

Population ecology of the nine-banded armadillo in Florida

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We used 15 years (1992–2006) of capture–mark–recapture (CMR) data obtained from a population of nine-banded armadillos (*Dasypus novemcinctus*) located at the Tall Timbers Research Station near Tallahassee, Florida and multistate CMR models to estimate and model capture probabilities, annual apparent survival, and transition probabilities between reproductive and nonreproductive states (for adult females only). Using an information theoretic approach, we then examined various influences on these parameters. Across all years, capture probability, p , was higher for adults than for yearlings, and higher for males than for females. There was also substantial yearly variation. Conditional on survival, the annual transition probability, ψ , for reproductive adult females to remain reproductive was 0.853 ± 0.044 ; the estimate for nonreproductive adult females to become reproductive was 0.388 ± 0.060 . Annual apparent survival, S , was lowest for juveniles ($S = 0.541 \pm 0.118$) and highest for reproductive adult females ($S = 0.753 \pm 0.034$). Contrary to expectation, these data provided no evidence for a cost of reproduction among adult females. Finally, annual apparent survival was lower for all animals during an extensive hardwood removal that occurred from 1998 to 2000 than in either preceding or subsequent years.

Key words: apparent survival, armadillo, capture probability, costs of reproduction, *Dasypus novemcinctus*, logging, mark–recapture analysis

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Estimates of demographic parameters, and how they covary with intrinsic and extrinsic environmental factors, are a fundamental requirement for understanding the population ecology of any species. In the ideal situation, this is accomplished by tracking all members of a population from birth until death (Clutton-Brock and Sheldon 2010). Impressively, this has been achieved (or at least approximated) in a growing number of species, including mammals such as primates, rodents, and ungulates. However, many mammals are more cryptic, and knowledge of population features is often very limited. One example is the nine-banded armadillo (*Dasypus novemcinctus*; hereafter referred to as “armadillo”), a primarily nocturnal, burrowing species that is largely asocial (Loughry and McDonough 2013; McBee and Baker 1982). Despite some intensive field studies, there have been no attempts to estimate demographic parameters for any population of armadillos. This undoubtedly stems, at least in part, from difficulties in capturing sufficient numbers of individually identified animals year after year in a species that is relatively long lived (although longevity is unknown in the wild, a best estimate is about 8–12 years; some captive animals have lived

>20 years—see Loughry and McDonough 2013). Indeed, the situation is equally bleak for all other species of Xenarthra (anteaters, sloths, and armadillos). This is unfortunate because it precludes the possibility of any intra- or interspecific comparisons that might identify important factors influencing the evolution of particular populations.

Recently, several techniques have been developed that allow estimation of demographic parameters using incomplete data. In this paper we use 15 years (1992–2006) of capture–mark–recapture (CMR) data collected from a population of nine-banded armadillos occupying Tall Timbers Research Station in northern Florida, and multistate CMR models (Amstrup et al. 2005; White and Burnham 1999), to generate estimates of capture probability, the transition probability between reproductive and nonreproductive states, and annual apparent survival. We then examine how these parameters covary with



age, sex, and time (year). We expected age to influence survival because data from the carapaces of dead animals collected at a site in Texas indicated that juveniles experienced a higher level of mortality than did adults, much of it due to predation (McDonough and Loughry 1997). Assuming the same holds true elsewhere, we hypothesized that estimates of survival for juveniles would be lower than those for adults.

Among adults, survival is often associated with the costs of reproduction. Because of these costs, the usual expectation, for both sexes, is that reproductive individuals should have lower survival than nonreproductive ones (Reznick 1985). This seems plausible for armadillos. For example, males appear to compete among themselves for access to females (McDonough 1997), and may have larger home ranges than females or nonreproductive males to increase encounters with receptive females (McDonough 2000). Likewise, virtually all female mammals experience energetic costs during reproduction (Gittleman and Thompson 1988; Speakman 2008). However, unlike most species of armadillos that only produce 1–2 young, female nine-banded armadillos compound these costs because they exhibit obligate polyembryony, whereby they routinely give birth to litters of genetically identical quadruplets from a single fertilized egg (Prodöhl et al. 1996). Indeed, Lengyel (2011) showed that reproductive females experienced a nearly 40% increase in mass-specific oxygen consumption and a 17% increase in mass-specific excretion of carbon dioxide. Beyond this, Superina and Loughry (2012) proposed that females may incur further nutritional costs because they must provide sufficient calcium for the young to develop their protective carapaces. Given these considerations, it seems logical to predict that reproductive armadillos should have lower survival than nonreproductive individuals.

