

POPULATION ECOLOGY OF MESOPREDATORS IN NORTH-CENTRAL FLORIDA

By

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To Dr. Katherine E. Troyer

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Abstract of Thesis Presented to the Graduate School
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Populations of mesopredators (mid-sized mammalian carnivores) are expanding in size and range amid declining apex predator populations and ever-growing human presence, leading to significant ecological impacts. Despite their obvious importance, population dynamics have scarcely been studied for most mesopredator species. Information on basic population parameters and processes under a range of conditions is necessary for managing these species. Here I investigate survival, recruitment, and population growth rate of two widely distributed and abundant mesopredators, the Virginia opossum (*Didelphis virginiana*) and the northern raccoon (*Procyon lotor*), using Pradel's temporal symmetry models and >6 years of monthly capture-mark-recapture data collected in a protected area in north-central Florida.

For opossums, monthly apparent survival probability was higher for females (0.86, 95% CI = 0.83–0.88) than for males (0.76, 95% CI = 0.72–0.79) and did not vary temporally. Recruitment rate was higher for males and varied monthly, with the highest recruitment in December (0.32, 95% CI = 0.14–0.58 for females; 0.57, 95% CI = 0.19–0.88 for males). Finally, realized population growth rate for opossums varied monthly

and, like recruitment, was highest in December (1.30, 95% CI = 1.01–1.68). Both recruitment and population growth rate were positively influenced by the monthly coefficient of variation of precipitation. There was no evidence of density-dependent influences on opossum population dynamics, nor was there evidence of competition from the raccoon.

For raccoons, monthly apparent survival probability was higher for females (0.95, 95% CI = 0.93–0.96) than for males (0.91, 95% CI = 0.89–0.92), while monthly recruitment rate was higher for males (0.09, 95% CI = 0.08–0.11) than for females (0.05, 95% CI = 0.04–0.07). Monthly realized population growth rate was 1.000 (95% CI = 0.995–1.004), indicating that this raccoon population has reached a stable equilibrium in this relatively undisturbed habitat. There was no evidence for substantial temporal variation in raccoon population growth rate or its components. My study is one of the first to quantify survival, recruitment, and realized population growth rate of opossums and raccoons using long-term data and rigorous statistical models. In doing so, I provide important insights into the population dynamics of two increasingly influential mesopredators.

CHAPTER 1 INTRODUCTION

Mesopredators are consumers of animal matter at middle levels of food webs. In the usual sense of the term, they are small-to-midsized carnivorous mammals, also called mesocarnivores (Prugh et al. 2009). They exist in ecosystems throughout the world in greater numbers than the larger apex predators or top carnivores, but they receive comparatively little research and conservation attention (Roemer et al. 2009). Given their adaptability, population resilience, and tolerance of human disturbance, mesopredators are likely to become increasingly influential in future ecosystems (Roemer et al. 2009). It is now more important than ever to study their ecology.

One of the major ecological impacts related to mesopredators involves mesopredator release, broadly defined as an increase in density, range expansion, or change in behavior of mesopredator species resulting from a reduction in the density or distribution of apex predator species (Prugh et al. 2009). Although it is not always possible to show that the decline of apex predators directly causes mesopredator overabundance, there is no doubt that explosions of mesopredator populations have occurred worldwide in recent years, with negative effects on many other species (Prugh et al. 2009; Ritchie and Johnson 2009). Mortality from predation is a common direct effect that can severely limit prey populations, especially through nest predation on birds and reptiles (Crooks and Soule 1999; Eagan et al. 2011; Garmestani and Percival 2005). As mesopredator populations increase, nest predation increases, resulting in lower nest survival and lower prey population size (Schmidt 2003).

Mesopredators also have important indirect effects on other species. Due to their flexible, omnivorous diets, mesopredators can fill a wide range of ecosystem roles. Not

only do they hunt seed dispersers, they can also be seed dispersers themselves (Roemer et al. 2009). They are often facultative scavengers and can negatively affect carrion-dependent species when they monopolize carrion resources—in one study, raccoons and opossums removed 93% of mouse carcasses for which the scavenger was identified (DeVault et al. 2011). Non-predatory roles for mesopredators have begun to get more research attention and might prove to have broader ecological consequences than previously realized (Roemer et al. 2009).

Mesopredator populations are also highly effective reservoirs of pathogens. These pathogens can infect populations of larger carnivores that might not have the same capacity to withstand epizootics (Roemer et al. 2009). Thus, mesopredator overabundance can negatively affect higher levels of food webs as well as lower levels. Mesopredators can also spread pathogens to domestic animals, such as pets and livestock (Elsheikha et al. 2004; Witmer et al. 2010), and even to humans (Brown et al. 2010; Dyer et al. 2013). The ecological, economic, and public health impacts of these species reach far in every dimension.

In their review of mesopredator ecology, Roemer et al. (2009) wrote that mammalian mesopredators “may be fundamentally important drivers of ecosystem function, structure, or dynamics.” Yet for many of these species, we lack basic ecological information that is crucial for developing effective management strategies. In particular, our knowledge of population ecology and the factors that affect mesopredator population dynamics is surprisingly incomplete. Without knowing how their populations function and respond to intrinsic and extrinsic factors, we cannot predict the ecological impacts of mesopredators. This study seeks to fill some of those knowledge gaps.

A central parameter in population ecology is realized population growth rate (Sibly and Hone 2002), or the ratio between the population size at time $t + 1$ and the population size at time t . Realized population growth rate indicates the magnitude and direction of change in population size over time, which directly affects the population's ecological impacts: the higher the growth rate, the greater the population's effects will become. In turn, population growth rate is determined by the rate of losses from the population and the rate of gains to the population. Two parameters often used to model these processes are apparent survival, which is the complement of loss, and recruitment rate, which represents gains. Apparent survival is the probability that an individual remains in the population from time t to time $t + 1$; individuals can leave the population through either death or permanent emigration. Recruitment rate quantifies the per capita additions of new individuals to the population from time t to time $t + 1$, either through immigration or maturation of young within the population (Williams et al. 2002). In the case of mesopredators, recruitment and population growth rate in particular have barely been studied. The three parameters described above—realized population growth rate and its determinants, survival and recruitment—are the focus of this study.

One common method of investigating population parameters is the analysis of capture-mark-recapture (CMR) data. CMR data are gathered by trapping, marking, and releasing animals at multiple capture occasions and recording the capture history of each individual (whether the individual was captured at each occasion). Such data can be analyzed using various models depending on the parameters of interest and the characteristics of the data (Williams et al. 2002). In this study, I use Pradel's (1996)

temporal symmetry models, which allows one to estimate apparent survival, recruitment, and realized population growth rate. These models are suitable for data from open populations in which individuals can immigrate and emigrate, an important consideration for potentially mobile mesopredators.

The two mesopredator species in this study are ubiquitous in the southeastern United States with typically broad ecological impacts: the Virginia opossum (*Didelphis virginiana*) and the northern raccoon (*Procyon lotor*). The population ecology of these species has not been studied thoroughly in this region, particularly in Florida. Little is known regarding demographic parameters such as survival and reproductive rates, and reports of population growth rates and factors that influence them are nonexistent. In this study, I apply rigorous statistical models to long-term (1992–1998) capture-mark-recapture datasets for both opossums and raccoons to investigate the population ecology of these important mesopredator species.

The study populations inhabit the Ordway-Swisher Biological Station (OSBS), a field station managed by the University of Florida. OSBS consists of more than 9,200 acres of protected habitat in north-central Florida and is used primarily as an outdoor teaching and research laboratory. Because the land is undeveloped, unexploited, and not open to the public, its wildlife populations can be studied in a relatively natural state. This presents a unique opportunity to study mesopredator population dynamics in habitats with little human disturbance.

The overall objective of this project is to investigate demographic parameters and population dynamics of opossums and raccoons at the relatively undisturbed Ordway-Swisher Biological Station, FL, using a long-term dataset. In Chapter 2, I investigate the

population ecology of opossums to determine estimates of survival, recruitment, and realized population growth rate and factors influencing these parameters. In Chapter 3, I conduct the same investigation for raccoons. By studying these two mesopredator species simultaneously, I am also able to compare their demographic parameters and population dynamic patterns. These analyses of long-term data using state-of-the-art modeling techniques are a significant contribution to our understanding of mesopredator population ecology in Florida.

CHAPTER 2 FACTORS INFLUENCING SURVIVAL, RECRUITMENT, AND POPULATION GROWTH RATE OF VIRGINIA OPOSSUMS

Anthropogenic alteration of ecosystems through processes such as habitat fragmentation, urbanization, and climate change is a global phenomenon of ever-growing severity (Bernstein et al. 2007; Ellis et al. 2010; Foley et al. 2005). Whereas these changes adversely affect many species and are considered to be an important cause of biodiversity loss worldwide (Fischer and Lindenmayer 2007; Mantyka-Pringle et al. 2012; Seto et al. 2012), some species often benefit and thrive amidst human impacts. One such group of species is small-to-midsized predators at intermediate levels of food webs, or mesopredators (Prugh et al. 2009).

