Population Dynamics of Nine-Banded Armadillos: Insights from a Removal Experiment

Colleen M. McDonough[1,*], J. Mitchell Lockhart[1], and W.J. Loughry[1]

Abstract - From 1992 to 2003, we captured and permanently marked 829 *Dasypus novemcinctus* (nine-banded armadillo) at the Tall Timbers Research Station in northern Florida. From 2004 to 2006, an attempt was made to eliminate all armadillos from Tall Timbers as part of an experiment to remove nest predators of *Colinus virginianus* (Northern Bobwhite). Data from armadillos killed at Tall Timbers during this period showed a rapid decline in previously marked individuals, with only 4 collected in 2006. Even though the resident population thus seemed to have been exterminated quickly, total numbers of armadillos collected remained stable over all 3 years. This did not appear to be due to an increase in reproductive success such that more juveniles were produced to replace the animals being lost. Rather, the data were more consistent with the hypothesis of immigration by adults into the population to colonize areas vacated by culled animals. This scenario supports previous reports of large numbers of transient armadillos that move extensively, and may provide insight into how armadillos have successfully invaded most of the southern United States in just the last 200 years. Finally, these findings also suggest that, at least in this area, culling animals is not likely to be an effective means of eliminating armadillo predation on quail eggs.

Introduction

Standard population biology models identify birth and death rates, and the rates of immigration versus emigration as key determinants of population size (e.g., Caughley 1977, Hastings 1997, Hedrick 1984, MacArthur and Connell 1966). Thus, in the face of heightened mortality, the only way for a population to remain stable is to enhance reproduction and/or to receive more immigrants. Conventional wisdom suggests increased immigration would be a less important factor because dispersal is risky, low frequency, and typically not focused in specific directions (Chepko-Sade and Halpin 1987, Clobert et al. 2001, Stenseth and Lidicker 1992). Consequently, the probability of large numbers of immigrants moving in to replace individuals lost through increased mortality would seem low.

Recently, conservation biologists have been interested in identifying attributes that might make a particular species a successful invader of new habitats (Sakai et al. 2001). One obvious such trait is vagility, as increased movement would presumably increase the probability of finding hospitable areas in which to thrive. Unlike the scenario described above, such populations might be able to recover quite quickly from population downturns, even without elevated reproductive rates, due to the extreme fluidity of individual movement patterns.

[1]Department of Biology, Valdosta State University, Valdosta, GA 31698-0015. [*]Corresponding author - cmcdonou@valdosta.edu.

Dasypus novemcinctus Linneaus (nine-banded armadillo) is a ubiquitous resident of the southern United States. However, its commonness in the US is a relatively recent phenomenon; armadillos were first noted in the Rio Grande River Valley of Texas in the 1820s (Humphrey 1974, Taulman and Robbins 1996). Coupled with one or more releases of captive armadillos in south-central Florida in the 1920s, the species has rapidly spread across much of the southern US, currently found as far north as southern Illinois and Nebraska (Freeman and Genoways 1998, Van Deelen et al. 2002) and possibly as far west as Arizona (M. Mares, Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Normal, OK, pers. comm.).

Taulman and Robbins (1996) estimated that armadillos were expanding their range in the US at the rate of 4 km/yr. This would suggest substantial movement by individuals out of established populations to colonize new areas. In a long-term study of patterns of recruitment and retention in an armadillo population, Loughry and McDonough (2001) found that a certain portion of the animals were long-term residents that moved very little (see also Gammons 2006). However, in addition, many animals were captured only once, seemingly as they passed through the area. These animals have been referred to as transients (Bond et al. 2000, Jacobs 1979). What determines whether an armadillo becomes a long-term resident versus a transient remains unknown at present, but it seems likely that transients are major factors in promoting the rapid range expansion of nine-banded armadillos in the United States.

Recent intensive studies of *Colinus virginianus* Linneaus (Northern Bobwhite) nests have identified nine-banded armadillos as an important mammalian predator of quail eggs (Staller 2001, Staller et al. 2005). Consequently, there has been interest among game managers in finding ways to limit this predation and improve quail production. One proposed option is to remove all potential mammalian predators from quail-nesting habitat. However, such an approach is only likely to be effective if culled animals are not replaced (via immigration or increased reproduction), so that predator populations are permanently reduced. In the case of nine-banded armadillos, the presence of transients and the rapid range expansion of this successful invader suggest there may be a considerable reservoir of individuals available to replace those lost.