If there are differential costs of reproduction between the sexes, then the standard prediction from life-history theory is that the sex experiencing higher costs should exhibit lower survival (Reznick 1985; Stearns 1989, 1992). As just described, male and female armadillos seem to incur costs associated with reproduction, but it is not clear how these costs compare with one another. Consequently, predicting a sex bias in survival is not possible. In fact, another alternative is that the costs of reproduction for each sex may be equivalent. This possibility is supported by studies that failed to find any obvious sexual dimorphism in morphology or differences in the time budgets of males and females (Ancona and Loughry 2010; Loughry and McDonough 2013). Thus, although no clear prediction can be made, analysis of sex-specific survival in armadillos may allow identification of which sex (if either) has higher costs of reproduction.

Finally, various environmental conditions can also influence survival. In the case of the Tall Timbers population, the most obvious instance of this involved an extensive program of hardwood removal that occurred from 1998 to 2000. Hardwoods are preferred habitat for armadillos at this site (McDonough et al. 2000), and their removal seemed to trigger a subsequent decline in the population (McDonough and Loughry 2005). By analyzing temporal (i.e., yearly) variation

in estimates of annual apparent survival we hoped to further document the effects of hardwood removal, with the prediction that survival would be lower during, and perhaps after, removal than in the years prior.

MATERIALS AND METHODS

Field methods.—Details of the study site and sampling methods can be found in Loughry and McDonough (2013). Briefly, data were collected at the Tall Timbers Research Station, located just north of Tallahassee, Florida (30°39'36"N, 84°12'0"W), during the summers (May–August) of 1992–2003. There were only 2 days of sampling in 1996 and 8 days in 2000. Sampling in other years was more extensive, with the number of sampling days ranging from 44 to 68 (McDonough and Loughry 2005; Robertson et al. 2000). Sampling consisted of nightly censuses that lasted from approximately 1600 h to 2400 h. Before dark, roads and trails were walked while searching for armadillos; after dark, spotlights and headlamps were used to locate animals while driving or walking along roads on the property. Except for 1996 and 2000, the number of hours spent in the field each year conducting censuses ranged from 238 to 489, and typically involved the participation of 2–7 field-workers.

All procedures for capturing and marking armadillos followed American Society of Mammalogists guidelines (Sikes et al. 2011) and were approved by the animal care committee at Valdosta State University. We attempted to capture and mark, or in the case of previously marked individuals, identify all animals discovered during nightly censuses. Armadillos were captured using long dip nets. Once caught, individuals were weighed, sexed, measured, marked for temporary visual identification with various shapes and colors of reflective tape glued to different areas of the carapace, and marked for permanent identification by injection of a passive induced transponder tag under the front carapace at its juncture with the neck. Body mass was used to assign captured animals to 1 of 3 age categories: juveniles (young of the year) were individuals weighing <2 kg, yearlings weighed 2–3 kg, and adults weighed >3 kg (Loughry and McDonough 1996). Although there is some overlap in body mass between yearlings and adults (McDonough et al. 1998), we have found body mass to be a fairly reliable criterion in assigning individuals to these broad age categories (Loughry and McDonough 2013).

Reproductive status of adult females was determined from inspection of the nipples as definitely lactating, possibly lactating, or definitely not lactating (Loughry and McDonough 1996). It is likely that the first 2 categories represent the reproductively active females present in the population each year (Loughry and McDonough 2013). In contrast, all adult males are physiologically capable of reproducing each year (Peppler 2008). Our data did not allow us to distinguish which males were reproductively active each year and which were not. Consequently, we were unable to test for survival differences between reproductive and nonreproductive adult males.

