Journal of Mammalogy, 95(2):421–430, 2014

Density dependence or climatic variation? Factors influencing survival, recruitment, and population growth rate of Virginia opossums

Elizabeth M. Troyer, Susan E. Cameron Devitt, Melvin E. Sunquist, Varun R. Goswami, and Madan K. Oli*

School of Natural Resources and Environment, 103 Black Hall, University of Florida, Gainesville, FL 32611, USA (EMT, VRG)

Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, University of Florida, Gainesville, FL 32611, USA (EMT, SECD, MES, VRG, MKO)

* *Correspondent: olim@ufl.edu*

Mesopredators play an increasingly important role in ecosystems where apex predators have been eliminated, but population ecology of these midsized mammalian carnivores remains poorly understood. We applied Pradel's temporal symmetry models to > 6 years of monthly capture–mark–recapture data and investigated factors influencing apparent survival, recruitment, and realized population growth rate of the Virginia opossum (*Didelphis virginiana*), an important mesopredator with unique life-history characteristics. Apparent survival did not vary temporally; monthly survival probabilities were 0.86 ± 0.01 (*SE*) for females and 0.76 ± 0.02 for males. Recruitment rate varied monthly, with the highest recruitment in December (0.32 ± 0.12 for females and 0.57 ± 0.22 for males). Realized population growth rate varied monthly and was also highest in December (1.30 ± 0.17). 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 (*Procyon lotor*), a sympatric and abundant mesopredator. Our study is the 1st to simultaneously report survival, recruitment, and population growth rate of Virginia opossums and to investigate factors influencing these rates. In doing so, we provide important insights into the population dynamics of an increasingly influential mesopredator.

Key words: *Didelphis virginiana*, mesopredator release, population dynamics, Pradel's capture–mark–recapture model, recruitment, survival

DOI: 10.1644/13-MAMM-A-164.1

Anthropogenic alteration of ecosystems through processes such as habitat fragmentation, urbanization, and climate change is a global phenomenon of ever-growing severity (Foley et al. 2005; Bernstein et al. 2007; Ellis et al. 2010). 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., Leirs et al. 1997; Goswami et al. 2011; Kneip et al. 2011). 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., Ozgul et al. 2010; Hostetler et al. 2012). 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 (Prugh et al. 2009; Brashares et al. 2010). 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 1st 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 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, pers. obs.) 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°42′0″N, 82°0′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% 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 with 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 1st year after their birth (Sunquist and Eisenberg 1993), and most only survive to breed for 1 year, which includes 2 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.

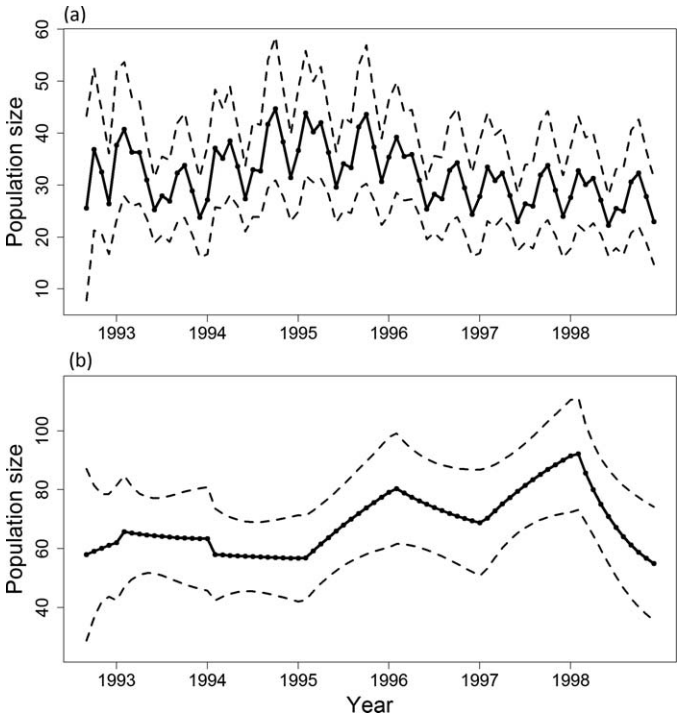

Fig. 1.—Estimates of a) Virginia opossum (*Didelphis virginiana*) and b) northern raccoon (*Procyon lotor*) population sizes derived from POPAN models, Ordway-Swisher Biological Station, Florida, September 1992 to December 1998. Dotted lines represent 95% confidence intervals of estimates.