From 1992 to 2003 we studied a population of nine-banded armadillos at the Tall Timbers Research Station. A major component of this study involved extensive mark-recapture sampling. Beginning in 2004, Tall Timbers contracted with the United States Department of Agriculture (USDA) to conduct a 3-year experiment in which all potential mammalian predators of Northern Bobwhite eggs were removed from the property. Thus, armadillos, along with other species such as *Lynx rufus* Schreber (bobcat), *Procyon lotor* Linneaus (raccoon), *Canis latrans* Say (coyote) and *Didelphis virginiana* Kerr (opossum), were trapped and killed from 2004 to 2006. This massive undertaking provided a unique opportunity to examine certain features of armadillo population dynamics. Specifically, data from these harvested animals allowed us to address the following questions: (1) How long did it take to remove the resident population of armadillos from Tall Timbers? (2) Once residents were gone, were they replaced—either from within the population by increased production of juveniles, or from without by increased immigration of adults into vacated spaces—or did the population show a steady decline toward local extinction? and (3) Is culling animals an effective means of reducing armadillo predation on quail eggs?

Study Site Description

Tall Timbers is located north of Tallahassee, FL (Leon County) at the border with Georgia. The 1600-ha property is situated along the north shore of Lake Iamonia and is bisected by a public road (County Road 12, Fig. 1). Major habitat types found there are: (1) hammocks, or bottomland hardwood forests, consisting primarily of: *Quercus* spp. (oak), *Fagus grandifolia* Ehrh. (American beech), and *Magnolia grandiflora* L. (southern magnolia); (2) fields, which were plowed annually and planted with *Zea mays* L. (corn), *Trifolium* spp. (clover), and *Urochloa ramosa* (L.) Nguyen (brown-top millet); and (3) upland pine, primarily consisting of *Pinus taeda* L. (loblolly), *P. echinata* P. Mill. (shortleaf), and some *P. palustris* P. Mill. (longleaf), along with some shrubby undergrowth (Brennan et al. 1998, McDonough et al. 2000).

Methods

Details of sampling conducted between 1992–2003 can be found in Loughry and McDonough (2001) and McDonough and Loughry (2005). Briefly, with the exceptions of 1996 and 2000, we censused the armadillo population at Tall Timbers for approximately 3 months each summer (see Robertson et al. 2000). Censuses were conducted at all hours, but primarily in the evenings, from about 16:00–24:00. We attempted to capture all animals observed while walking or driving along roads and trails on the property. For each captured animal, various body-size measurements, weight, and sex were recorded (Loughry and McDonough 1996), and the reproductive condition of females was assessed by examination of the nipples (see Loughry and McDonough 1996). In addition, one or more small pieces of ear tissue were obtained for genetic analyses using an ear notcher (e.g., Prodöhl et al. 1996), and the spatial location of the animal was obtained with a handheld GPS unit (Loughry and McDonough 1998). Animals were permanently marked with passive induced transponder (PIT) tags injected under the front carapace immediately behind the neck. These PIT tags, coupled with natural markings such as scars, missing tail segments, etc. (Loughry et al. 2002), and the fact that ear notches were taken from different locations on each ear for each animal, allowed us to reliably identify individual armadillos when recaptured during subsequent years.

Elimination of armadillos at Tall Timbers was conducted from 1 March–30 September of 2004–2006. Extermination was accomplished in two ways:

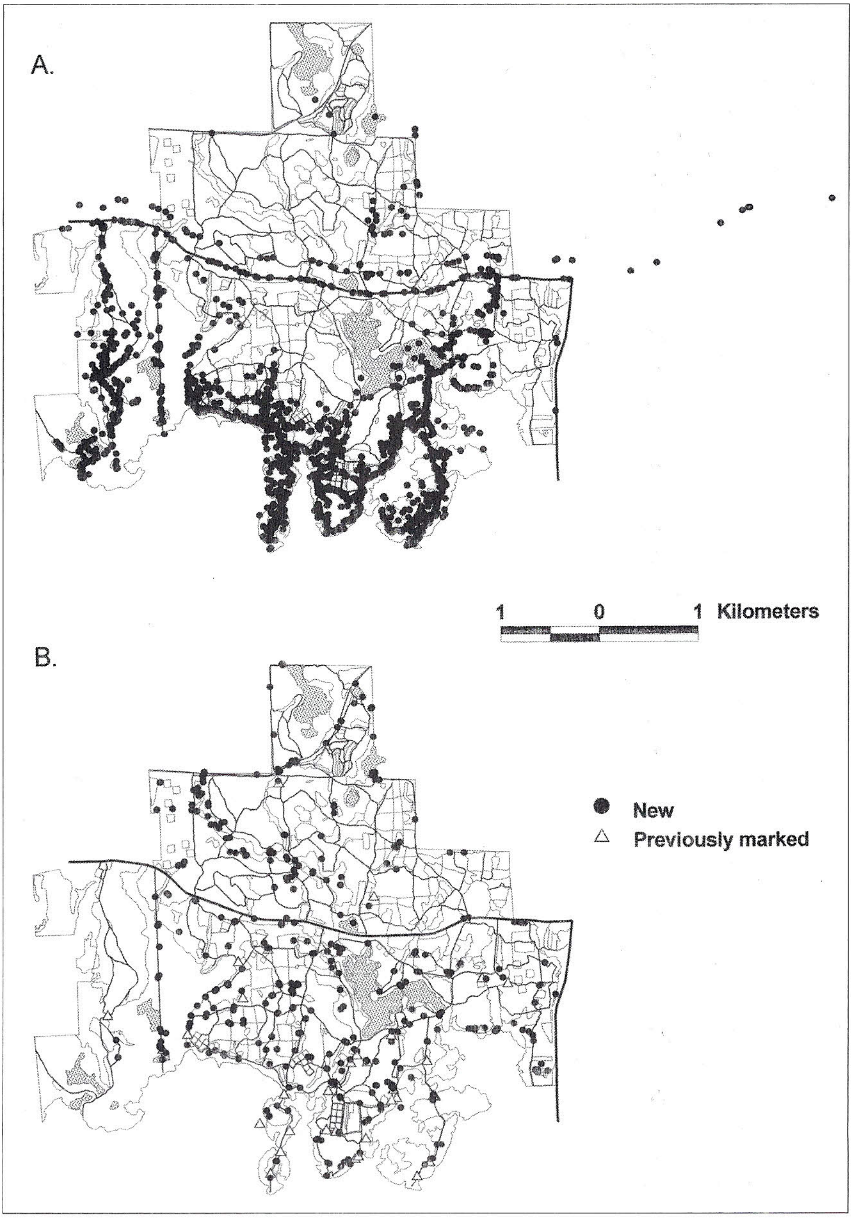

Figure 1. Map of Tall Timbers Research Station showing locations of sampled armadillos. A. Locations (n = 2047) of animals sampled via mark-recapture from 1992 to 2003 (modified from McDonough and Loughry 2005). Data include multiple locations from the same individuals to provide the broadest depiction of the sampled area. B. Locations (n = 451) of animals harvested by the USDA, 2004–2006. Not all locations are depicted in either figure because of extreme overlap among some points. Stippled areas represent open water; the lower edge of the property is bounded by Lake Iamonia.

with baited leg-hold and live traps and by shooting animals encountered while on the property. Traps were used for catching not only armadillos, but all mammalian predators of interest. A total of 125 traps were placed at a variety of locations on the property for an average of 25,625 trap-nights per year. Culled animals were sexed and weighed. Weights were used to assign individuals to age classes as juveniles or adults (Loughry and McDonough 1996; note that for the purposes of this study, yearling individuals were categorized as adults). All culled animals were part of a larger wildlife disease study (J.M. Lockhart et al., unpubl. data) in which the carcasses were dissected, but unfortunately no data on female reproductive condition (pregnant, lactating, etc.) were taken.

In addition to Tall Timbers, the USDA replicated their experiment at three other sites. Armadillos were harvested from Pebble Hill Plantation, located just south of Thomasville, GA, from 2001 to 2003. They were also removed from two separate tracts at Pinebloom Plantation, located just west of Albany, GA. Pinebloom A was harvested from 2001 to 2003, and Pinebloom B from 2004 to 2006. Although we did not have baseline data from these sites, we include some data from them to assess how generalized the results were from Tall Timbers.

Prior to 2004, simple mark-recapture estimates of population size indicated an armadillo population at Tall Timbers numbering approximately 400 individuals (Lincoln-Peterson index calculated between successive years from 1992 to 2003; C.M. McDonough, unpubl. data). In general, slightly less than 40% of the animals caught in any given year were residents that had been caught previously (Table 1). New animals were either juveniles or adults that had never been caught before. Of these adults, some were only caught in one year and never again, while others settled in the population and were recaptured in later years.