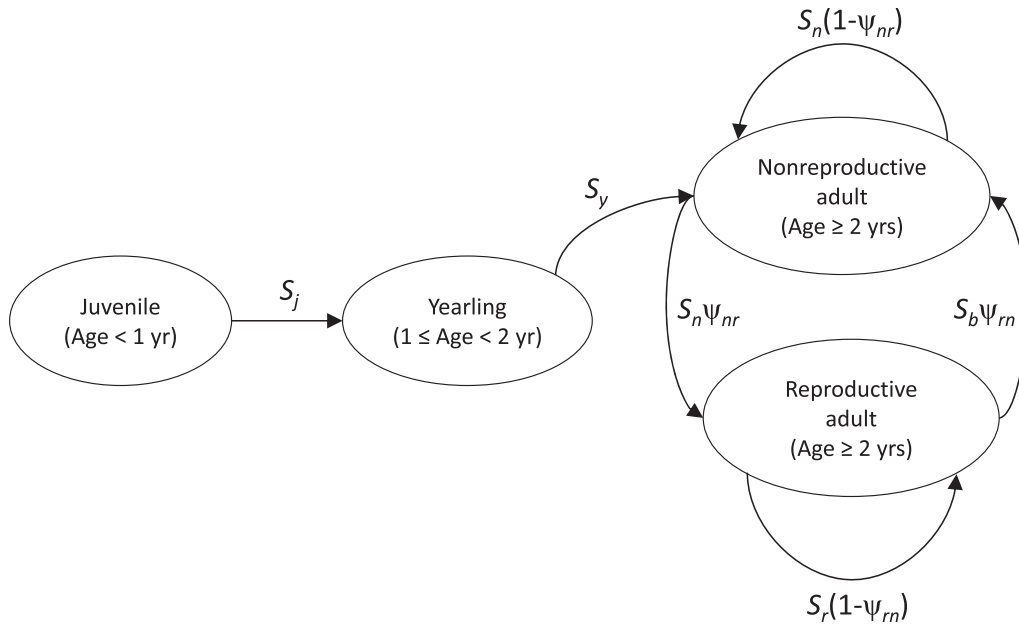


Fig. 1.—Life cycle graph used to describe the life history of nine-banded armadillos. See text for definitions of stages. Symbols are: S_j = apparent annual survival probability of juveniles; S_y = apparent annual survival probability of yearlings; S_n = apparent annual survival probability of nonreproductive adults; S_r = apparent annual survival probability of reproductive adults; ψ_{nr} = probability that a nonreproductive adult becomes reproductive the following year, conditional on survival; and ψ_{rm} = probability that a reproductive adult becomes nonreproductive the following year, conditional on survival.

Although our fieldwork terminated at the end of 2003, some data were available from 2004 to 2006 because of an experiment at Tall Timbers designed to remove nest predators of northern bobwhite (*Colinus virginianus*—see McDonough et al. 2007). Armadillos do eat quail eggs (Staller et al. 2005), and so were culled from the property as part of the experiment. We were granted access to these specimens to identify any individuals that had been captured and marked as part of our earlier sampling. Nest predators were culled from March to October of each year; this work involved the full-time, daily efforts of 2–3 technicians from the United States Department of Agriculture. Thus, the sampling in these years, although not concentrated solely in our study areas, was sufficiently intensive as to be comparable with that conducted by us (McDonough et al. 2007).

Survival analysis.—We used a multistate CMR modeling framework (Williams et al. 2001) to estimate and model capture probability (p), annual apparent survival (S), and transition probabilities (ψ). The multistate CMR models were implemented in Program MARK using the RMark interface to build models for MARK (Laake and Rextad 2009; White and Burnham 1999). We considered 4 stages on the basis of age and reproductive status: <1 year old = juveniles; ≥ 1 and <2 year old = yearlings; and ≥ 2 years old = adults (Fig. 1). For the reasons stated above, adult females, but not adult males, were further divided into nonreproductive and reproductive stages. Juveniles survive with annual survival probability S_j and all survivors become yearlings the following year. Yearlings survive with annual survival rate S_y and all

surviving yearlings become nonreproductive adults the following year. Although some yearlings could potentially become reproductive (Peppler 2008), none did so in our sample. Consequently, the probability of transition from yearling to reproductive adult was not estimable. Nonreproductive and reproductive adults survive the year with annual survival rate S_n and S_r , respectively. Additionally, nonreproductive adult females that survive the year become reproductive adults the following year with probability ψ_{nr} , and remain nonreproductive with probability $(1 - \psi_{nr})$. Finally, reproductive adult females that survive the year become nonreproductive adults the following year with probability ψ_{rm} , and remain reproductive with probability $(1 - \psi_{rm})$. Transitions from the juvenile to yearling stage and from the yearling to nonreproductive adult stage were fixed to 1.0, because all survivors automatically make these transitions. Transitions from nonreproductive and reproductive stages to yearling or juvenile stages, from yearling to juvenile, and from juvenile to adult were fixed to 0 because these transitions are not biologically feasible. Data limitations did not allow us to test for temporal variation in ψ . Also, because the reproductive status of males could not be accurately determined, data on adult males were used for estimating and modeling p and S , but not for the analysis of ψ .

We used a sequential approach to the modeling process. First, we determined an appropriate model structure for the capture probability, p . To do so, we constrained survival and transition probabilities to be stage specific (i.e., $S[\text{stage}]$ and $\psi[\text{stage}]$), allowed p to be constant, then examined how p was