Mammalian mesopredators exist in ecosystems throughout the world in greater numbers than the larger apex predators or top carnivores, but they receive comparatively little research and conservation attention (Roemer et al. 2009). Mesopredators play diverse ecological roles: they can suppress populations of prey species (Crooks and Soule 1999), outcompete specialist species (DeVault et al. 2011), and serve as reservoirs and vectors of pathogens (Roemer et al. 2009). They also tend to flourish in human-dominated landscapes (DeStefano and DeGraaf 2003; Klinkowski-Clark et al. 2010). Not surprisingly, mesopredator populations have exploded worldwide in recent decades, with negative effects for many other species (Prugh et al. 2009). Given their adaptability, population resilience, and tolerance of human disturbance, mesopredators are likely to become increasingly influential in future ecosystems (Roemer et al. 2009). It is now more important than ever to understand how and why their populations thrive in a variety of both natural and human-modified habitats.

Population growth rate is the central parameter in population ecology, and determining factors and processes that underlie changes in this parameter is an important goal in ecological research (Sibly and Hone 2002). Population growth rate in turn depends on its underlying vital rates: survival, or individuals remaining in the population; and recruitment, or individuals joining the population. These rates can be influenced by density-dependent (DD) and density-independent (DID) factors, and there is a growing body of research investigating the relative importance of DD versus DID factors in population dynamics (e.g., Goswami et al. 2011; Kneip et al. 2011; Leirs et al. 1997). Climatic variables, an important subset of DID factors, have received special attention in recent years due to the increasing focus on the impacts of climate change on population dynamics (e.g., Hostetler et al. 2012; Ozgul et al. 2010). For many mesopredator species, however, population dynamics remain poorly understood, even though such information is crucial for understanding potential impacts of mesopredator release on biodiversity in anthropogenically modified ecosystems (Brashares et al. 2010; Prugh et al. 2009). In particular, the relative influence of DD and DID factors in driving mesopredator population dynamics, and the potential responses of these populations to climate change and interspecific competition, are largely unknown. Studying mesopredator populations under natural conditions is an important first step in understanding how anthropogenic change affects these dynamics.

One particularly important mesopredator species in the United States is the Virginia opossum, *Didelphis virginiana*. The opossum has been implicated as an important nest predator of songbirds (Crooks and Soule 1999) and is a vector for several pathogens that can infect humans or livestock, most notably those causing

Chagas's disease (Brown et al. 2010), bovine tuberculosis (Witmer et al. 2010), and equine protozoal myeloencephalitis (Elsheikha et al. 2004). On the other hand, Keesing et al. (2009) found that opossums in southeastern New York could reduce the spread of Lyme disease and other tick-borne illnesses by killing over 95% of ticks that attempt to parasitize them. Opossums are highly human-tolerant and thrive in suburban landscapes (DeStefano and DeGraaf 2003); as a result, their many ecological impacts are often heightened in these areas. However, factors and processes influencing survival, recruitment, and population growth rate of this important mesopredator in both natural and human-modified areas remain relatively unknown (but see Kanda et al. 2009).

Our overall goal was to test for factors influencing apparent survival probability, recruitment rate, and realized population growth rate of opossums using detailed, long-term capture-mark-recapture data and Pradel's (1996) temporal symmetry models. Our study population inhabited a relatively undisturbed area under natural conditions, so our results can serve as a baseline for comparison with populations in more human-dominated areas. We tested the following hypotheses regarding the above parameters: (1) Survival and recruitment rates would differ by sex and vary based on time of year due to different dispersal behaviors and the strongly seasonal nature of opossum reproduction (Sunquist and Eisenberg 1993). (2) Population growth rate would vary based on time of year due to the variation in its underlying vital rates. (3) Population growth rate and its components would be positively affected by mean precipitation. Higher precipitation usually leads to higher primary productivity and increases opossum food resources such as mast-producing plants. (4) Survival, recruitment, and population

growth rate would be negatively affected by low temperatures. Opossums are not particularly cold-tolerant, and the duration of their activity period decreases strongly with decreasing temperature (Ryser 1995), potentially limiting their foraging ability in the cold. (5) DID factors would have a greater influence on population growth rate than DD factors. Opossums at the study site exist at a relatively low density (Sunquist and Eisenberg 1993), possibly too low to experience any significant effects of density dependence. In addition, populations of species with fast life histories tend to fluctuate with environmental variation (Promislow and Harvey 1990). (6) Population growth rate would be negatively affected by raccoon population size. Raccoons are more aggressive and intelligent than opossums (M. E. Sunquist, personal observation) and are therefore likely to be the superior competitors when these species are sympatric and overlap in resource use.

Materials and Methods

Study Area and Species

We conducted our study at the Ordway-Swisher Biological Station (OSBS), a field station managed by the University of Florida that contains more than 9,200 acres of protected habitat in north-central Florida (about 29.7°N and 82.0°W). The mosaic of habitat types within OSBS includes sandhills, xeric hammock, upland mixed forest, swamps, marshes, and lakes, with a riverine system that connects to the St. John's River. Precipitation and temperature in the region are strongly seasonal, with about 60 percent of annual rainfall occurring between May and September. The temperature occasionally falls below freezing between December and March. Primary productivity is correlated with rainfall and therefore is also seasonal (Sunquist and Eisenberg 1993).

The Virginia opossum is distributed from southernmost Canada throughout the eastern United States and as far south as Costa Rica (Gardner and Sunquist 2003). OSBS is therefore near the middle of its latitudinal range. The opossum has an unusually fast life history for its body size compared to most other mammalian mesopredators: relatively quick maturation followed by a condensed period of rapid reproduction, and then early senescence and death (Bielby et al. 2007). Both male and female opossums are sexually mature in the first year after their birth (Sunquist and Eisenberg 1993), and most only survive to breed for one year, which includes two breeding seasons. With an average litter size of 7 in the southern part their range, this results in an average lifetime reproductive output of 14 young per female (Sunquist and Eisenberg 1993), creating the potential for a high yearly per capita population growth rate.

Field Methods

Opossums were trapped at OSBS as part of a capture-mark-recapture field study on mesopredators. Monthly trapping efforts ran from September 1992 to December 1998, resulting in a total of 76 capture occasions. A total of 25 Tomahawk live traps were set at approximately 0.4-km intervals along a major flow-through drainage on the station. Traps were active for two consecutive nights per month, except in March and May, when they were active for four consecutive nights. Captured individuals were marked, weighed, measured, sexed, and released at the capture location. Data on size and sex ratio of litters were collected from female opossums, and the pouch young were also marked. Field methods followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Animal Care and Use Committee at the University of Florida (approval number A023).

Opossum and Raccoon Population Size

In order to test for the effects of density dependence and interspecific competition on opossum survival, recruitment, and population growth rate, we used capture-mark-recapture data from the aforementioned field study, in which raccoons were trapped as well as opossums. We applied superpopulation or POPAN models (Schwarz and Arnason 1996; Williams et al. 2002) to these datasets to derive monthly estimates of opossum and raccoon population size. Frequent movement of animals into and out of the study area necessitated the use of an open population model. Estimates of population size were sufficient as a measure of density because the size of the study area remained constant throughout the study. Opossum and raccoon population size estimates are provided in Figure 2-1.

Climatic Covariates

To test for the effects of climatic variables, we used historical temperature and precipitation data from the weather station at the Gainesville Regional Airport, Florida, which is 25 km west of OSBS. The available data included daily rainfall, daily maximum temperature, and daily minimum temperature for 1992 through 1998. We calculated the mean and coefficient of variation for each of these variables by month; we then used these six monthly variables as climatic covariates.

Capture-Mark-Recapture Analyses

We used two parameterizations of Pradel's (1996) temporal symmetry model to estimate and model survival, recruitment, and population growth rate. The first parameterization (ϕ and λ parameterization) estimates apparent survival probability (ϕ), recapture probability (p), and realized population growth rate (λ). The second parameterization (ϕ and f parameterization) estimates recruitment (f) rate instead of

population growth rate. These analyses, as well as those that involved POPAN models, were carried out using program MARK (White and Burnham 1999) version 6.2 implemented through the RMark package for program R (Laake and Rexstad 2010) version 2.15.2. We used an information-theoretic approach for model selection, with Akaike's information criterion corrected for small sample size (AIC_c) as a measure of model parsimony (Burnham and Anderson 2002; Williams et al. 2002).

We first determined the best model structure for recapture probability and fixed it to that structure for all subsequent analyses. We then conducted analyses to establish the appropriate base model for survival and population growth rate (using the ϕ and λ parameterization) and recruitment (using the ϕ and f parameterization). Base models were selected from model sets including the effects of sex, time (capture occasion), a linear temporal trend (modeled as a change in equal increments from one occasion to the next throughout the study), month, season, year, and additive and interactive effects of these variables. We chose biologically relevant seasons based on preliminary analyses and our knowledge of opossum phenology in the study area: January–February (first breeding season), May–June (second breeding season), July–September (wet nonbreeding season), and October–December and March–April (dry nonbreeding season).

After selecting a base model for each parameter, we tested for additive and interactive effects of density dependence (without time lags, and with time lags of one and two months) with single covariates in the base model. We conducted the same set of analyses for climatic and raccoon density covariates (grouped together as density-independent covariates). Finally, if there was evidence for both DD and DID effects, we

investigated additive and interactive effects of the covariates in the top DD model and the top DID model for each parameter.

We used RELEASE TEST 2 + 3 to assess goodness of fit. The test revealed no evidence for lack of fit or overdispersion ($\chi^2_{279} = 123.85$, $P = 1.00$, $\hat{c} = 0.44$).

Results

Over the course of the field study, there were 815 captures of 332 individual opossums. This included 454 captures of 152 individual females and 361 captures of 180 individual males. Therefore, the average number of captures per individual was close to 3 for females and 2 for males.