Due to a combination of factors, including drought and an extensive removal of hardwoods, the armadillo population at Tall Timbers declined between 2001–2003 (McDonough and Loughry 2005). Analyzing the effects of harvesting could potentially be biased by the atypical conditions occurring during this period. To minimize this problem we performed two sets of analyses. First, we used data from just 2003 as the most recent exemplar of the unharvested condition (Table 1). We then used long-term data, obtained by averaging yearly values from 1992 to 2002 (Table 1), to obtain a

Table 1. Demography of *D. novemcinctus* (nine-banded armadillo) during 12 years of mark-recapture sampling at Tall Timbers Research Station. Data for 1992–2002 are yearly averages ± SD. Total caught includes some animals that could not be assigned to a particular age/sex category.

	1992–2002	2003
Total caught	132.44 ± 59.99	58
Adult males	57.78 ± 28.46	24
Adult females	51.00 ± 29.24	24
Juvenile males	11.44 ± 5.39	5
Juvenile females	10.56 ± 7.40	4
Number of recaptures	50.75 ± 33.80	15

more general picture of how harvesting impacted the population. With these data, we used chi-square tests to compare proportions of juveniles and proportions of previously marked animals in the population before and during harvesting. We also used chi-square tests to determine if any sex differences occurred among the new and recaptured animals collected during harvesting (versus the null hypothesis of a 50:50 sex ratio in each case), and to examine year-to-year changes in the numbers of animals collected at each of the four harvested sites (performed by comparing the proportion of total animals collected at each site in pair-wise tests between years).

Results

We marked a total of 829 armadillos from 1992 to 2003; 451 animals were removed by the USDA from 2004 to 2006. Armadillos are not normally considered easily trappable animals, but these results indicate trapping was surprisingly effective. Coupled with opportunistic shooting of animals, it thus appears culling of armadillos each year was thorough and extensive. Visual inspection of locations where we live-caught animals (Fig. 1A) and locations where armadillos were trapped or shot (Fig. 1B) indicate our marked population was subject to intense harvesting by the USDA (note that both figures only depict successful captures; sampling in both instances was more extensive because some areas were sampled where no armadillos were ever caught). Thus, we are confident the results we report are not due to some form of sampling bias.

The marked population of armadillos at Tall Timbers was rapidly eliminated: of the 41 marked animals collected, 78% were taken in 2004 (Table 2). The proportion of marked animals collected in 2004 was significantly greater than in 2005 (χ^2= 20.86, $P < 0.0001$) and 2006 ($\chi^2 = 23.81$, $P < 0.0001$); the proportion of marked animals collected in 2005 versus 2006 did not differ ($\chi^2 = 0.001$, $P = 0.96$). Likewise, the proportion of marked animals collected in 2004 was similar to that in 2003 (χ^2= 0.24, $P = 0.62$), but the proportions in 2005 and 2006 were significantly lower (both $P < 0.0001$). Use of longer-term data from 1992–2002 showed the proportion of marked animals in the culled samples was significantly lower in all 3 years

Table 2. Demography of *D. novemcinctus* (nine-banded armadillo) killed at Tall Timbers Research Station during 3 years of intensive culling. All previously marked animals were adults when killed (M = male, F = female). Total killed is larger than the sums of values for age/sex classes because some animals were missing data and so could not be assigned to a particular age and sex group.

	2004	2005	2006
Total killed	149	149	153
Adult males	56	65	59
Adult females	54	49	66
Juvenile males	16	17	11
Juvenile females	17	8	5
Number marked (M/F)	32 (16/16)	5 (2/3)	4 (2/2)

(all $P < 0.003$). There were no sex differences in animals collected at Tall Timbers, either among previously marked animals (all $P > 0.48$) or among new adults (all $P > 0.32$) or juveniles (all $P > 0.25$).

The proportion of armadillos collected each year did not change significantly (pair-wise comparisons between years, all $P > 0.83$, Fig. 2). Interestingly, a similar pattern was found at one of the three other sites that also harvested armadillos for three years (Pinebloom A: pair-wise comparisons between years, all $P > 0.38$, see Fig. 2). At the other two (Pinebloom B and Pebble Hill), proportions of collected animals were significantly greater in year 1 than in year 2 (both $P < 0.003$) and year 3 (both $P < 0.0005$), but not between year 2 and year 3 (both $P > 0.08$, see Fig. 2).