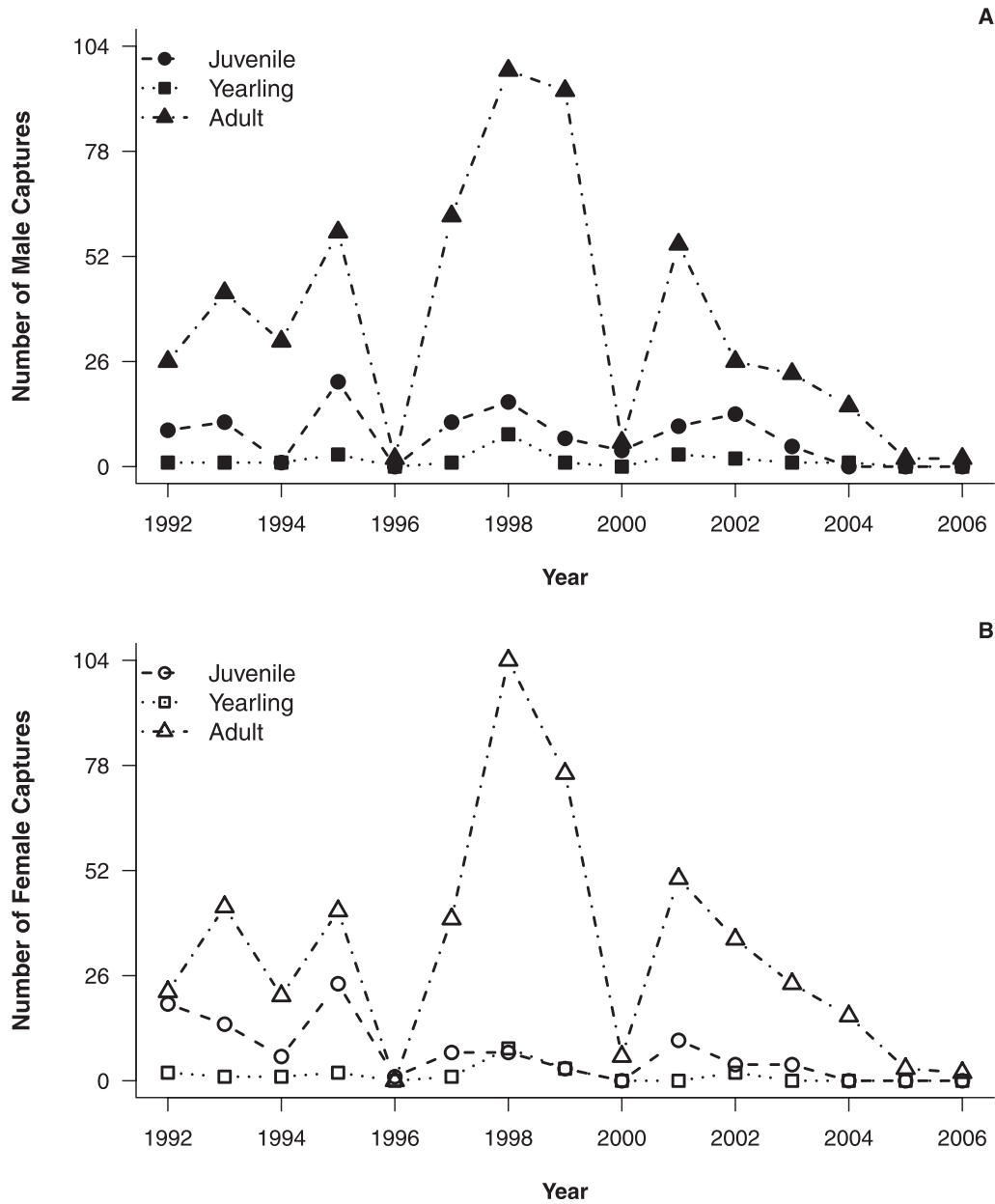


Fig. 2.—Summary of the number of male (A) and female (B) nine-banded armadillos captured by age class for each year of the study.

affected by stage, sex, and time, plus additive and interactive effects of these three variables. We used an information theoretic approach on the basis of the Akaike information criterion corrected for small sample size (AICc—Burnham and Anderson 2002) to identify the most parsimonious (or best) model structure for p ; model structure for p was fixed to that with the lowest AICc value for subsequent analyses. Next, we modeled ψ as a constant parameter (i.e., unaffected by any covariate), and also allowed it to be affected by stage. As stated previously, a sex effect on ψ could not be evaluated due to the lack of reliable data on the reproductive status of adult males. The effect of stage, sex, time, and additive and interactive effects of these variables on S was investigated next, with p and ψ fixed at those with lowest AICc values based on the

preceding analyses. Finally, using the most parsimonious model structure for p , ψ , and S thus identified, we tested for the effect of hardwood removal on apparent survival rates.

We used AICc for model comparison and statistical inferences, and to select the most parsimonious model from a candidate model set (Burnham and Anderson 2002). Model comparison was based on differences in AICc values (ΔAICc). The model with the lowest AICc value was considered the most parsimonious or the best model; models that differed from each other by $\Delta\text{AICc} \leq 2$ were considered to be equally well supported by the data. A goodness-of-fit test implemented in UCARE (Choquet et al. 2009) revealed no lack of fit or overdispersion ($\chi^2 = 21.998$, $d.f. = 33$; $\hat{c} = 0.666$). Consequent-