Recapture Probability

The best model for recapture probability ($\Delta AIC_c < 8$) included an interactive effect of sex and season. Based on this model, females (0.31 ± 0.02 [SE] to 0.43 ± 0.04) had a higher recapture probability during nonbreeding seasons than males (0.26 ± 0.04 to 0.29 ± 0.03), while males (0.37 ± 0.05 to 0.53 ± 0.06) had a higher recapture probability during breeding seasons than females (0.14 ± 0.03 to 0.46 ± 0.04). Because this model was well supported, we fixed recapture probability to this structure for all subsequent analyses.

Apparent Survival Probability

We found strong evidence that survival differed between sexes—all the well-supported models ($\Delta AIC_c < 19$; Table 2-1) included an effect of sex, with higher survival probabilities for females than for males. Although models that included additive effects of sex with temporal trend and year were also well supported, the 95% confidence intervals for the effect sizes (i.e., regression coefficients on a logit scale, or β parameters) of trend and year included zero, indicating little evidence for these effects.

We therefore used the sex effect model as the primary base model for subsequent analyses, because this model was well-supported ($\Delta AIC_c = 0.16$) and had fewer parameters compared to other competing models. Based on this model, females (0.86 ± 0.01) had a higher monthly apparent survival than males (0.76 ± 0.02). Annual survival probability was therefore 0.16 for females and 0.04 for males.

There was no evidence that population density affected survival probability. The base model performed better than all models that included population density with and without time lags as covariates (Table 2-2). In addition, the 95% confidence intervals for the β parameters of all density covariates included 0. This further indicates that population density has little or no effect on survival.

The analyses testing for effects of DID factors on survival probability revealed five factors with $\Delta AIC_c < 2$: mean precipitation with a one-month lag (mean_precip_{t-1}), variation in maximum temperature with a one-month lag (cv_maxT_{t-1}), precipitation variability with a two-month lag (cv_precip_{t-2}), precipitation variability with no time lag (cv_precip), and mean precipitation with a two-month lag (mean_precip_{t-2}), all with an additive effect of sex (Table 2-3). However, the 95% confidence intervals for the β parameters for all five of these covariates included 0, suggesting that none of these factors had a biologically meaningful effect. Since we did not find sufficient evidence that any covariates influenced survival, it was not necessary to investigate relative and combined effects of DD and DID covariates on this parameter.

Recruitment Rate

The best-supported model for recruitment rate, with a weight of 0.96, included an additive effect of month and sex (Table 2-4). For both sexes, f in May and November was too small to be estimable; we therefore fixed its value at zero for these months.

Recruitment rate was consistently higher for males than for females. Recruitment was highest in December (0.32 ± 0.12 for females and 0.57 ± 0.22 for males), and lowest in May and November (fixed to 0 for both sexes) (Figure 2-2).

We found no evidence for density dependence in recruitment rate. The base model was better supported than all DD models, and no DD model had $\Delta AIC_c < 2$ (Table 2-5). The 95% confidence intervals for the effect sizes of all density covariates included 0, further indicating that density did not influence recruitment rate.

The only DID covariate substantially influencing recruitment rate ($\Delta AIC_c < 2$) was precipitation variability with no time lag (cv_precip), which had a positive effect on recruitment ($\beta = 3.3$, 95% CI = 1.5–5.0). The top DID model included an interaction of this covariate with month; the second-best model indicated a possible interaction with sex as well (Table 2-6). Because we found no evidence supporting DD models, no further analysis was needed to compare DD and DID covariates. Recruitment rate was therefore driven primarily by climatic influences.

Realized Population Growth Rate

Like recruitment rate, population growth rate exhibited monthly variation; however, there was no evidence that population growth rate differed between sexes (Table 2-7). The population growth rate estimated from the top model ($\lambda(\text{month})$) was lowest in November (0.69 ± 0.05), and highest in December (1.30 ± 0.17). The overall pattern in population growth rate showed a decrease from December to April, an increase from April to August, a steady decrease from August to November, and a sharp increase from November to December (Figure 2-2).

We found no evidence for density dependence in population growth rate. No models with DD terms performed better than the base model (Table 2-8); 95% confidence intervals of β parameters for DD terms in models with $\Delta AIC_c < 2$ included 0.

The covariate in the best-supported DID model ($\Delta AIC_c < 3$) was precipitation variability with no time lag (*cv_precip*), which had a positive effect on population growth rate ($\beta = 0.31$, 95% CI = [0.13, 0.49]). This model included an interaction between *cv_precip* and month (Table 2-9). The lack of evidence for density dependence allowed us to conclude without further analysis that opossum population growth rate at OSBS was driven primarily by density-independent climatic factors.

Discussion

Population fluctuations are caused by underlying factors and processes that remain relatively unknown for many mesopredator species. This is particularly serious given their worldwide population explosions in the wake of apex predator declines and burgeoning human development (Letnic et al. 2011; Prugh et al. 2009). These mesopredator explosions exert significant effects on ecosystems through increased predation and disease transmission, and they can be devastating to biodiversity (Brashares et al. 2010; Crooks and Soule 1999; Ripple et al. 2013). Our goal in this study was to provide baseline information regarding the population ecology of an important mesopredator species, the Virginia opossum, by analyzing a long-term dataset gathered from a population inhabiting relatively natural habitats.

As we hypothesized, apparent survival probability and recruitment rate were dependent on sex. Male opossums are much more likely to disperse out of the population than females (Wright et al. 1995) and therefore are also more likely to be recruited from outside. Recruitment rate has not been previously studied for the Virginia

opossum, and little information on this parameter is available for other mesopredator species. Survival probabilities of opossums and other mesopredators have been better studied (Chamberlain et al. 1999; Kamler et al. 2003; Kasparian et al. 2004), but much variation exists between populations and species regarding factors that influence survival. For example, survival probabilities of several mesopredator species in a protected area of Kansas, including opossums, did not differ between sexes; annual survival for opossums was 0.06, comparable to our estimates of 0.04-0.16 and much lower than annual survival rates for other mesopredators in the study, which all exceeded 0.70 (Kamler and Gipson 2004).

While recruitment varied throughout the year as expected, survival did not vary substantially over time. This suggests that opossum survival in our study area is relatively unaffected by changing food resources or climatic conditions. The fact that this population is not limited by inter- or intra-specific competition further indicates that resources are not limiting in this system. By contrast, other studies of similarly-sized mammals have found direct effects of resource availability on population dynamics (Gentile et al. 2004). It is unclear whether our results are due to abundant resources or an inability of the population to approach its carrying capacity for other reasons as yet unknown.

Variation in precipitation had a greater effect on population growth rate and recruitment than mean precipitation did. This indicates that the amount of rainfall is less important to opossum population dynamics than how evenly rainfall is distributed throughout the month. The importance of within-year climatic variability as opposed to climatic means in driving population dynamics has been gaining recognition in recent

years, and other studies have begun to find that climate variability is more influential for other similarly-sized mammals as well (e.g., Campbell et al. 2012). This has important implications for future population trends in these species, given that the most confident predictions regarding global climate change indicate that climatic patterns are likely to become more variable, with a greater frequency of extreme events (Bernstein et al. 2007).

Contrary to our hypothesis, we found no evidence for effects of temperature on population growth rate or its components. In north-central Florida, periods of low temperature might be too mild and brief to have any significant effects on opossum population dynamics. In the more northern parts of their range, however, cold winter temperatures probably limit the distribution of opossums by decreasing overwinter survival (Kanda and Fuller 2004), and temperature in general has been shown to influence population dynamics in many other species (Fordham et al. 2012; Galiano et al. 2013; Korpela et al. 2013).

As expected, DID factors were more important than DD factors in driving opossum population dynamics. There was no evidence for the effect of population density on demographic parameters we examined. A potential explanation for the lack of density dependence is that this population might exist at a comparatively low density for opossums (see Conner et al. 1983) and is therefore well below the carrying capacity of our relatively undisturbed study site. Although the relative effects of DD and DID factors on population dynamics are a growing area of research, few studies have explicitly investigated these effects in mesopredator species (but see Levi and Wilmers 2012). Studies that have focused on other small mammals have demonstrated

combined effects of DD and DID factors (e.g., Goswami et al. 2011; Kneip et al. 2011; Leirs et al. 1997), in contrast to our study; this probably results from higher densities or an increased sensitivity to density-dependent effects of the study populations.

Finally, we found no evidence that raccoon population size influenced opossum population dynamics. Despite the potential for competition over food resources, several other studies have reported a similar lack of evidence that raccoons limit opossum populations or activity patterns (Carver et al. 2011; Kasparian et al. 2004). Intraguild competition among mammalian mesopredators has received moderate research attention, and although many studies have shown that mesopredator populations can limit each other through competition (Casanovas et al. 2012; Linnell and Strand 2000), others have found no evidence for competitive exclusion (e.g., Prange and Gehrt 2007). It is possible that mesopredator species with generalist habitat and dietary preferences may coexist more easily than other ecologically similar species, especially if they can exploit anthropogenic resources (Fischer et al. 2012). When mesopredators are not limited by competition in such environments, their populations can reach extremely high densities, heightening detrimental ecological effects such as disease transmission (Bateman and Fleming 2012).

