (patchsize*t) p,c (.) N (.)}	334.355	110.99	0.00000	0.0000	27.000	278.439
{Phi, lambda (patchsize*t) p,c (all .)}	412.282	188.92	0.00000	0.0000	33.000	343.416

Table 20. 2004 Models Using Pradel Robust Design with Groups

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi, lambda (gr*t) p,c,N (gr)}	697.008	0.00	0.99691	1.0000	28.000	638.947
{Phi, lambda (gr*t) p,c (gr) N (.)}	709.508	12.50	0.00192	0.0019	28.000	651.447
{Phi, lambda (gr*t) p,c (gr) N (t)}	710.626	13.62	0.00110	0.0011	35.000	637.399
{Phi, lambda (gr*t) p,c,N (.)}	717.490	20.48	0.00004	0.0000	26.000	663.713
{Phi, lambda (gr*t) p,c (.) N (gr)}	719.508	22.50	0.00001	0.0000	27.000	663.591
{Phi, lambda (gr*t) p,c all . N (gr)}	719.508	22.50	0.00001	0.0000	27.000	663.591
{Phi (gr) lambda (gr*t) p,c (gr) N (gr*t)}	807.012	110.00	0.00000	0.0000	32.000	740.319
{Phi, lambda (gr+t) p,c,N (gr)}	858.455	161.45	0.00000	0.0000	20.000	817.400
{Phi (t) lambda (.) p,c (.)}	877.237	180.23	0.00000	0.0000	47.000	777.369
{Phi, lambda (.) p,c (.)}	882.777	185.77	0.00000	0.0000	42.000	794.110
{Phi, lambda (t) p,c (.)}	882.866	185.86	0.00000	0.0000	47.000	782.999
{Phi, lambda (gr) p,c (.)}	884.541	187.53	0.00000	0.0000	44.000	791.412
{Phi (.) lambda (t) p,c (.)}	884.961	187.95	0.00000	0.0000	47.000	785.094

Table 21. 2004 Models Using Link Barker with Individual Covariates

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (t) f (PS*t)}	1346.410	0.00	0.43380	1.0000	23.000	1297.458
{Phi (t) p (.) f (PS*t)}	1346.979	0.57	0.32629	0.7522	19.000	1306.969
{Phi (t) p (t) f (PS+t)}	1349.474	3.06	0.09371	0.2160	18.000	1311.670
{Phi (PS+t) p (t) f (PS+t)}	1349.649	3.24	0.08586	0.1979	19.000	1309.639
{Phi (PS+t) p (.) f (PS+t)}	1351.091	4.68	0.04176	0.0963	15.000	1319.835
{Phi (t) p (t) f (PS)}	1353.958	7.55	0.00996	0.0230	15.000	1322.701
{Phi (PS*t) p (t) f PS*t)}	1354.433	8.02	0.00785	0.0181	29.000	1291.705
{Phi (t) p (t) f (t)}	1359.058	12.65	0.00078	0.0018	18.000	1321.253

Table 22. 2004 Models Using Link Barker with Groups

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (gr) p (t) f (gr*t)}	1351.883	0.00	0.38923	1.0000	19.000	169.329
{Phi (t) p (t) f (gr*t)}	1353.494	1.61	0.17392	0.4468	22.000	164.252
{Phi (t) p (.) f (gr*t)}	1353.805	1.92	0.14891	0.3826	18.000	173.456
{Phi (gr) p (t) f (gr+t)}	1354.901	3.02	0.08608	0.2212	16.000	178.929
{Phi (gr) p (t) f (t)}	1355.115	3.23	0.07735	0.1987	14.000	183.475
{Phi (gr) p (.) f (gr*t)}	1355.707	3.82	0.05751	0.1478	14.000	184.067
{Phi (t) p (t) f (t)}	1356.864	4.98	0.03226	0.0829	17.000	178.710
{Phi (gr) p (gr) f (gr*t)}	1357.666	5.78	0.02160	0.0555	15.000	183.866
{Phi (t) p (t) f (gr)}	1358.658	6.77	0.01316	0.0338	15.000	184.858

Table 23. 2005 Models Using Conventional Robust Design

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (a1) p,c (.) N (.) Markov migr}	-169.681	0.00	0.52935	1.0000	20.000	0.000
{Phi (a1) gammas (.) p,c (.) N (.) Markov migr}	-167.341	2.34	0.16436	0.3105	17.000	0.000
{Phi (a1) p,c (.) N (.) no migr}	-166.620	3.06	0.11457	0.2164	15.000	0.000
{Phi (a1+PS) p,c (.) N (.) Markov migr}	-165.792	3.89	0.07573	0.1431	22.000	0.000
{Phi (a1) p,c (.) N (.) random migr}	-165.683	4.00	0.07173	0.1355	18.000	0.000
{Phi (a1+PS) p,c (.) N (PS) Markov migr}	-163.610	6.07	0.02544	0.0481	23.000	0.000
{Phi (.) p,c (.) N (.) Markov migr}	-161.396	8.28	0.00841	0.0159	19.000	0.000
{Phi (a1+PS) p,c (.) N (t) Markov migr}	-159.997	9.68	0.00418	0.0079	27.000	0.000
{Phi (a1) p,c (.) N (t) Markov migr}	-159.505	10.18	0.00327	0.0062	27.000	0.000
{Phi (a1+PS) p,c (all .) N (.) Markov migr}	-158.075	11.61	0.00160	0.0030	10.000	0.000
{Phi (a1*PS) p,c (.) N (t) Markov migr}	-157.772	11.91	0.00137	0.0026	28.000	0.000