Table 1.—Model comparisons testing for the effects of stage, sex, time, and their additive and interactive effects on 4 parameters. (a) Capture probability (p). For these analyses, transition (ψ) and apparent survival probabilities (S) were constrained to be stage specific (i.e., ψ [stage], and S [stage]). (b) Transition probability (ψ). For these analyses, p was fixed at the best model structure in (a) model 3, and S was modeled as S (stage). (c) Survival probability (S). For these analyses, p was fixed at the best model structure in (a) model 3, and ψ was fixed at the best model structure in (b) model 2. (d) Effect of hardwood removal on S . For these analyses, model structure for p was fixed at that in (a) model 3, ψ was fixed at that in (b) model 2, and S was fixed at that in (c) model 4. Symbols are: K = number of parameters in the model; AICc = Akaike information criterion corrected for small sample size; Δ AICc = difference in AICc between the minimum AICc model and the i th model; and model weight = Akaike weight (probability that the i th model is the best model in the candidate model set). An asterisk (*) indicates an interactive effect, a plus sign (+) indicates an additive effect, a period (.) indicates a constant parameter value; time indicates temporal (yearly) variation; and *manage* is a dummy variable indicating hardwood removal activity in our study site (1992–1997: before removal; 1998–2000: during removal; and 2001–2006: after removal). See Fig. 1 for details on stages. The most parsimonious models are in bold typeface.

Model number	Parameters	K	AICc	Δ AICc	Weight
(a) Capture probability (p)					
3	p(stage + sex + time)	25	2,659.678	0.000	0.922
5	p (stage + time)	24	2,664.831	5.153	0.070
8	p (time + sex)	22	2,669.480	9.802	0.007
9	p (time)	21	2,673.037	13.359	0.001
7	p (stage * time)	61	2,729.276	69.598	0.000
6	p (stage)	11	2,993.083	333.405	0.000
4	p (stage + sex)	12	2,993.320	333.642	0.000
2	p (sex)	9	3,003.576	343.898	0.000
1	p (.)	8	3,004.148	344.470	0.000
(b) Transition probability (ψ)					
2	ψ(stage)	25	2,659.678	0.000	1.000
1	ψ (.)	23	2,687.359	27.681	0.000
(c) Survival probability (S)					
4	S(stage)	25	2,659.678	0.000	0.427
5	S (stage + sex)	26	2,661.228	1.550	0.197
1	S (.)	22	2,661.284	1.606	0.191
2	S (sex)	23	2,661.459	1.781	0.175
6	S (stage + time)	38	2,668.310	8.632	0.006
5	S (stage + sex + time)	39	2,670.161	10.483	0.002
8	S (time)	35	2,672.556	12.878	0.001
2	S (sex + time)	36	2,673.290	13.612	0.001
7	S (stage * time)	76	2,723.426	63.748	0.000
(d) Effect of hardwood removal on S					
2	S(stage + manage)	27	2,656.377	0.000	0.426
6	S (stage * manage)	33	2,657.309	0.932	0.268
4	S (stage + sex + manage)	28	2,658.354	1.977	0.159
1	S (stage)	25	2,659.678	3.301	0.082
3	S (stage + sex)	26	2,661.228	4.851	0.038
5	S ((stage + sex) * manage)	36	2,661.854	5.477	0.028

ly, quasilikelihood adjustments were not necessary. In what follows, all means are reported $\pm 1 SE$.

RESULTS

A total of 1,292 captures of 828 armadillos was recorded during our study. Excluding individuals with missing information on age, sex, or reproductive status (the latter for females only), there were 390 females and 422 males in the sample. There were 207, 43, and 1,026 captures of juveniles, yearlings, and adults respectively. The mean number of recaptures was 1.60 ± 0.97 . As shown in Fig. 2, sex and age composition, as well as the total number of individuals in our sample, varied substantially during the study.

Preliminary analyses performed to identify appropriate model structure for capture probability (p) revealed that this

parameter was best described with an additive effect of stage, sex, and time, indicating stage- and sex-specific differences, as well as temporal variation (Table 1a). On the basis of this model, p was consistently lower among yearlings compared with adults, and males generally had higher capture probabilities than females across all years; p for all stages substantially varied over time (Figs. 3A and 3B).

The model that allowed transition probability (ψ) to be stage specific was better supported than the one that constrained ψ to be constant (Table 1b). On the basis of this model, conditional on survival, the probability that nonreproductive females became reproductive the following year was 0.388 ± 0.060 ; the rest remained nonreproductive. For females that were reproductive, the probability that they would reproduce again the following year was quite high ($\psi = 0.853 \pm 0.044$; Fig. 3C). For further analyses, we fixed model structure for p to that