Reports of population growth rates for mesopredators are scarce. The only other published study that reported a population growth rate for Virginia opossums was done in central Massachusetts at the northern edge of the opossum's range (Kanda et al. 2009). This study found an annual growth rate of 1.26 in a source-sink population system that relied on urban habitat to support opossums during the harsh northern winters. This value indicates a relatively rapidly growing population at the boundary of

the opossum's expanding distribution (Kanda 2005), whereas we found no evidence that our study population was increasing or decreasing annually. High population growth rates at range edges coupled with much lower, stable rates in the range interior are typical of invading species (Arim et al. 2006; Loughry et al. 2013). Populations of Virginia opossums and other mesopredators could be exhibiting this pattern; consequently, these species might function as native invaders (Carey et al. 2012). In addition, since these studies on opossum population growth rate focused on populations in nearly opposite environments, in terms of both climate and human impact, it is likely that factors driving population dynamics were also different. This illustrates the importance of studying population dynamics in multiple settings in order to truly understand the influence of climate and anthropogenic change—especially in the case of mesopredators, many of which have large distributions that can span across biomes.

Our study shows that mesopredator population dynamics in a relatively undisturbed habitat can be driven almost solely by DID factors—in particular, by short-term climatic variation, which will probably increase as our climate continues to change (Bernstein et al. 2007). Human disturbance is likely to augment the success of mesopredator populations, even with intense urbanization (Bateman and Fleming 2012; Smith and Engeman 2002). We can be reasonably sure that opossums and similar mesopredators will continue to thrive amid future environmental changes, potentially expanding in both population size and distribution, and the expansion of these species could have potentially devastating effects on biodiversity (Brashares et al. 2010; Ritchie and Johnson 2009). However, without detailed knowledge of the factors that influence

their population ecology, particularly their population growth rates, we cannot predict or effectively manage these mesopredator explosions. It is also important to investigate how these dynamics differ between populations in natural habitats and those in modified habitats. Our study provides baseline information for a relatively undisturbed opossum population in Florida. The only way we can reach a true understanding of mesopredator population dynamics is through the use of long-term data to conduct detailed investigations of covariate effects on many more species in diverse habitats around the world.

Table 2-1. Base model comparison table for apparent survival probability of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\phi(\text{Time} + \text{sex})$	23	0.000	0.269
2	$\phi(\text{sex})$	22	0.164	0.248
3	$\phi(\text{year} + \text{sex})$	28	0.693	0.190
4	$\phi(\text{Time} \times \text{sex})$	24	2.000	0.099
5	$\phi(\text{season} + \text{sex})$	25	2.381	0.082
6	$\phi(\text{season} + \text{year} + \text{sex})$	31	2.891	0.063
7	$\phi(\text{season} \times \text{sex})$	28	4.921	0.023
8	$\phi(\text{year} \times \text{sex})$	34	5.263	0.019
9	$\phi(\text{season} + \text{year} \times \text{sex})$	37	7.646	0.006
10	$\phi(\text{month} + \text{year} + \text{sex})$	39	12.923	0.000

Note: Pradel's temporal symmetry analysis of apparent survival probability (ϕ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, trend (Time), time, year, month, and season to determine the most parsimonious base model for ϕ . Only the top ten models are included. K is the number of parameters, ΔAIC_c is the difference between each model's AIC_c (Akaike's Information Criterion corrected for small sample size) and the AIC_c of the top-ranked model, and weight is the Akaike weight or model probability.

Table 2-2. Density-dependent model comparison table for apparent survival probability of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\phi(\text{sex})$	21	0.000	0.250
2	$\phi(\text{sex} + N_{t-1})$	22	0.416	0.203
3	$\phi(\text{sex} + N_{t-2})$	22	0.678	0.178
4	$\phi(\text{sex} + N)$	22	1.589	0.113
5	$\phi(\text{sex} \times N_{t-2})$	23	1.834	0.100
6	$\phi(\text{sex} \times N_{t-1})$	23	1.959	0.094
7	$\phi(\text{sex} \times N)$	23	2.826	0.061
8	$\phi(\cdot)$	20	21.434	0.000
9	$\phi(N_{t-1})$	21	22.075	0.000
10	$\phi(N_{t-2})$	21	22.472	0.000

Note: Pradel's temporal symmetry analysis of apparent survival probability (ϕ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of opossum density (N) on ϕ , including time lags of one and two months. Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-3. Density-independent model comparison table for apparent survival probability of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\phi(\text{sex} + \text{mean_precip}_{t-1})$	22	0.000	0.104
2	$\phi(\text{sex} + \text{cv_maxT}_{t-1})$	22	0.542	0.079
3	$\phi(\text{sex} + \text{cv_precip}_{t-2})$	22	0.588	0.077
4	$\phi(\text{sex})$	21	1.549	0.048
5	$\phi(\text{sex} + \text{cv_precip})$	22	1.808	0.042
6	$\phi(\text{sex} + \text{mean_precip}_{t-2})$	22	1.923	0.040
7	$\phi(\text{sex} \times \text{mean_precip}_{t-1})$	23	2.117	0.036
8	$\phi(\text{sex} \times \text{cv_maxT}_{t-1})$	23	2.478	0.030
9	$\phi(\text{sex} \times \text{cv_precip})$	23	2.596	0.028
10	$\phi(\text{sex} \times \text{cv_precip}_{t-2})$	23	2.697	0.027

Note: Pradel's temporal symmetry analysis of apparent survival probability (ϕ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of climatic variables and raccoon density (Ncoon) on ϕ , including time lags of one and two months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and cv_precip), maximum temperature (mean_maxT and cv_maxT), and minimum temperature (mean_minT and cv_minT). Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-4. Base model comparison table for recruitment rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$f(\text{month} + \text{sex})$	21	0.000	0.961
2	$f(\text{season} \times \text{sex})$	18	7.132	0.027
3	$f(\text{month} + \text{year} + \text{sex})$	27	9.382	0.009
4	$f(\text{season} + \text{sex})$	15	12.219	0.002
5	$f(\text{month} + \text{year} \times \text{sex})$	33	15.378	0.000
6	$f(\text{season} \times \text{sex} + \text{year})$	24	16.277	0.000
7	$f(\text{month} \times \text{sex})$	34	17.228	0.000
8	$f(\text{month})$	20	19.931	0.000
9	$f(\text{season} + \text{year} + \text{sex})$	21	21.340	0.000
10	$f(\text{sex})$	12	24.772	0.000

Note: Pradel's temporal symmetry analysis of recruitment rate (f) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, trend (Time), time, year, month, and season to determine the most parsimonious base model for f . Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-5. Density-dependent model comparison table for recruitment rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$f(\text{month} + \text{sex})$	21	0.000	0.368
2	$f(\text{month} + \text{sex} + N_{t-2})$	22	2.013	0.134
3	$f(\text{month} + \text{sex} + N_{t-1})$	22	2.086	0.130
4	$f(\text{month} + \text{sex} + N)$	22	2.108	0.128
5	$f(\text{month} + \text{sex} \times N)$	23	2.736	0.094
6	$f(\text{month} + \text{sex} \times N_{t-1})$	23	3.133	0.077
7	$f(\text{month} + \text{sex} \times N_{t-2})$	23	3.485	0.064
8	$f(\text{month} \times N_{t-2} + \text{sex})$	31	10.509	0.002
9	$f(\text{month} \times N_{t-1} + \text{sex})$	31	11.433	0.001
10	$f(\text{month} \times N_{t-2} + \text{sex} \times N_{t-2})$	32	11.573	0.001

Note: Pradel's temporal symmetry analysis of recruitment rate (f) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of opossum density (N) on f , including time lags of one and two months. Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-6. Density-independent model comparison table for recruitment rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$f(\text{month} \times \text{cv_precip} + \text{sex})$	31	0.000	0.425
2	$f(\text{month} \times \text{cv_precip} + \text{sex} \times \text{cv_precip})$	32	1.254	0.227
3	$f(\text{month} \times \text{cv_precip}_{t-2} + \text{sex})$	31	2.087	0.150
4	$f(\text{month} \times \text{cv_precip}_{t-2} + \text{sex} \times \text{cv_precip}_{t-2})$	32	4.060	0.056
5	$f(\text{month} + \text{sex} + \text{mean_maxT}_{t-1})$	22	7.171	0.012
6	$f(\text{month} + \text{sex} + \text{cv_minT}_{t-2})$	23	7.426	0.010
7	$f(\text{month} + \text{sex} + \text{cv_minT}_{t-1})$	22	7.877	0.008
8	$f(\text{month} + \text{sex} + \text{mean_maxT})$	22	7.884	0.008
9	$f(\text{month} + \text{sex})$	21	8.560	0.006
10	$f(\text{month} + \text{sex} \times \text{Ncoon}_{t-2})$	23	9.170	0.004

Note: Pradel's temporal symmetry analysis of recruitment rate (f) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of climatic variables and raccoon density (Ncoon) on f , including time lags of one and two months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and cv_precip), maximum temperature (mean_maxT and cv_maxT), and minimum temperature (mean_minT and cv_minT). Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-7. Base model comparison table for realized population growth rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\lambda(\text{month})$	22	0.000	0.631
2	$\lambda(\text{month} + \text{sex})$	23	1.689	0.271
3	$\lambda(\text{month} \times \text{sex})$	34	4.685	0.061
4	$\lambda(\text{month} + \text{year})$	28	8.234	0.010
5	$\lambda(\text{season})$	14	8.546	0.009
6	$\lambda(\text{season} \times \text{sex})$	18	8.666	0.008
7	$\lambda(\text{month} + \text{year} + \text{sex})$	29	9.857	0.005
8	$\lambda(\text{season} + \text{sex})$	15	10.243	0.004
9	$\lambda(\text{month} + \text{year} \times \text{sex})$	35	12.793	0.001
10	$\lambda(\text{season} + \text{year})$	20	17.300	0.000

Note: Pradel's temporal symmetry analysis of realized population growth rate (λ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, trend (Time), time, year, month, and season to determine the most parsimonious base model for λ . Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-8. Density-dependent model comparison table for realized population growth rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\lambda(\text{month})$	22	0.000	0.437
2	$\lambda(\text{month} + N)$	23	1.561	0.200
3	$\lambda(\text{month} + N_{t-1})$	23	1.693	0.187
4	$\lambda(\text{month} + N_{t-2})$	23	1.824	0.175
5	$\lambda(\text{month} \times N_{t-2})$	34	15.052	0.000
6	$\lambda(\text{month} \times N_{t-1})$	34	16.142	0.000
7	$\lambda(\text{month} \times N)$	34	16.310	0.000
8	$\lambda(.)$	11	24.769	0.000
9	$\lambda(N_{t-1})$	12	25.804	0.000
10	$\lambda(N_{t-2})$	12	26.544	0.000

Note: Pradel's temporal symmetry analysis of realized population growth rate (λ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of opossum density (N) on λ , including time lags of one and two months. Only the top ten models are included. See Table 2-1 for explanations of column headings.