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 (Hazelhurst, Wisconsin) were set at approximately 0.4-km intervals along a major flow-through drainage on the station. Traps were active for 2 consecutive nights per month, except in March and May, when they were active for 4 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.—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 data sets 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 Fig. 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 6 monthly variables as climatic covariates. Values of these covariates are provided in Appendix I.

Capture–mark–recapture analyses.—We used 2 parameterizations of Pradel's (1996) temporal symmetry model to estimate and model survival, recruitment, and population growth rate. The 1st parameterization (φ and λ parameterization) estimates apparent survival probability (φ), recapture probability (p), and realized population growth rate (λ). The 2nd parameterization (φ and f parameterization) estimates recruitment rate (f) 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 1st 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 on the basis of preliminary analyses and our knowledge of opossum phenology in the study area: January–February (1st breeding season), May–June (2nd 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 1 and 2 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 ($\chi^2_{279} = 123.85$, $P = 1.00$, $\hat{c} = 0.44$).

Table 1.—Model comparison table for 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. We ran 3 model sets: a) effects of sex, trend (Time), time, year, month, and season to determine the most parsimonious base model for φ; b) effects of opossum density (*N*) on φ, including time lags of 1 and 2 months; and c) effects of climatic variables and raccoon density (*N*coon) on φ, including time lags of 1 and 2 months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and *cv*_precip), maximum temperature (mean_max*T* and *cv*_max*T*), and minimum temperature (mean_min*T* and *cv*_min*T*). In section a), we used the lambda parameterization, setting *p* to season × sex and λ to month. In sections b) and c), we used the recruitment parameterization, setting *p* to season × sex and *f* to month + sex. Only the top 10 models are included for each set. *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.

No.	Model	*K*	ΔAIC_c	Weight
a) Base model				
1	φ(time + sex)	23	0.000	0.269
2	φ(sex)	22	0.164	0.248
3	φ(year + sex)	28	0.693	0.190
4	φ(time × sex)	24	2.000	0.099
5	φ(season + sex)	25	2.381	0.082
6	φ(season + year + sex)	31	2.891	0.063
7	φ(season × sex)	28	4.921	0.023
8	φ(year × sex)	34	5.263	0.019
9	φ(season + year × sex)	37	7.646	0.006
10	φ(month + year + sex)	39	12.923	0.000
b) Density dependence				
1	v(sex)	21	0.000	0.250
2	φ(sex + N_{t-1})	22	0.416	0.203
3	φ(sex + N_{t-2})	22	0.678	0.178
4	φ(sex + *N*)	22	1.589	0.113
5	φ(sex × N_{t-2})	23	1.834	0.100
6	φ(sex × N_{t-1})	23	1.959	0.094
7	φ(sex × N)	23	2.826	0.061
8	v(.)	20	21.434	0.000
9	φ(N_{t-1})	21	22.075	0.000
10	φ(N_{t-2})	21	22.472	0.000
c) Environmental covariates				
1	φ(sex + mean_precip$_{t-1}$)	22	0.000	0.104
2	φ(sex + *cv*_maxT_{t-1})	22	0.542	0.079
3	φ(sex + *cv*_precip$_{t-2}$)	22	0.588	0.077
4	φ(sex)	21	1.549	0.048
5	φ(sex + *cv*_precip)	22	1.808	0.042
6	φ(sex + mean_precip$_{t-2}$)	22	1.923	0.040
7	φ(sex × mean_precip$_{t-1}$)	23	2.117	0.036
8	φ(sex × *cv*_maxT_{t-1})	23	2.478	0.030
9	φ(sex × *cv*_precip)	23	2.596	0.028
10	φ(sex × *cv*_precip$_{t-2}$)	23	2.697	0.027