Numbers of juveniles collected were low (Table 2) and the proportion of juveniles in the population each year did not differ significantly from numbers live-caught in 2003 (all $P > 0.38$) or 1992–2002 (all $P > 0.17$), indicating production of juveniles did not increase with the onset of harvesting. Further, comparisons of proportions of juveniles in the culled population each year showed a significant decrease between 2004 and 2006 ($\chi^2 = 6.57$, $P = 0.009$; other pair-wise comparisons between years were not significant, all $P > 0.15$), the opposite of what might be expected if increased reproduction was responsible for the replacement of culled individuals.

Discussion

Our data document remarkable constancy of the armadillo population at Tall Timbers in the face of intensive harvesting. As discussed below, it seems unlikely this was due to increased production and retention of

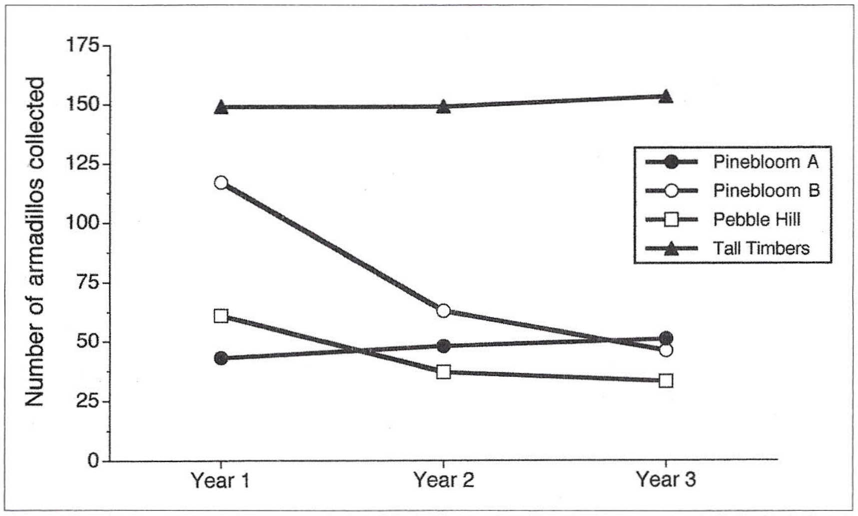

Figure 2. Numbers of *D. novemcinctus* (nine-banded armadillo) culled by the USDA at four sites over three years. Sampling at Pebble Hill and Pinebloom A occurred from 2001 to 2003, and at Tall Timbers and Pinebloom B from 2004 to 2006.

juveniles in their natal population. Rather, it appears there was a substantial pool of animals in the surrounding habitat available to immigrate in and rapidly replace individuals that were removed.

Although a crude estimate, Lincoln-Peterson calculations of armadillo population size at Tall Timbers suggested nearly 400 individuals inhabited the site per year. However, the population appeared to be in decline during 2001–2003 due to the effects of a prolonged drought and habitat alterations resulting from an extensive hardwood removal (McDonough and Loughry 2005). Thus, at the start of harvesting by the USDA, the total population at Tall Timbers was probably much lower. If so, then assuming minimal replacement, the numbers of animals culled in 2004 and 2005 (Table 2) should have virtually eliminated the entire population. Yet, remarkably, the number of armadillos taken in 2006 actually slightly exceeded the numbers taken in each of the previous two years.

One might expect the rapid elimination of the marked animals at Tall Timbers to result in an overall decline in the population. However, the proportion of armadillos collected each year did not change significantly (Fig. 2), as also was the case with the population at the Pinebloom A Tract.