Table 2-9. Density-independent model comparison table for realized population growth rate of Virginia opossums.

No.	Model	K	ΔAIC_c	Weight
1	$\lambda(\text{month} \times \text{cv_precip})$	34	0.000	0.486
2	$\lambda(\text{month} \times \text{cv_precip}_{t-2})$	34	3.476	0.085
3	$\lambda(\text{month} + \text{mean_maxT})$	23	3.697	0.077
4	$\lambda(\text{month} + \text{mean_maxT}_{t-1})$	23	4.292	0.057
5	$\lambda(\text{month} \times \text{cv_minT}_{t-1})$	34	5.064	0.039
6	$\lambda(\text{month} + \text{cv_minT}_{t-2})$	23	5.778	0.027
7	$\lambda(\text{month} + \text{mean_minT})$	23	6.040	0.024
8	$\lambda(\text{month} + \text{mean_maxT}_{t-2})$	23	6.620	0.018
9	$\lambda(\text{month} + N_{\text{coon}})$	23	6.644	0.018
10	$\lambda(\text{month})$	22	6.809	0.016

Note: Pradel's temporal symmetry analysis of realized population growth rate (λ) of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of climatic variables and raccoon density (N_{coon}) on λ , including time lags of one and two months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and cv_precip), maximum temperature (mean_maxT and cv_maxT), and minimum temperature (mean_minT and cv_minT). Only the top ten models are included. See Table 2-1 for explanations of column headings.

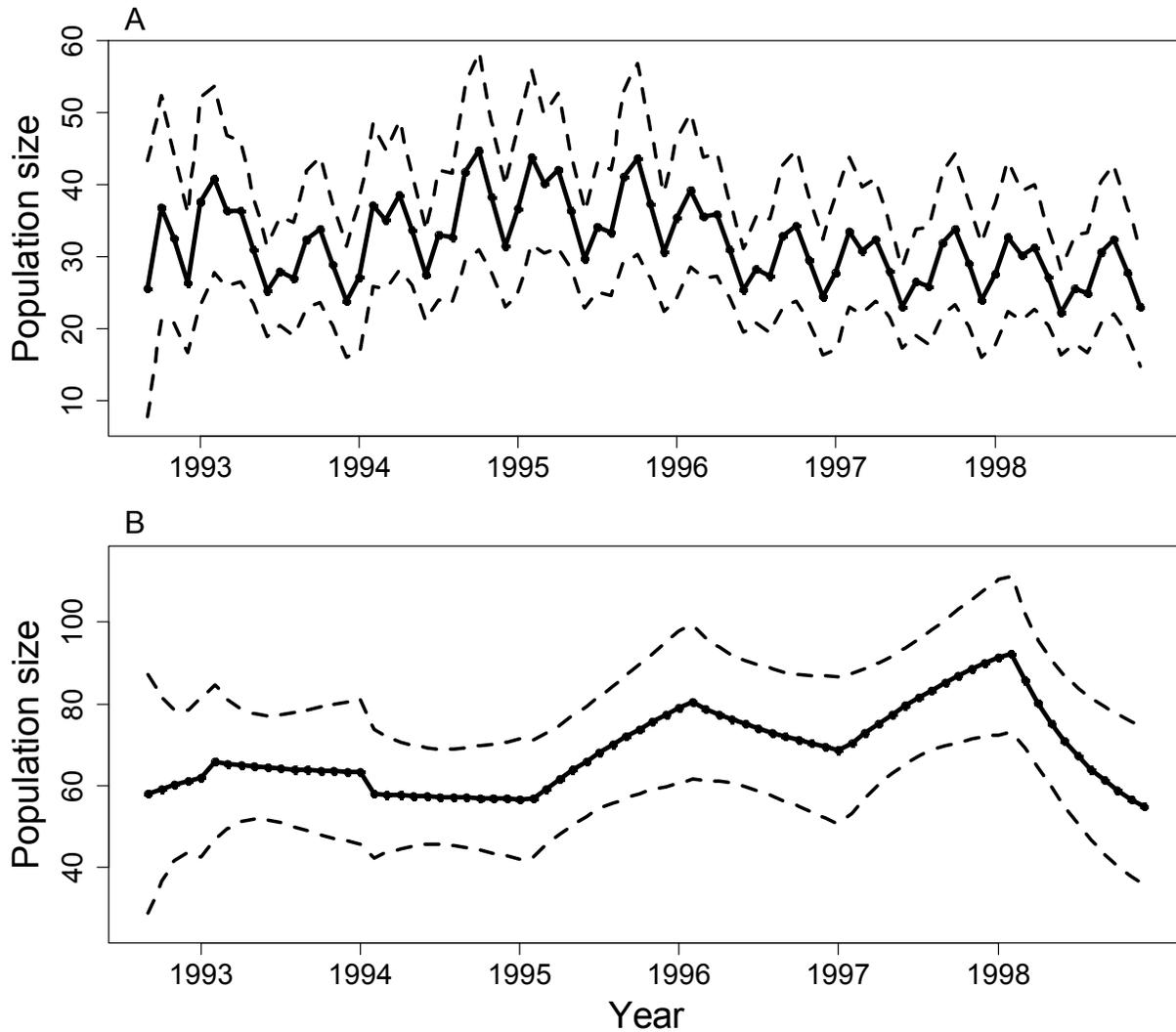


Figure 2-1. Mesopredator population sizes at the Ordway-Swisher Biological Station, FL. Estimates of A) Virginia opossum (*Didelphis virginiana*) and B) northern raccoon (*Procyon lotor*) population sizes derived from POPAN models, September 1992 to December 1998. Dotted lines represent 95% confidence intervals of estimates.