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. On the basis of 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), whereas 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 1a) 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 0, 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 with other competing models. On the basis of 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 1b). 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 5 factors with $\Delta AIC_c < 2$: mean precipitation with a 1-month lag (mean_precip$_{t-1}$), variation in maximum temperature with a 1-month lag (*cv*_maxT_{t-1}), precipitation variability with a 2-month lag (*cv*_precip$_{t-2}$), precipitation variability with no time lag (*cv*_precip), and mean precipitation with a 2-month lag (mean_precip$_{t-2}$), all with an additive effect of sex (Table 1c). However, the 95% confidence intervals for the β parameters for all 5 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 2a). For both sexes, *f* in May and November was too small to be estimable; we therefore fixed its value at 0 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; Fig. 2a).

Table 2.—Model comparison table for 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. We ran 3 model sets: a) effects of sex, trend (Time), time, year, month, and season to determine the most parsimonious base model for f; b) effects of opossum density (N) on f, including time lags of 1 and 2 months; and c) effects of climatic variables and raccoon density (Ncoon) on f, including time lags of 1 and 2 months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and cv_precip), maximum temperature (mean_max$T$ and cv_max$T$), and minimum temperature (mean_min$T$ and cv_min$T$). We set φ to sex and p to season × sex in all model sets. Only the top 10 models are included for each set. 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.

No.	Model	K	ΔAIC_c	Weight
a) Base model				
1	f(month + sex)	21	0.000	0.961
2	f(season × sex)	18	7.132	0.027
3	f(month + year + sex)	27	9.382	0.009
4	f(season + sex)	15	12.219	0.002
5	f(month + year × sex)	33	15.378	0.000
6	f(season × sex + year)	24	16.277	0.000
7	f(month × sex)	34	17.228	0.000
8	f(month)	20	19.931	0.000
9	f(season + year + sex)	21	21.340	0.000
10	f(sex)	12	24.772	0.000
b) Density dependence				
1	f(month + sex)	21	0.000	0.368
2	f(month + sex + N_{t-2})	22	2.013	0.134
3	f(month + sex + N_{t-1})	22	2.086	0.130
4	f(month + sex + N)	22	2.108	0.128
5	f(month + sex × N)	23	2.736	0.094
6	f(month + sex × N_{t-1})	23	3.133	0.077
7	f(month + sex × N_{t-2})	23	3.485	0.064
8	f(month × N_{t-2} + sex)	31	10.509	0.002
9	f(month × N_{t-1} + sex)	31	11.433	0.001
10	f(month × N_{t-2} + sex × N_{t-2})	32	11.573	0.001
c) Environmental covariates				
1	f(month × cv_precip + sex)	31	0.000	0.425
2	f(month × cv_precip + sex × cv_precip)	32	1.254	0.227
3	f(month × cv_precip$_{t-2}$ + sex)	31	2.087	0.150
4	f(month × cv_precip$_{t-2}$ + sex × cv_precip$_{t-2}$)	32	4.060	0.056
5	f(month + sex + mean_maxT_{t-1})	22	7.171	0.012
6	f(month + sex + cv_minT_{t-2})	23	7.426	0.010
7	f(month + sex + cv_minT_{t-1})	22	7.877	0.008
8	f(month + sex + mean_max$T$)	22	7.884	0.008
9	f(month + sex)	21	8.560	0.006
10	f(month + sex × Ncoon$_{t-2}$)	23	9.170	0.004

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 2b). 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% confidence interval [CI] = 1.5–5.0). The top DID model included an interaction of this covariate with month; the 2nd-best model indicated a possible interaction with sex as well (Table 2c). 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 3a). The population growth rate estimated from the top model (λ[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 (Fig. 2b).