So from where did all these animals come? Based on the data in Table 2, it seems unlikely they were resident animals that managed to escape capture in previous years. Indeed, animals marked by us from 1992 to 2003 were nearly gone after just one year of harvesting, suggesting much of the resident population was quickly eliminated. Given that fact, maintenance of a stable population size at Tall Timbers in the face of such an intense harvesting effort only seems possible if either there was (a) a considerable increase in reproduction, producing enough juveniles to replace animals being lost, and/or (b) increased immigration into the population by animals colonizing areas vacated by culled individuals. Our data are most consistent with the latter hypothesis, since increased reproduction seems unlikely. Female nine-banded armadillos give birth to a single litter of genetically identical quadruplets each year (Prodöhl et al. 1996), although not all females reproduce every year. Thus, replacement of culled animals by reproduction would require either an increase in the number of reproductive females and/or increased survivorship of juveniles. Neither seems likely because (a) the numbers of juveniles collected each year was not significantly increased over that seen in earlier years, and (b) many pregnant and lactating females were probably killed in the spring and summer, presumably resulting in the loss of many litters. Studies of territorial species have documented many instances of non-territorial floaters that exist within a population waiting to fill any vacancies that might occur (reviews in Greenwood and Harvey 1982, Kokko and Sutherland 1998, Pen and Weissing 2000, Reed et al. 1999, Smith 1978). It is not clear if such individuals exist in nine-banded armadillo populations. However, even if they do, the harvesting protocol should have eliminated them as well, so it seems unlikely replacements for culled animals came from any within-population source.

Given our results, the most likely explanation for the continued high abundance of armadillos at Tall Timbers is that culled animals were rapidly replaced by immigrants. Even though relatively close to an urban environment, Tall Timbers is not an isolated island of suitable armadillo habitat and may not represent a distinct population. Large tracts of relatively undisturbed land border the property and presumably harbor many armadillos. These areas represent a potentially large reservoir of individuals that could replace those lost at Tall Timbers. Of course, this assumes these individuals move sufficiently to discover the newly available openings. Our previous work has shown that some armadillos are long-term residents that remain in the same areas year after year (up to 10 years; Loughry and McDonough 2001). However, an additional component of the population is made up of individuals that are caught once and never again. Bond et al. (2000) referred to these individuals as transients, suggesting they were temporary members of the population, captured as they moved through the area. The existence of transients would seem necessary to explain the rapid and continued range expansion of nine-banded armadillos in the United States, which can only be generated by the movement of individuals out of established populations to colonize new areas. Thus, even if floaters do not exist within armadillo populations, the extensive movements of transient individuals would suggest sufficient vagility and fluidity to not only colonize new habitats, but also to fill vacancies created in established populations (Gammons 2006). Further understanding of armadillo population dynamics will require identifying the factors that distinguish transients from residents, coupled with genetic analyses of gene flow between populations to identify the extent and sources of immigrants into established populations.

Given the nature of this study, only immigration could be the major source of new individuals in the population because juveniles and reproductive adults were continually eliminated. Obviously, under more natural conditions reproduction and immigration would undoubtedly both contribute to maintaining population levels. However, our data indicate that immigration can maintain population size even in the absence of much reproductive input. High juvenile mortality (McDonough and Loughry 1997), coupled with the fact that we found no evidence that reproduction increased in the face of population decline (and in fact decreased in 2006), would suggest that, even under more natural conditions, immigration may be more important than reproduction in restoring population size. Of course, this is more likely to be true in areas saturated with armadillos, where individuals from surrounding habitats can easily move into vacated areas. Immigration is probably less important (and reproduction more important) in more isolated populations, e.g., along the expanding northern edge of the species' range.

The data from the first year of harvesting in 2004 show a population substantially larger than that observed in 2003. As stated above, mark-recapture data indicated a population in decline from 2001 to 2003, probably due to the combined effects of drought and habitat changes associated with extensive logging of hardwoods on the property. More animals might be expected from sampling in 2004 because the sampling period was over twice as long (7 months in 2004 versus 3 months in 2003) and the area sampled was larger. With regard to the latter, we did catch and mark armadillos in almost all areas of the property (Fig. 1A), but our sampling was primarily concentrated in the bottomland hardwoods along the lakefront; sampling in the northern part of the property (in particular north of County Road 12) was much less extensive. In contrast, USDA sampling was more equally distributed across the entire property and so might have contributed to the increased sample size obtained. Nonetheless, much of the habitat in the other areas sampled by the USDA was upland pine, and previous work has shown that few armadillos are normally found there (McDonough et al. 2000). Thus, it appears that, while increased sampling effort may have contributed somewhat to the increased numbers of animals collected in 2004, the population may also have been recovering from the decline associated with drought and hardwood removal, suggesting the effects of these impacts were not as long-lasting as previously supposed (McDonough and Loughry 2005). This is, perhaps, not surprising in such a successful invasive species as nine-banded armadillo. The rapid range expansion of this species in the US would seem to require properties such as resiliency and an ability to quickly adjust to new conditions, a view reinforced by the data presented here.