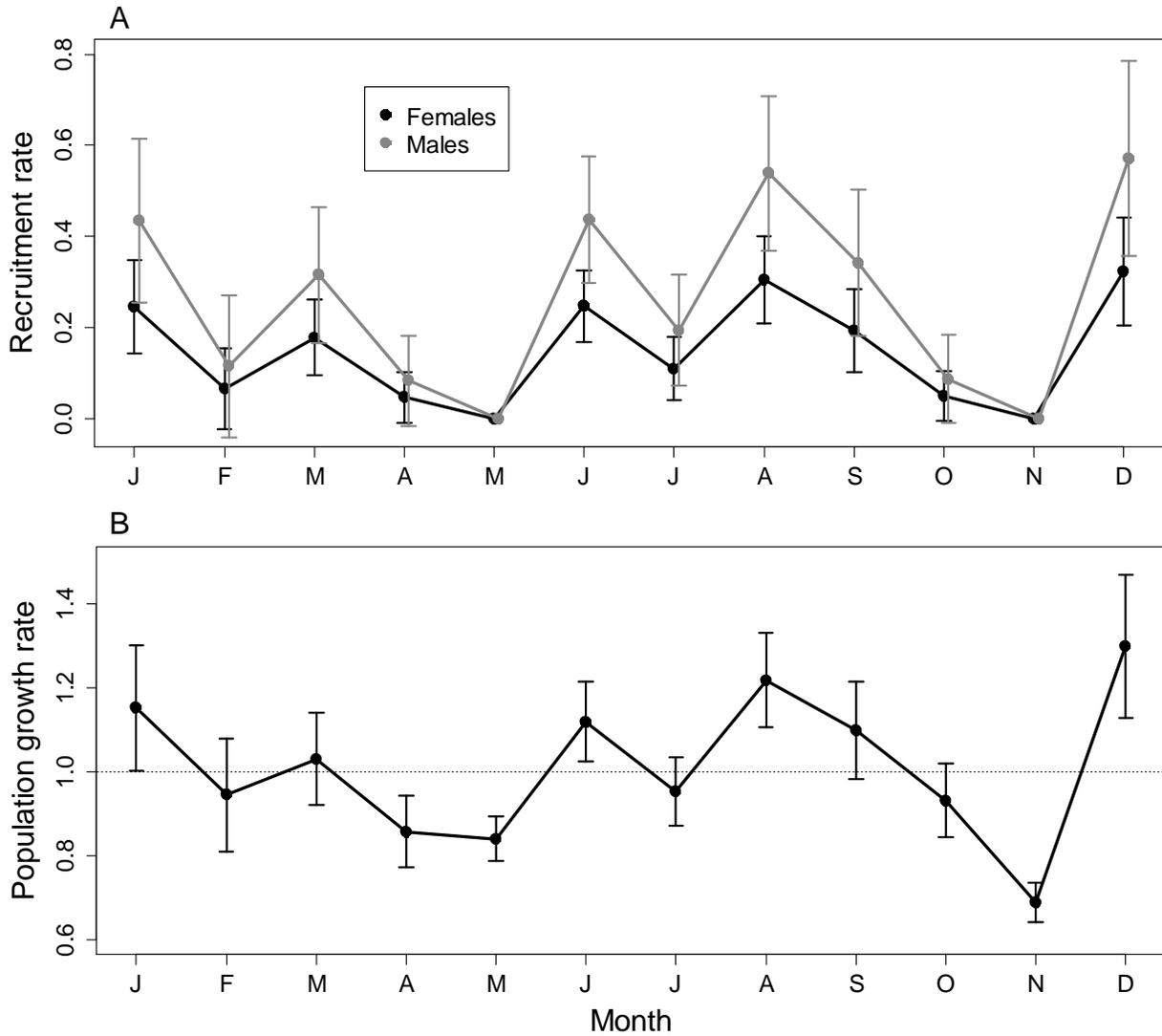


Figure 2-2. Population parameter estimates for Virginia opossums. Estimates of A) recruitment rate and B) realized population growth rate of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, FL. Estimates and standard errors are from the top-ranked base model for each parameter, which included the additive effects of month and sex for recruitment (Table 2-4) and the effect of month for population growth rate (Table 2-7).

CHAPTER 3 SURVIVAL, RECRUITMENT, AND POPULATION GROWTH RATE OF NORTHERN RACCOONS

Mesopredators, or predators at middle levels of food webs, are important contributors to ecosystem function and have significant impacts on a wide range of species (Prugh et al. 2009). They can exert their influence through many means, including predation (Crooks and Soule 1999), competition with specialist species (DeVault et al. 2011), and the spread of pathogens (Roemer et al. 2009). These effects are often heightened by the resilience and rapid growth of mesopredator populations, particularly in the presence of human settlements (DeStefano and DeGraaf 2003). Basic information on mesopredator population ecology and dynamics, though crucial for developing effective conservation and management strategies, is lacking for many of these species.

One particularly abundant and widely distributed mesopredator species in the United States is the northern raccoon, *Procyon lotor*. The raccoon has become a highly successful species in the past century with dramatic increases in both abundance and distribution, probably due to its skill in exploiting anthropogenic resources as well as the decimation of North American large carnivore populations (Zeweloff 2002). In addition, the raccoon has been introduced to Japan (Asano et al. 2003), to the former Soviet Union (Aliev and Sanderson 1966), and across mainland Europe (Beltran-Beck et al. 2012); population control efforts in these areas are hampered by insufficient knowledge of raccoon population ecology outside their native range.

As an abundant mesopredator, the raccoon has significant impacts on other species. Predation by raccoons has been shown to suppress the reproductive success of songbirds (Schmidt 2003), waterfowl (Frey and Conover 2006), and sea turtles

(Garmestani and Percival 2005), and to regulate some populations of the white-footed mouse, *Peromyscus leucopus*, (Eagan et al. 2011) and the endangered Key Largo woodrat, *Neotoma floridana smalli* (Winchester et al. 2009). The raccoon also serves as a reservoir and vector for many diseases and parasites, including rabies, canine distemper, and raccoon roundworm (Page et al. 1998). Some of these diseases can harm less-resilient populations of other species, such as the critically endangered island fox, *Urocyon littoralis*, (Timm et al. 2009), and others can infect livestock and interfere with farming operations (Atwood et al. 2009). Because they tend to thrive in the presence of human settlements, raccoons often become nuisance animals and can even pose a threat to humans as carriers of rabies (McLean 1971).

It is obvious that raccoons have significant impacts on ecology, economics, and public health and that their population dynamics are central to these impacts. However, little is known about their population ecology. In particular, estimates of raccoon population growth rates and factors influencing population growth and its components, survival and recruitment, remain largely unknown.

Our goal was to investigate demographic parameters and population dynamics of raccoons in a relatively undisturbed area using a detailed, long-term dataset and state-of-the-art modeling techniques. We estimated and modeled apparent survival, recruitment, and realized population growth rate and tested the following hypotheses regarding these parameters: (1) Males would have lower apparent survival and higher recruitment than females, because males are more likely to disperse away from their natal population and join other populations (Zaveloff 2002). (2) Survival, recruitment, and population growth rate would be positively associated with mean precipitation,

because higher precipitation results in higher primary productivity. This should bolster the availability of raccoon food resources such as hard and soft mast. (3) Population growth rate and its components would decrease with lower minimum temperatures. Since Florida raccoons are reproductively isolated from more northern populations (Cullingham et al. 2008), they might be less adapted to the cold. (4) Population growth rate would covary more strongly with survival than with recruitment. Raccoons have somewhat slow life histories with several breeding opportunities per lifetime, and population growth rates of species characterized by slow life histories tend to be more strongly influenced by survival than reproductive rates (Oli and Dobson 2005, 2003; Promislow and Harvey 1990).

Materials and Methods

Study Area and Species

We carried out fieldwork at the Ordway-Swisher Biological Station (OSBS), a field station located in north-central Florida (about 29.7°N and 82.0°W). OSBS is managed by the University of Florida and comprises more than 9,200 acres of protected habitat that is maintained in a fairly natural, undisturbed state. The station has a mosaic of dry and wet habitat types, including sandhills, xeric hammock, upland mixed forest, swamps, marshes, and lakes, as well as a riverine system connecting to the St. John's River. Precipitation and temperature in the region vary seasonally—about 60 percent of annual rainfall occurs between May and September, and the temperature occasionally falls below freezing between December and March. Primary productivity, which is correlated with rainfall, is also seasonal (Sunkvist and Eisenberg 1993).

The northern raccoon is a common medium-sized carnivore across much of the United States. Some aspects of the life history and ecology of raccoons have been fairly

well studied, particularly in the Midwest. In most parts of their range, the mating season lasts from January through March, peaking in February (Zaveloff 2002). Pregnancies last around two months, resulting in a birth peak in April (Zaveloff 2002). In the Southeast, mating generally begins later and lasts longer (Zaveloff 2002). For example, raccoons in the mangrove swamps of southern Florida mate from March through August and give birth between May and October, with no well-defined breeding season (Bigler et al. 1981). Litter sizes vary positively with latitude and female body size (Ritke 1990), commonly averaging between 3 and 4 (Clark et al. 1989; Fritzell et al. 1985; Payne and Root 1986).

Females are sexually mature in the first breeding season after their birth, although yearlings usually have much lower pregnancy rates than adults (Zaveloff 2002). If a female does not become pregnant in the regular breeding season or loses her litter soon after birth, she can experience a second estrus and produce a litter later in the year, but one litter per female per year seems to be the limit (Zaveloff 2002). Most adult raccoons survive to breed for more than one season, but few live beyond five years (Lotze and Anderson 1979). Johnson (1970) reported an average longevity of 3.1 years for raccoons in Alabama, USA.

Field Methods

Raccoons were trapped once per month from September 1992 to December 1998 (76 occasions) as part of a capture-mark-recapture field study on mesopredators at OSBS. A total of 25 Tomahawk live traps were set at approximately 0.4-km intervals along a major flow-through drainage on the station. Traps were active for four consecutive nights in March and May and for two consecutive nights in all other months; we treated these multi-day trapping periods as single capture occasions in our

analyses. Captured individuals were marked, weighed, measured, sexed, and released at the capture location. Field methods were approved by the Animal Care and Use Committee at the University of Florida (approval number A023).

Climatic Covariates

We obtained historical measurements of daily precipitation, daily maximum temperature, and daily minimum temperature from the weather station at the Gainesville Regional Airport, Florida, 25 km west of OSBS. We calculated the mean and coefficient of variation of each variable for each month from 1992 through 1998 and used these six monthly variables (mean and CV of precipitation, mean and CV of maximum temperature, and mean and CV of minimum temperature) as covariates to test for climatic effects on raccoon population dynamics.

Capture-Mark-Recapture Analyses

We used two parameterizations of Pradel's (1996) temporal symmetry model to estimate and model survival, recruitment, and population growth rate. One (ϕ and λ parameterization) estimates apparent survival probability (ϕ), recapture probability (p), and realized population growth rate (λ); the other (ϕ and f parameterization) estimates recruitment (f) rate instead of population growth rate. We carried out all analyses using program MARK (White and Burnham 1999) version 6.2 implemented through the RMark package for program R (Laake and Rexstad 2010) version 2.15.2. For model selection, we used an information-theoretic approach with Akaike's information criterion corrected for small sample size (AIC_c) to determine model parsimony and make statistical inferences (Burnham and Anderson 2002; Williams et al. 2002).

Pradel's model is sensitive to trap response, or differences in capture probabilities of marked vs. unmarked individuals (Hines and Nichols 2002). Several

raccoons in this study appeared to be “trap happy” and repeatedly reentered traps to retrieve bait (M. Sunquist, pers. obs.). To reduce bias caused by trap response, we removed all individuals that were caught on 5 or more consecutive occasions from the data.