We found no evidence for density dependence in population growth rate. No models with DD terms performed better than the base model (Table 3b); 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 3c). 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 (Prugh et al. 2009; Letnic et al. 2011). These mesopredator explosions exert significant effects on ecosystems through increased predation and disease transmission, and they can be devastating to biodiversity (Crooks and Soule 1999; Brashares et al. 2010; 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 data set 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

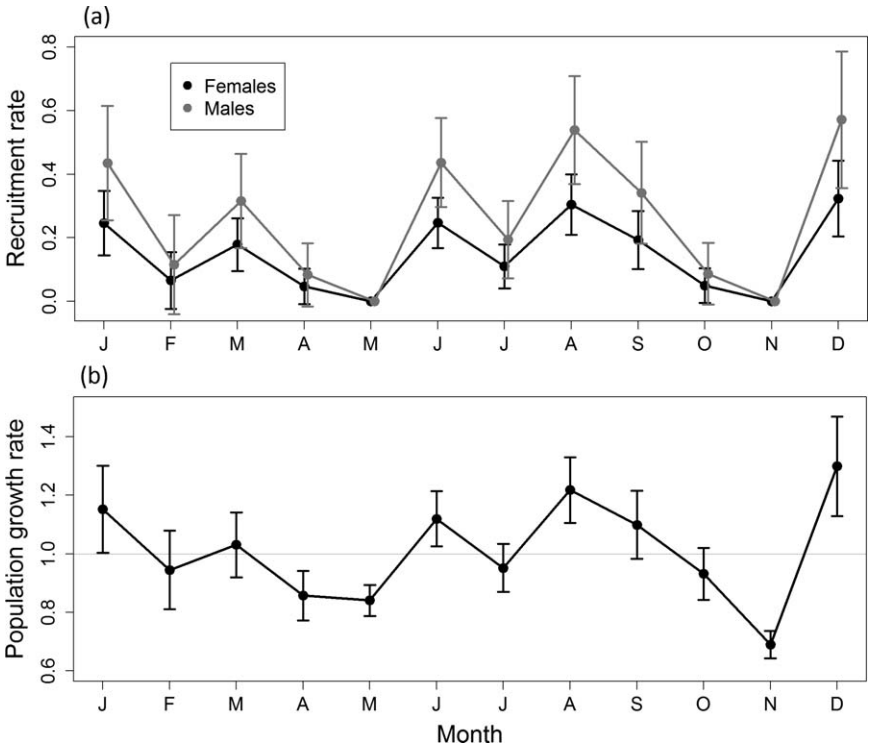

Fig. 2.—a) Recruitment rate and b) realized population growth rate of Virginia opossums (*Didelphis virginiana*) at the Ordway-Swisher Biological Station, Florida. Estimates and *SE*s are from the top-ranked model for each parameter, which included the additive effects of month and sex for recruitment (Table 2a) and the effect of month for population growth rate (Table 3a).

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 with 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).

Although 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 intraspecific 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

Table 3.—Model comparison table for 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. We ran 3 model sets: a) effects of sex, trend (Time), year, month, and season to determine the most parsimonious base model for λ; b) effects of opossum density (*N*) on λ, including time lags of 1 and 2 months; and c) effects of climatic variables and raccoon density (*N*coon) on λ, including time lags of 1 and 2 months. Climatic variables included the monthly mean and coefficient of variation of precipitation (mean_precip and *cv*_precip), maximum temperature (mean_max*T* and *cv*_max*T*), and minimum temperature (mean_min*T* and *cv*_min*T*). We set φ to sex and *p* to season × sex in all model sets. Only the top 10 models are included for each set. *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.

No.	Model	*K*	ΔAIC_c	Weight
a) Base model				
1	λ(month)	22	0.000	0.631
2	λ(month + sex)	23	1.689	0.271
3	λ(month × sex)	34	4.685	0.061
4	λ(month + year)	28	8.234	0.010
5	λ(season)	14	8.546	0.009
6	λ(season × sex)	18	8.666	0.008
7	λ(month + year + sex)	29	9.857	0.005
8	λ(season + sex)	15	10.243	0.004
9	λ(month + year × sex)	35	12.793	0.001
10	λ(season + year)	20	17.300	0.000
b) Density dependence				
1	λ(month)	22	0.000	0.437
2	λ(month + *N*)	23	1.561	0.200
3	λ(month + N_{t-1})	23	1.693	0.187
4	λ(month + N_{t-2})	23	1.824	0.175
5	λ(month × N_{t-2})	34	15.052	0.000
6	λ(month × N_{t-1})	34	16.142	0.000
7	λ(month × *N*)	34	16.310	0.000
8	λ(.)	11	24.769	0.000
9	λ(N_{t-1})	12	25.804	0.000
10	λ(N_{t-2})	12	26.544	0.000
c) Environmental covariates				
1	λ(month × *cv*_precip)	34	0.000	0.486
2	λ(month × cv_precip_{t-2})	34	3.476	0.085
3	λ(month + mean_max*T*)	23	3.697	0.077
4	λ(month + mean_maxT_{t-1})	23	4.292	0.057
5	λ(month × *cv*_minT_{t-1})	34	5.064	0.039
6	λ(month + *cv*_minT_{t-2})	23	5.778	0.027
7	λ(month + mean_min*T*)	23	6.040	0.024
8	λ(month + mean_maxT_{t-2})	23	6.620	0.018
9	λ(month + Ncoon)	23	6.644	0.018
10	λ(month)	22	6.809	0.016