There are at least two questions regarding our data that we cannot answer at present. First, why were so many more armadillos collected at Tall Timbers than any other site (see Fig. 2)? All four sites were intentionally designed to be replicates, so the difference cannot be explained by differences in sampling effort or size of the sampled areas. In addition, Tall Timbers possesses similar habitat features as the other sites, so there are no obvious characteristics of this one site that would suggest it is somehow superior for armadillos. Perhaps a broader, metapopulation perspective of surrounding areas might be relevant, but at present no obvious explanation exists for this difference between sites. Second, we have argued above that immigration of transients allowed maintenance of the Tall Timbers population in the face of extensive harvesting. However, because animals continued to be killed each year of the study, we cannot know the long-term fate of these individuals. Clearly, transients moved into the areas vacated by culled animals. But, did they settle in these areas or continue as transients? Now that culling of animals has ceased at Tall Timbers, this question could be answered by tracking the population over the next few years.

This study was possible because of the interest in assessing the impact of nest-predator removal on Northern Bobwhite reproductive success. Given that a large suite of mammalian predators was eliminated at Tall Timbers (n = 1446 individuals collected from all species combined; J.M. Lockhart, unpubl. data), it is possible the experiment generated positive results. However, looking specifically at the armadillo data, it is hard to envision harvesting as an effective management strategy. At 2 of the 4 sites where harvesting occurred, the numbers of armadillos taken remained stable over the 3 years of the experiment (Pinebloom A and Tall Timbers, see Fig. 2); harvesting did impact populations at the other 2 sites, where the number of animals collected in the third year of the study was 50% or less of that taken in the first year (Fig. 2). There are no data available to assess to what extent these populations may have rebounded after harvesting ended, but the data from Tall Timbers suggest replacement can be very rapid. Harvesting is difficult, labor-intensive work. Given its minimal impact in 2 populations and, in particular, the rapid replacement of individuals at Tall Timbers, it would seem that, even if partially effective in the short-term, unless there is a long-term commitment to persistent culling, such a strategy is ultimately doomed to failure in controlling armadillo populations.

Acknowledgments

We thank the staff of Tall Timbers Research Station for allowing us to work there for so many years. We also thank the USDA personnel, Hardy S. Drew, John C. Griffin, Lucas B. Harvard III, Daymond W. Hughes, Patrick H. Stalvey, and Orin B. White, Jr., who collected all the animals. We are grateful to the Guest Editor, Lenny Brennan, and two anonymous reviewers for their helpful comments. Our work at Tall Timbers was funded over the years by Faculty Research Awards from Valdosta State University, Earthwatch, and the American Philosophical Society.

Literature Cited

Bond, B.T., M.I. Nelson, and R.J. Warren. 2000. Home-range dynamics and den use of nine-banded armadillos on Cumberland Island, Georgia. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 54:414–424.

Brennan, L.A., R.T. Engstrom, S.M. Hermann, S.T. Lindeman, W.K. Moser, K. McGorty, J. Noble, and W.E. Palmer. 1998. A five-year land-management plan for Tall Timbers Research Station property: 1998–2002. Tall Timbers Research Station, Tallahassee, FL. 106 pp.

Caughley, G. 1977. Analysis of Vertebrate Populations. John Wiley and Sons, New York, NY. 234 pp.

Chepko-Sade, B.D., and Z.T. Halpin (Eds.). 1987. Mammalian Dispersal Patterns. University of Chicago Press, Chicago, IL. 342 pp.

Clobert, J., E. Danchin, A.A. Dhondt, and J.D. Nichols (Eds.). 2001. Dispersal. Oxford University Press, Oxford, UK. 452 pp.

Freeman, P.W., and H.H. Genoways. 1998. Recent northern records of the nine-banded armadillo (Dasypodidae) in Nebraska. Southwestern Naturalist 43:491–504.

Gammons, D. 2006. Radiotelemetry studies of armadillos in southwestern Georgia. M.Sc. Thesis. University of Georgia, Athens, GA. 75 pp.

Greenwood, P.J., and P.H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13:1–21.

Hastings, A. 1997. Population Biology: Concepts and Models. Springer, New York, NY.

Hedrick, P.W. 1984. Population Biology: The Evolution and Ecology of Populations. Jones and Bartlett, Boston, MA. 445 pp.