The first step in our analyses was to determine the best model structure for recapture probability; we then fixed p to that structure for all subsequent analyses. Next, we determined the most parsimonious base model for survival and population growth rate (using the ϕ and λ parameterization) and recruitment (using the ϕ and f parameterization). We selected base models from model sets that included the effects of sex, time (capture occasion), month, season, and additive and interactive effects between sex and the other variables. We considered four biologically relevant seasons based on preliminary analyses and climatic patterns of the region: March–May (spring), June–August (summer), September–November (fall), and December–February (winter).

Once we had selected a base model for each parameter, we planned to test for additive and interactive effects of individual climatic covariates with the base model, including no time lag and time lags of one and two months. These climatic covariates are described above. However, we found little evidence for temporal variation in the parameters (see results), so we did not test for the effects of time-varying climatic factors.

We tested goodness of fit using RELEASE TEST 2 + 3. We found no evidence for lack of fit or overdispersion ($\chi^2_{346} = 252.58$, $P = 1.00$, $\hat{c} = 0.73$).

Results

There were 1,095 captures of 348 raccoons over the course of the field study. Of these individuals, 7 were captured on more than 5 consecutive occasions and were

therefore excluded from analyses. The final dataset included 983 captures of 341 raccoons, with 343 captures of 112 females and 640 captures of 229 males (Figure 3-1). The average number of captures per individual was close to 3 for both sexes, but overall there were twice as many males in the study as females.

Recapture Probability

The best model for recapture probability included an additive effect of season and sex (Table 3-1). Recapture probabilities based on this model were consistently higher for males than females; estimates were highest in spring (0.266, 95% CI = 0.234–0.302 for males; 0.193, 95% CI = 0.164–0.226 for females) and lowest in fall (0.157, 95% CI = 0.134–0.184 for males; 0.110, 95% CI = 0.091–0.132 for females). Since this model had a $\Delta AIC_c > 2$ and a model weight > 3 times greater than that of any other model, we fixed recapture probability to this structure for all subsequent analyses.

Apparent Survival Probability

All well-supported models for survival probability ($\Delta AIC_c < 18$, Table 3-2) included an effect of sex, providing strong evidence that survival differed between sexes. The top model included no temporal variation in survival; estimates were 0.947 for females (95% CI = 0.934–0.958) and 0.908 for males (95% CI = 0.893–0.920). This model had a $\Delta AIC_c > 3$ and a model weight > 5 times greater than any model that allowed survival to vary monthly or seasonally.

Recruitment Rate

Recruitment rate differed between sexes ($\Delta AIC_c < 13$, Table 3-3). Estimates of monthly recruitment from the top model, which included a sex difference with no temporal variation, were 0.091 for males (95% CI = 0.078–0.106) and 0.054 for females (95% CI = 0.042–0.067). The low ΔAIC_c between this model and the second model

(which included an additive effect of sex and season) suggested some evidence for seasonal variation in recruitment. However, the 95% confidence intervals for the β parameters of all seasons in the {season + sex} model included zero, and the 95% confidence intervals for the real estimates from this model overlapped between all seasons. This suggested little or no evidence for discernible seasonal variation in recruitment rate.

Realized Population Growth Rate

The best-supported model for population growth rate was the constant parameter model, which estimated a monthly growth rate of 1.000 (95% CI = 0.995–1.004). This indicates that our study population may have reached a stable equilibrium. Three other models had a $\Delta AIC_c < 2$ (Table 3-4); these included the effects of season, sex, and the combination of these two variables. The effect sizes of these variables, however, did not provide evidence that population growth rate varied seasonally or between sexes: the 95% confidence intervals of all β parameters for season and sex included zero. In addition, all 95% confidence intervals of the real estimates overlapped.

Neither population growth rate nor its components (survival and recruitment) varied over time (monthly or seasonally); consequently, we did not test for the influence of temporal climatic covariates on these parameters.

Discussion

Mesopredators constitute one of the most ecologically influential groups of vertebrates in the modern world, particularly as apex predator populations continue to decline and human presence continues to increase (Brashares et al. 2010; Prugh et al. 2009; Ritchie and Johnson 2009). It is becoming ever more important to understand their population dynamics in order to predict their population explosions and mitigate

their potentially harmful effects on ecosystems and other species. But research on mesopredator population ecology is remarkably scarce and limited in scope, often using coarse-scale data with little or no investigation of environmental influences on demographic parameters (e.g., Kamler and Gipson 2004; Urbanek et al. 2009). Our goal in this study was to report rigorous estimates of survival, recruitment, and population growth rate based on a long-term dataset and to test for factors influencing these parameters in a ubiquitous mesopredator, the northern raccoon.

Consistent with our hypothesis, male raccoons had lower apparent survival and higher recruitment, probably due to the movement of dispersing males into and out of the study area. The same pattern has been found for Virginia opossums in this system, an ecologically similar mesopredator species that also exhibits male-biased dispersal (Troyer et al. In press). In other mesopredator populations, sex differences in survival are often not present; clearly, the conditions in each system influence whether one sex will have higher survival than the other, but most studies do not investigate what those conditions are (Chamberlain et al. 1999; Hasbrouck et al. 1992; Kamler and Gipson 2004).

Precipitation and temperature determine primary productivity and thus also influence higher levels of food webs. Because rainfall and temperatures in our study site vary over time, we expected some evidence of temporal variation in some or all of the population parameters we studied, and we expected climatic covariates to explain some of that variation. In fact, many other studies have found links between population dynamics and climatic variables (Campbell et al. 2012; Fordham et al. 2012; Galiano et al. 2013). However, we found no evidence that either the population growth rate or its

components varied over time. Raccoons are highly adaptable in terms of diet and habitat tolerance, and the climate in Florida is relatively mild with a low range of variation. These factors likely minimized temporal variation in demographic parameters and diminished the influence of climatic variation on raccoon population dynamics.

In contrast, a sympatric population of Virginia opossums showed monthly variation in population growth rate and recruitment, strong covariation between these parameters, and a positive association of these parameters with precipitation variability (CV) (Troyer et al. In press). While opossums and raccoons are ecologically similar as mesopredators, they follow different life history strategies—opossums live a “fast” life, with rapid reproduction and early senescence; raccoons live a “slow” life, with smaller litters spaced over longer lifespans (Promislow and Harvey 1990). In addition, opossums have clearly-defined breeding seasons (Sunquist and Eisenberg 1993), while Florida raccoons can apparently breed year-round (M. Sunquist, pers. obs.). These different strategies appear to have resulted in distinct population dynamic patterns. In general, population size is less temporally variable in species with slow life histories than in those with fast life histories. The relative influence of vital rates on population growth rate also depends on life history strategy, in that population growth rate tends to be more sensitive to survival in “slow” species and to recruitment in “fast” species (Oli 2004; Oli and Dobson 2003). This example further illustrates the importance of detailed studies on the population ecology of individual mesopredator species. Even though these species often have similar diets, habitat preferences, and levels of human tolerance, dissimilarities in their reproductive schedules can cause their populations to function differently and have different responses to environmental changes.

As mentioned earlier, Pradel's model is sensitive to trap response; in particular, trap-happy behavior in the study animals can result in positively biased estimates of population growth rate (Hines and Nichols 2002; Nichols and Hines 2002). To minimize the effects of trap response, we identified 7 individuals as trap-happy and removed them from our analyses. However, we cannot completely rule out the possibility that some of our estimates and inferences were affected.

Although some aspects of raccoon ecology have been studied intensively (e.g., Beasley et al. 2012; Beasley et al. 2011; Fritzell et al. 1985; Gehrt et al. 2002; Nixon et al. 2009), there has been little focus on raccoon population dynamics and the factors and processes underlying population growth rate. For many other mesopredator species, basic population ecology is poorly understood, which can hamper efforts to determine drivers of mesopredator population dynamics and factors that allow mesopredators to thrive in a variety of habitats. As human impacts continue to grow in magnitude around the world (Bernstein et al. 2007; Ellis et al. 2010; Foley et al. 2005), human-tolerant mesopredators will continue to increase in distribution and impact as well, with potentially devastating consequences for biodiversity (Brashares et al. 2010; Prugh et al. 2009). Even in ecosystems where mesopredators are less abundant, these species play diverse roles affecting many other species (Roemer et al. 2009). In order to understand what drives their population dynamics, we need more long-term studies in diverse habitats investigating the effects of potential factors on population growth rates and underlying vital rates.

Table 3-1. Base model comparison table for recapture probability of northern raccoons.

No.	Model	K	ΔAIC_c	Weight
1	$p(\text{season} + \text{sex})$	19	0.000	0.682
2	$p(\text{season} \times \text{sex})$	22	2.463	0.199
3	$p(\text{month} + \text{sex})$	27	3.517	0.117
4	$p(\text{month} \times \text{sex})$	38	13.117	0.001
5	$p(\text{season})$	18	13.726	0.001
6	$p(\text{month})$	26	16.714	0.000
7	$p(\text{sex})$	16	43.433	0.000
8	$p(\text{time} + \text{sex})$	91	51.297	0.000

Note: Pradel's temporal symmetry analysis of recapture probability (p) of northern raccoons (*Procyon lotor*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, time, month, and season to determine the most parsimonious base model for p . Only the top eight models are included. K is the number of parameters, ΔAIC_c is the difference between each model's AIC_c (Akaike's Information Criterion corrected for small sample size) and the AIC_c of the top-ranked model, and weight is the Akaike weight or model probability.

Table 3-2. Base model comparison table for apparent survival probability of northern raccoons.