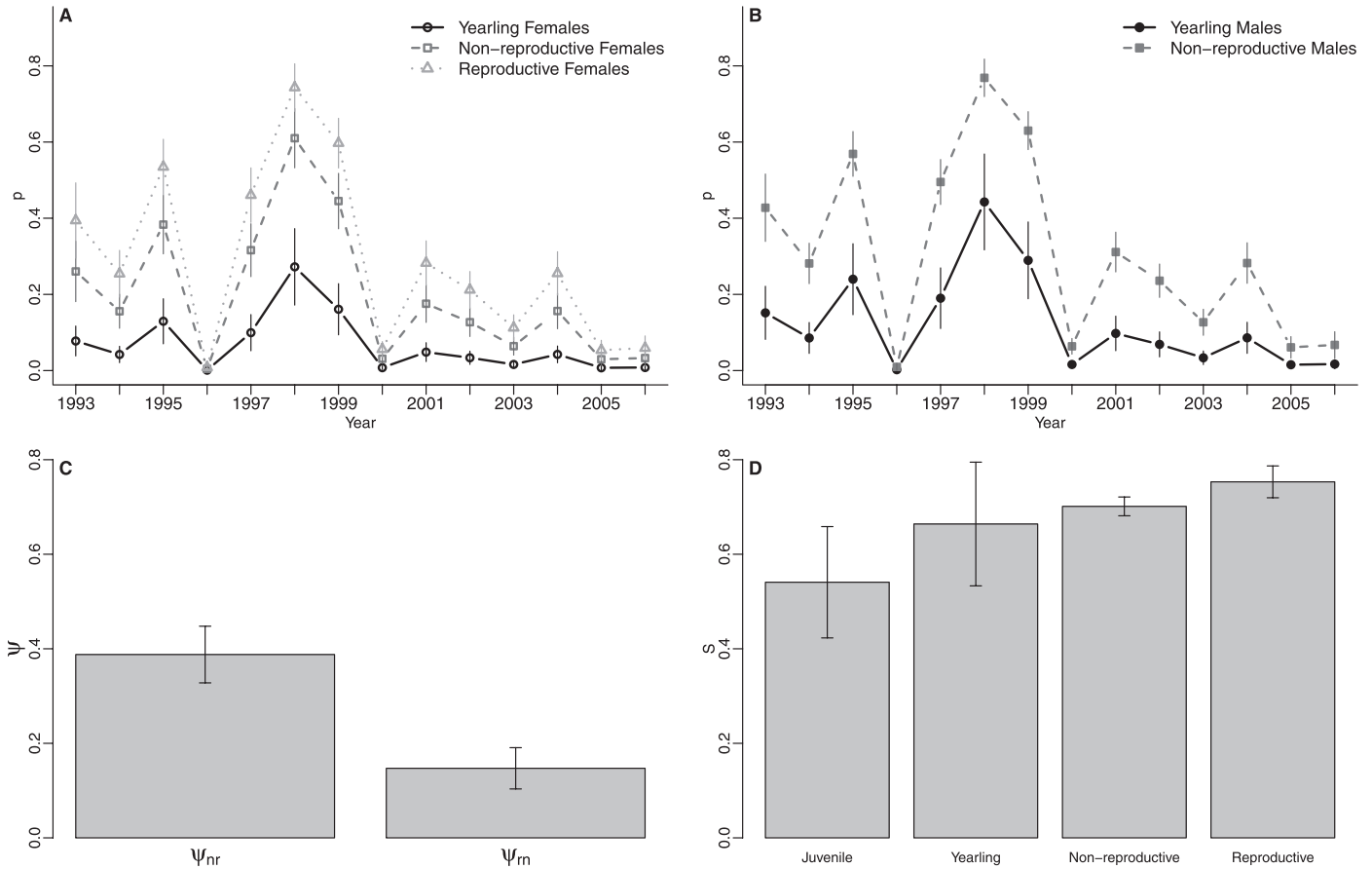


Fig. 3.—Parameter estimates on the basis of the best-supported multistate capture–mark–recapture model (Table 1c, model 4). The model structure was: ($S[\text{stage}]p[\text{stage} + \text{sex} + \text{time}] \psi [\text{stage}]$). (A) Stage-specific capture probability (p) through time for female armadillos; (B) stage-specific p through time for male armadillos. Reproductive status was not determined for adult males; thus all males were categorized as nonreproductive; (C) stage-transition probabilities (ψ) for adult females. Note that, although not depicted, $1 - \psi$ represents the probability of an individual remaining in the same stage as previously; and (D) stage-specific apparent survival probability (S). Vertical lines represent the standard error associated with each estimate. See Fig. 1 for explanation of state transition probabilities.

in model 3 in Table 1a, and ψ to that in model 2 in Table 1b, because these models had the lowest AICc values.

The most parsimonious model for S allowed survival to vary among stages (model 4, Table 1c). On the basis of this model, juveniles (0.541 ± 0.118) and yearlings (0.664 ± 0.131) had lower annual apparent survival than adults, and reproductive females (0.753 ± 0.034) had a slightly higher survival compared with nonreproductive females (0.701 ± 0.020 ; Fig. 3D). Although models that included a sex effect and an additive effect of sex and stage on S also received some support, evidence for sex-specific differences was weaker than stage-specific differences in survival.

Finally, we used ($p[\text{age} + \text{sex} + \text{time}] \psi[\text{stage}]S[\text{stage}]$) as a base model and tested for the effect of hardwood removal on S . The lowest AICc model included an additive effect of stage and hardwood removal on survival; a model that included an interactive effect of stage and hardwood removal was equally well supported. Both of these models indicated that stage-specific survival was lower when hardwoods were being removed, compared with before or after the hardwood removal (Fig. 4).