Humphrey, S.R. 1974. Zoogeography of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. BioScience 24:457–462.

Jacobs, J.F. 1979. Behavior and space-usage patterns of the nine-banded armadillo (*Dasypus novemcinctus*) in southwestern Mississippi. M.Sc. Thesis. Cornell University, Ithaca, NY. 132 pp.

Kokko, H., and W.J. Sutherland. 1998. Optimal floating and queuing strategies: Consequences for density dependence and habitat loss. American Naturalist 152:354–366.

Loughry, W.J., and C.M. McDonough. 1996. Are road kills valid indicators of armadillo population structure? American Midland Naturalist 135:53–59.

Loughry, W.J., and C.M. McDonough. 1998. Spatial patterns in a population of nine-banded armadillos (*Dasypus novemcinctus*). American Midland Naturalist 140:161–169.

Loughry, W.J., and C.M. McDonough. 2001. Natal recruitment and adult retention in a population of nine-banded armadillos. Acta Theriologica 46:393–406.

Loughry, W.J., C.M. McDonough, and E.G. Robertson. 2002. Patterns of anatomical damage in a population of nine-banded armadillos *Dasypus novemcinctus* (Xenarthra, Dasypodidae). Mammalia 66:111–122.

MacArthur, R.H., and J.H. Connell. 1966. The Biology of Populations. John Wiley and Sons, New York, NY. 200 pp.

McDonough, C.M., and W.J. Loughry. 1997. Patterns of mortality in a population of nine-banded armadillos, *Dasypus novemcinctus*. American Midland Naturalist 138:299–305.

McDonough, C.M., and W.J. Loughry. 2005. Impacts of land management practices on a population of nine-banded armadillos in northern Florida. Wildlife Society Bulletin 33:1198–1209.

McDonough, C.M., M.A. Delaney, P.Q. Le, M.S. Blackmore, and W.J. Loughry. 2000. Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America. Revista de Biología Tropical 48:109–120.

Pen, I., and F.J. Weissing. 2000. Optimal floating and queuing strategies: The logic of territory choice. American Naturalist 155:512–526.

Prodöhl, P.A., W.J. Loughry, C.M. McDonough, W.S. Nelson, and J.C. Avise. 1996. Molecular documentation of polyembryony and the micro-spatial dispersion of clonal sibships in the nine-banded armadillo, *Dasypus novemcinctus*. Proceedings of the Royal Society, London, Series B 263:1643–1649.

Reed, J.M., T. Boulinier, E. Danchin, and L.W. Oring. 1999. Informed dispersal: Prospecting of birds for breeding sites. Current Ornithology 15:189–259.

Robertson, E.G., C.M. McDonough, and W.J. Loughry. 2000. Changes in observability of adult nine-banded armadillos over the summer: Observer effect or seasonal decline? Florida Field Naturalist 28:161–172.

Sakai, A.K., F.W. Allendorf, J.S. Holt, D.M. Lodge, J. Molofsky, K.A.With, S. Baughman, R.J. Cabin, J.E. Cohen, N.C. Ellstrand, D.E. McCauley, P. O'Neil, I.M. Parker, J.N. Thompson, and S.G. Weller. 2001. The population biology of invasive species. Annual Review of Ecology and Systematics 32:305–332.

Smith, S.M. 1978. The "underworld" in a territorial species: Adaptive strategy for floaters. American Naturalist 112:571–582.

Staller, E.L. 2001. Identifying predators and fates of Northern Bobwhite nests using miniature video cameras. M.Sc. Thesis. University of Georgia, Athens, GA. 53 pp.

Staller, E.L., W.E. Palmer, J.P. Carroll, R.P. Thornton, and D.C. Sisson. 2005. Identifying predators at Northern Bobwhite nests. Journal of Wildlife Management 69:124–132.

Stenseth, N.C., and W.Z. Lidicker. (Eds.). 1992. Animal Dispersal: Small Mammals as a Model. Chapman and Hall, London, UK. 365 pp.

Taulman, J.F., and L.W. Robbins. 1996. Recent range expansion and distributional limits of the nine-banded armadillo (*Dasypus novemcinctus*) in the United States. Journal of Biogeography 23:635–648.

Van Deelen, T.R., J.D. Parrish, and E.J. Heske. 2002. A nine-banded armadillo (*Dasypus novemcinctus*) from central Illinois. Southwestern Naturalist 47:489–491.