No.	Model	K	ΔAIC_c	Weight
1	$\phi(\text{sex})$	19	0.000	0.819
2	$\phi(\text{season} + \text{sex})$	22	3.449	0.146
3	$\phi(\text{month} + \text{sex})$	30	6.839	0.027
4	$\phi(\text{season} \times \text{sex})$	25	9.166	0.008
5	$\phi(.)$	18	18.038	0.000
6	$\phi(\text{season})$	21	21.533	0.000
7	$\phi(\text{month})$	29	24.632	0.000
8	$\phi(\text{month} \times \text{sex})$	41	26.343	0.000

Note: Pradel's temporal symmetry analysis of apparent survival probability (ϕ) of northern raccoons (*Procyon lotor*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, time, month, and season to determine the most parsimonious base model for ϕ . Only the top eight models are included. See Table 3-1 for explanations of column headings.

Table 3-3. Base model comparison table for recruitment rate of northern raccoons.

No.	Model	K	ΔAIC_c	Weight
1	$f(\text{sex})$	9	0.000	0.654
2	$f(\text{season} + \text{sex})$	12	1.792	0.267
3	$f(\text{season} \times \text{sex})$	15	5.591	0.040
4	$f(\text{month} + \text{sex})$	20	5.706	0.038
5	$f(.)$	8	13.283	0.001
6	$f(\text{season})$	11	14.667	0.000
7	$f(\text{month})$	19	18.363	0.000
8	$f(\text{month} \times \text{sex})$	31	24.687	0.000

Note: Pradel's temporal symmetry analysis of recruitment rate (f) of northern raccoons (*Procyon lotor*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, time, month, and season to determine the most parsimonious base model for f . Only the top eight models are included. See Table 3-1 for explanations of column headings.

Table 3-4. Base model comparison table for realized population growth rate of northern raccoons.

No.	Model	K	ΔAIC_c	Weight
1	$\lambda(.)$	8	0.000	0.288
2	$\lambda(\text{season})$	11	0.315	0.246
3	$\lambda(\text{sex})$	9	1.144	0.163
4	$\lambda(\text{season} + \text{sex})$	12	1.567	0.132
5	$\lambda(\text{month})$	19	2.031	0.104
6	$\lambda(\text{month} + \text{sex})$	20	3.353	0.054
7	$\lambda(\text{season} \times \text{sex})$	15	6.284	0.012
8	$\lambda(\text{month} \times \text{sex})$	31	20.616	0.000

Note: Pradel's temporal symmetry analysis of realized population growth rate (λ) of northern raccoons (*Procyon lotor*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998, testing for effects of sex, time, month, and season to determine the most parsimonious base model for λ . Only the top eight models are included. See Table 3-1 for explanations of column headings.

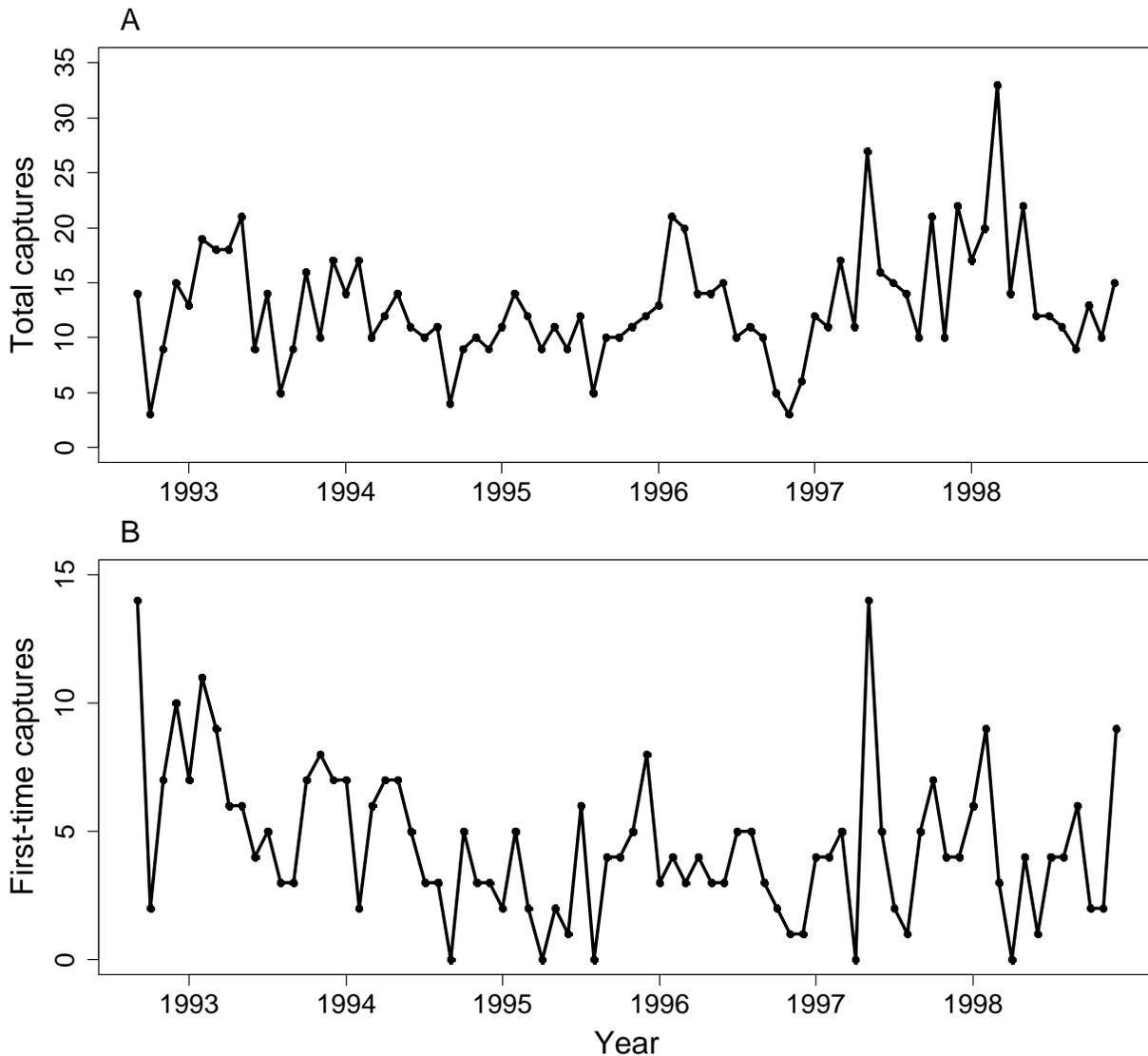


Figure 3-1. Field study results for northern raccoons. Number of A) total captures and B) first-time captures of northern raccoons (*Procyon lotor*) at the Ordway-Swisher Biological Station, Florida, from September 1992 to December 1998. Total captures include captures of all marked and unmarked individuals at each occasion; first-time captures indicate new individuals added to the overall study sample at each occasion.

CHAPTER 4 CONCLUSION

Opossums and raccoons share similar diets, habitat preferences, and levels of human tolerance. As mesopredators, they fill many of the same ecological roles. However, this study revealed important differences between the two species in demographic parameters and factors influencing them, which can influence their respective ecological impacts. Opossums have faster life histories—earlier maturation, rapid reproduction, and earlier senescence (Promislow and Harvey 1990)—and short, distinct breeding seasons. In Chapter 2, I found that opossum recruitment and realized population growth rate varied over time and were influenced by climatic variables. Raccoons, on the other hand, have slower life histories and no distinct breeding season in Florida. In Chapter 3, I found that, in contrast to opossums, recruitment and realized population growth rate of raccoons were fairly stable, with no evidence of temporal variation, and were apparently not substantially influenced by moderate climatic variation (at least in Florida). In addition, apparent survival probability was higher and recruitment rate was lower for raccoons than for opossums. For both species, survival did not vary temporally; I attribute this lack of substantial temporal variation in survival to mild climatic conditions and little temporal variation in the availability of resources for these adaptable, generalist mesopredators. Although these two species are sympatric and ecologically similar, their population dynamics differ in several ways, which could have important implications for management strategies.

Because these results come from natural, undisturbed populations, they can serve as a baseline for comparison to opossum and raccoon populations in more disturbed, human-dominated areas. In particular, these study populations were not

expanding; they maintained relatively stable sizes over the course of the study, which might be considered the natural state for mesopredator populations. Further work in this area could investigate mesopredator effects on other species in the absence of human disturbance, at both the Ordway-Swisher Biological Station and other undisturbed sites. By extrapolation, one could assume that increased human impact would increase mesopredator population sizes and thereby heighten mesopredator impacts on other species (Schmidt 2003).

We can be reasonably sure that opossums, raccoons, and similar mesopredators will continue to thrive amid future environmental changes, potentially expanding in both population size and distribution. As human populations increase and natural habitats are lost and fragmented worldwide, more and more wildlife will live in close proximity to human settlements. Mesopredator species often thrive under these conditions (Bateman and Fleming 2012; DeStefano and DeGraaf 2003). Climate change will also influence the future of these species, but the nature of this influence will likely differ between species depending on how their populations function. This study is the first to provide rigorous estimates of population growth rate and its underlying vital rates for raccoons and opossums in a natural habitat and the one of the first to directly investigate factors influencing these parameters. Comparative studies of mesopredator population ecology in relatively undisturbed versus heavily disturbed habitats, including some quantification of mesopredator impacts on communities in each habitat type, would allow us to better understand how mesopredator populations respond to human disturbance and how these responses might affect community structure in general.

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BIOGRAPHICAL SKETCH

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