DISCUSSION

This study provides the first rigorous estimates of demographic parameters for nine-banded armadillos, or any xenarthran. As such, it represents a critical first step toward future intra- and interspecific comparative analyses. We also identified a variety of factors that contributed to variation in parameter estimates. In what follows, we discuss each of our main findings in turn.

Capture probability varied with age, sex, and time. Age- and sex-specific variation was probably influenced by movement patterns, with individuals that moved little being more likely to be captured than those ranging more widely. Female armadillos give birth in early spring and share burrows with their young for much of the following summer (Loughry and McDonough 2013). Thus, the high capture probability of reproductive females may have resulted from their restricted movements as they remained close to the burrows containing their young. In contrast, the low capture probability of yearlings may have been due to their more extensive movements as they prospected for a home range in which to settle (Loughry and McDonough 2001). Along the same lines, several authors have

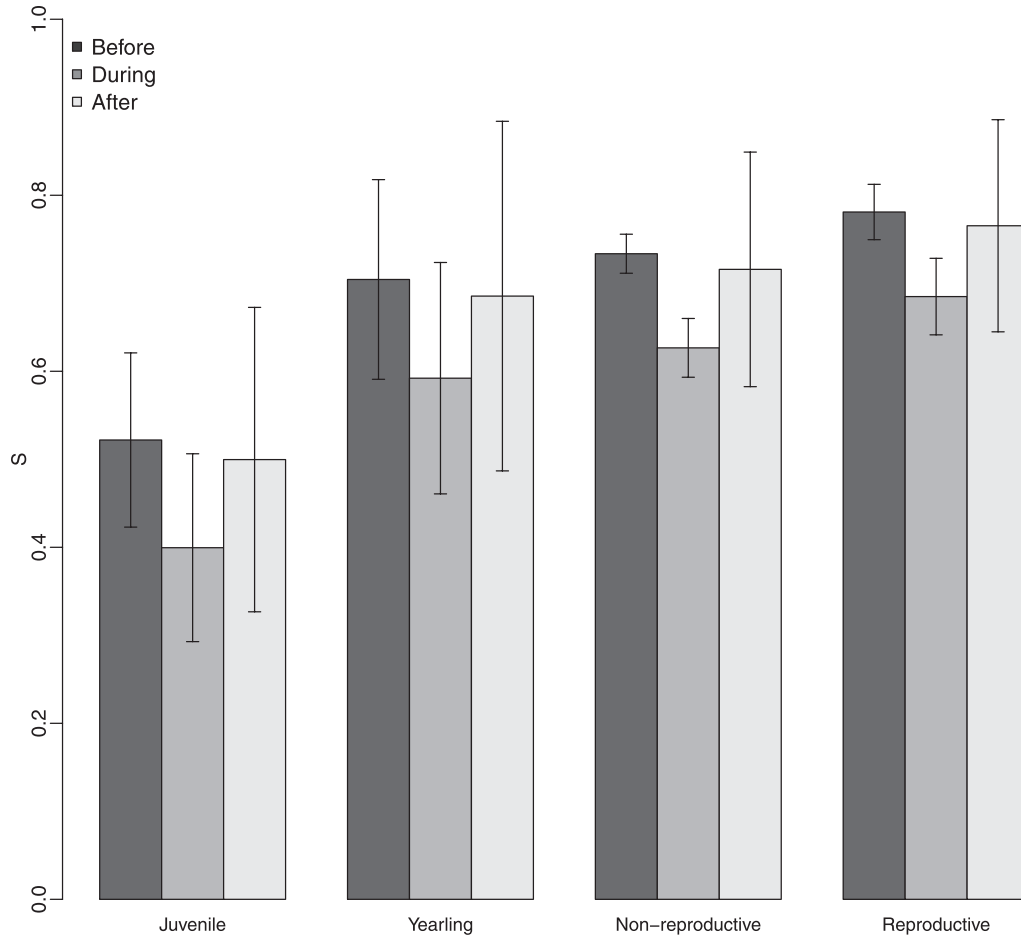


Fig. 4.—Survival estimates on the basis of the best-supported multistate capture–mark–recapture model that addressed the impact of hardwood management on survival: $S(\text{stage} + \text{management})p(\text{stage} + \text{sex} + \text{time})\psi(\text{stage})$. The survival probabilities (S) associated with each age/reproductive category for times before, during, and after hardwood removal are represented by different shades of gray.

noted that populations of armadillos consist of a core of long-term residents and about an equal number of “transients” that may be caught once or twice as they move through an area, but are rarely seen again (Bond et al. 2000; Jacobs 1979; Loughry and McDonough 2001). Reproductive adults (particularly females) would seem most likely to be residents and, thus, captured frequently, whereas yearlings and nonreproductive adults may often be transients, resulting in lower capture probabilities. Limited movement seems a less plausible explanation for the high capture probability of males. Instead, that may be linked with the increased activity and conspicuousness of males as the breeding season commences in midsummer (June and July—Loughry and McDonough 2013; McDonough 1997).