Table 24. 2005 Models Using Pradel Robust Design with Individual Covariates

Model	Delta AICc	AICc AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) lambda (t) p,c (.) N (.)}	263.740	0.00	0.50239	1.0000	23.000	215.600
{Phi (t) lambda (t) p,c (.) N (t)}	264.720	0.98	0.30768	0.6124	27.000	207.767
{Phi (t) lambda (PS+t) p,c (.) N (t)}	266.875	3.14	0.10477	0.2085	28.000	207.697
{Phi (t) lambda (PS*t) p,c (.) N (t)}	268.250	4.51	0.05268	0.1049	32.000	200.084
{Phi (t) lambda (.) p,c (.) N (t)}	270.195	6.46	0.01992	0.0397	24.000	219.865
{Phi (.) lambda (t) p,c (.) N (t)}	272.323	8.58	0.00687	0.0137	24.000	221.993
{Phi (t) lambda (t) p,c (all .) N (.)}	273.938	10.20	0.00307	0.0061	13.000	247.246
{Phi (PS*t) lambda (t) p,c (.) N (t)}	274.249	10.51	0.00262	0.0052	32.000	206.084

Table 25. 2005 Models Using Pradel Robust Design with Groups

Model	Delta AICc	AICc AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) lambda (t) p,c (.) N (t)}	670.382	0.00	0.46722	1.0000	27.000	613.429
{Phi (t) lambda (t) p,c (.) N (.)}	670.440	0.06	0.45405	0.9718	23.000	622.300
{Phi (gr*t) lambda (t) p,c (.) N (.)}	675.384	5.00	0.03833	0.0820	28.000	616.205
{Phi (t) lambda (gr) p,c (.) N (t)}	675.636	5.25	0.03378	0.0723	24.000	625.306
{Phi (gr) lambda (t) p,c (.) N (t)}	679.061	8.68	0.00609	0.0130	25.000	626.532
{Phi (gr*t) lambda (gr*t) p,c (.) N (.)}	684.978	14.60	0.00032	0.0007	33.000	614.543
{Phi (gr*t) lambda (gr*t) p,c (.) N (gr)}	685.867	15.48	0.00020	0.0004	34.000	613.154
{Phi (gr*t) lambda (gr*t) p,c (.) N (gr*t)}	694.860	24.48	0.00000	0.0000	42.000	603.592

Table 26. 2005 Models Using Link Barker with Individual Covariates

Model	Delta AICc	AICc AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (.) f (.)}	918.824	0.00	0.46775	1.0000	7.000	904.453
{Phi (.) p (.) f (.)}	920.705	1.88	0.18267	0.3905	3.000	914.626
{Phi (t) p (.) f (PS)}	920.920	2.10	0.16401	0.3506	8.000	904.442
{Phi (t) p (.) f (t)}	922.594	3.77	0.07102	0.1518	11.000	899.708
{Phi (PS) p (.) f (.)}	922.680	3.86	0.06805	0.1455	4.000	914.549
{Phi (t) p (.) f (PS+t)}	924.733	5.91	0.02438	0.0521	12.000	899.682
{Phi (.) p (.) f (t)}	925.637	6.81	0.01552	0.0332	7.000	911.266
{Phi (t) p (t) f (t)}	928.582	9.76	0.00356	0.0076	15.000	896.950
{Phi (t) p (.) f (PS*t)}	928.887	10.06	0.00306	0.0065	15.000	897.254

Table 27. 2005 Models Using Link Barker with Groups

Model	Delta AICc	AICc	Model Weight	Likelihood	#Par	Deviance
{Phi (t) p (.) f (.)}	918.824	0.00	0.36181	1.0000	7.000	94.339
{Phi (gr) p (.) f (.)}	920.431	1.61	0.16199	0.4477	4.000	102.186
{Phi (t) p (.) f (gr)}	920.515	1.69	0.15540	0.4295	8.000	93.922
{Phi (gr) p (.) f (gr)}	920.636	1.81	0.14626	0.4042	5.000	100.324
{Phi (.) p (.) f (.)}	920.705	1.88	0.14130	0.3905	3.000	104.512
{Phi (gr*t) p (.) f (.)}	924.762	5.94	0.01858	0.0514	12.000	89.598
{Phi (.) p (.) f (t)}	925.637	6.81	0.01200	0.0332	7.000	101.151
{Phi (gr*t) p (.) f (t)}	928.684	9.86	0.00261	0.0072	16.000	84.714
{Phi (gr*t) p (.) f (gr*t)}	937.216	18.39	0.00004	0.0001	21.000	81.894
{Phi (gr*t) p (t) f (gr*t)}	941.389	22.56	0.00000	0.0000	24.000	79.064