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., Leirs et al. 1997; Goswami et al. 2011; Kneip et al. 2011), 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 (Kasparian et al. 2004; Carver et al. 2011). 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 (Linnell and Strand 2000; Casanovas et al. 2012), 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 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 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 (Smith and Engeman 2002; Bateman and Fleming 2012). 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 (Ritchie and Johnson 2009; Brashares et al. 2010). 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.

Resumen

Los meso-depredadores juegan un papel cada vez más importante en los ecosistemas donde los depredadores ápice han sido reducidos o eliminados; sin embargo, se conoce poco sobre la ecología poblacional de estos mamíferos carnívoros de tamaño mediano. Nosotros aplicamos modelos simétricos temporales de Pradel a datos mensuales de marcaje, captura y recaptura (de más de 6 años) e investigamos los factores que influencian la sobrevivencia aparente, el reclutamiento y la tasa de crecimiento poblacional de la zarigüeya de Virginia (*Didelphis virginiana*); el único marsupial que habita al norte de la frontera Mexicana y un importante meso-depredador con características de historia de vida únicas. La sobrevivencia aparente fue diferente entre sexos y no presentó variación temporal, con probabilidades de sobrevivencia mensual de 0.86 $\pm$ 0.01 (EE) para hembras y 0.76 $\pm$ 0.02 para machos. La tasa de reclutamiento fue diferente entre sexos y varió mensualmente, con un mayor reclutamiento en diciembre (0.32 $\pm$ 0.12 para hembras y 0.57 $\pm$ 0.22 para machos). La tasa de crecimiento poblacional también varió mensualmente y fue mayor en diciembre (1.30 $\pm$ 0.17). Las tasas de reclutamiento y crecimiento poblacional fueron influenciadas positivamente por los coeficientes de variación mensual de la precipitación. No hubo evidencia de un efecto de la densidad sobre la dinámica poblacional de esta zarigüeya, ni evidencia de competencia con el mapache (*Procyon lotor*), un meso-depredador simpátrico y abundante. Nuestros resultados sugieren que la dinámica poblacional de esta zarigüeya es más fuertemente influenciada por la variación climática que por la competencia inter o intra-específica. Nuestro estudio es el primero en reportar simultáneamente las tasas de sobrevivencia, de reclutamiento y de crecimiento poblacional para la zarigüeya de Virginia, y en investigar los factores que influencian estas tasas con un análisis riguroso de datos de campo tomados sobre un largo periodo tiempo. De esta manera, aportamos información importante sobre la dinámica poblacional de un meso-depredador cada vez más influyente.

Acknowledgments

This study was supported by the Ordway-Swisher Biological Station, the School of Natural Resources and Environment, and the Department of Wildlife Ecology and Conservation, University of Florida. We are grateful to B. J. Swanson, N. Yoccoz, and an anonymous reviewer for many helpful suggestions and thoughtful comments. We thank O. E. Murillo-García for Spanish translation of the summary and the numerous volunteers who assisted in data collection. Finally, we thank the late J. F. Eisenberg for his support and active involvement in trapping and data collection. He was always a stimulating partner on the trap line.

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Submitted 3 July 2013. Accepted 24 September 2013.

Associate Editor was Bradley J. Swanson.