Several factors may have contributed to temporal variation in capture probability. First, and most obvious, is sampling effort. There was considerable variation in time spent in the field and the number of individuals involved in sampling each year at Tall Timbers (see McDonough and Loughry 2005), and this undoubtedly had an effect on capture success as well as capture probability. Second is weather. For example, armadillos were very scarce in 1994 when 2 tropical storms dumped

substantial rain on Tall Timbers, which resulted in flooding of parts of our study sites. Finally, there is human disturbance. Although logging may have decreased survival, it likely enhanced capture probability because animals were forced to move more as a result of being displaced from their normal home range, and armadillos were more conspicuous and easier to catch in the denuded landscape created by hardwood removal.

Analyses of transition probabilities focused on the transition between reproductive states for adult females. Our data indicate that once a female begins reproducing she is likely to continue to do so, but only about 39% of nonreproductive females transition to become reproductive each year. These findings are consistent with previous work, from multiple sites, that showed that about one-third of adult females are classified as not lactating each year (Loughry and McDonough 2013), and genetic data that identified only a small number of females as mothers of captured young (Loughry et al. 1998; Prodöhl et al. 1998). Collectively, these results suggest that a substantial number of females forego reproduction in any particular year. Given that armadillos reproduce just once a year (Loughry and McDonough 2013), skipping reproduction would seem to

represent a sizeable cost to a female's lifetime fitness. Why females might do this is unknown, but may reflect the energetic or nutritional costs associated with reproduction (Lengyel 2011; Superina and Loughry 2012). An important topic for future work will be to unravel the influences on the likelihood of reproduction among adult female armadillos.

Because of costs associated with reproduction, theory predicts lower survival for reproductive than nonreproductive individuals (Reznick 1985; Stearns 1989, 1992). Contrary to this expectation, we found that reproductive females survived slightly better than nonreproductive females. Once again, whether this indicates that only high-quality females in good condition can afford reproduction is unknown. In any case, whatever the costs associated with reproduction might be in armadillos, our analyses support the hypothesis that they are equivalent for males and females. This conclusion is based on the fact that there were no sex differences in survival within any age class. A lack of differential costs and an absence of sex differences in survival is perhaps expected, given previous work that documented no obvious sexual dimorphism in morphology (Loughry and McDonough 2013) or sex differences in time budgets (Ancona and Loughry 2010).

Among the factors considered in our study, age had the strongest influence on survival, with younger animals surviving less well than older ones. These results are consistent with age-specific survival patterns in many species of mammals (e.g., Hostetler et al. 2009; Kneip et al. 2011; Ozgul et al. 2006; Slade and Balph 1974), and also agree well with previous work in armadillos that documented high juvenile mortality, much of it due to predation (McDonough and Loughry 1997). Whether due to mortality or the disappearance of juveniles as the result of other phenomena such as dispersal, the lower apparent survival of juveniles is also reflected in the fact that a higher percentage of adults were retained in the Tall Timbers population from year to year compared with the percentage of juveniles that were recruited (Loughry and McDonough 2001).

Regardless of age class, another major impact on survival was the hardwood removal that occurred at Tall Timbers from 1998 to 2000. Survival was lower for all armadillos during the logging period. Thus, even though, for the reasons mentioned earlier, more animals were captured during the logging period (at least in the 1st year or 2, see Fig. 2), few of them persisted in the population. Lower survival undoubtedly contributed to the decline in population that began toward the end of the logging period and continued through 2003 (McDonough and Loughry 2005). Whether the population has been able to fully recover from this disturbance is unknown (but see McDonough et al. 2007). In any case, our findings highlight the potentially negative consequences of logging, and may have relevance for populations of armadillos (including other species) found throughout Latin America, where deforestation is an ongoing and major impact on many habitats.

Nine-banded armadillos have colonized much of the southern United States in less than 200 years, and continue to expand northward (Loughry and McDonough 2013; Taul-

man and Robbins 1996). As with any "invasive" species, there is great interest in understanding why armadillos have been so successful. Among other factors, demographic parameters clearly must play some contributing role. For example, one might speculate that armadillo populations grow rapidly due to high survival, reproduction, or a combination of the two. Like many colonizing species (Hedrick 1984), our data show that armadillos exhibit low juvenile and high adult survival, but we did not find much evidence that they have corresponding high rates of reproduction (see also Loughry et al. 1998). Thus, how this dramatic range expansion has been accomplished remains puzzling (but see Sol et al. 2012 for a possible explanation). The demographic parameters we have estimated can be incorporated into models to explore population dynamics (e.g., Hostetler et al. 2009, 2012). Such an exercise might provide a better understanding of how the intrinsic properties of armadillo populations have promoted range expansion.

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