Despite undergoing a rapid range expansion throughout the southeastern United States during the last 150 years, reliable data on nine-banded armadillo (*Dasypus novemcinctus*) space use patterns are lacking. In addition, although nuisance armadillos are often live-captured and translocated, no studies have compared movements between resident and translocated animals. Therefore, from June 2005 to June 2006 I used radiotelemetry to (1) investigate the home range and habitat use of resident armadillos, and (2) compare movements between resident and translocated individuals in order to evaluate the appropriateness of translocation. Armadillo home ranges differed seasonally, with the largest home ranges occurring during the summer. Armadillos avoided mature pine and agriculture habitats, so active conservation and restoration of longleaf pine forests may result in future decreases in armadillo populations. Release site fidelity of translocated animals was low suggesting that translocation of nuisance armadillos should be minimized.

INDEX WORDS: armadillo, *Dasypus novemcinctus*, habitat use, home range, radiotelemetry, translocation
RADIOTELEMETRY STUDIES OF ARMADILLOS IN SOUTHWESTERN GEORGIA

by

DANIEL GAMMONS

B.S., Ferrum College, 2003

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment
of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2006
“The nine-banded armadillo, an outstanding oddity among North American mammals…”

--Kalmbach 1944

“Armadillos are stupid animals in many respects.”

--Taber 1945
ACKNOWLEDGEMENTS

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CHAPTER 1
INTRODUCTION AND JUSTIFICATION, THESIS FORMAT, AND LITERATURE REVIEW
INTRODUCTION AND JUSTIFICATION

Prior to the mid-1850s, the distribution of nine-banded armadillos (*Dasypus novemcinctus*) within the United States was restricted to southern Texas (Taulman and Robbins 1996). Since that time, armadillos have undergone a rapid range expansion throughout the Southeast and now likely number between 30 and 50 million in the United States (Gilbert 1995). Because armadillos have long been thought to be significant predators of ground-nesting birds, their diet has been extensively studied (Kalmbach 1944, Fitch et al. 1952, Breece and Dusi 1985, Wirtz et al. 1985, Sikes et al. 1990, Osborn et al. 2000). In addition, numerous studies have been devoted to determining the impact of their unusual mode of reproduction—obligate polyembryony, where females consistently give birth to litters of identical quadruplets—on their behavior and population structure, especially in regard to the potential for kin selection (reviewed in Loughry et al. 1998). Yet, despite their ubiquitous presence, status as a nuisance animal for both urban and rural landowners (Chamberlain 1980, Hawthorne 1994, Mengak 2003, Schaefer and Hostetler 2003), and potential to alter ecosystems where they were previously absent, reliable estimates of their basic space-use patterns are lacking. A better understanding of armadillo home range and habitat use may help in developing management strategies to minimize their negative impacts or reduce their populations.

Armadillos are generally associated with hardwood bottoms (Inbar and Mayer 1999, McDonough 2000), but only 1 study has explicitly examined their habitat use patterns (McDonough et al. 2000). A number of studies have examined armadillo home ranges, but many have been based on opportunistic visual observations of marked animals (Clark 1951, Fitch et al. 1952, Layne and Glover 1977, Breece and Dusi 1985, Suttkus and Jones 1999, McDonough 2000). This method generally limits the opportunity for both multiple relocations of individuals
and for nocturnal observations, which are essential for reliable estimates because armadillos are primarily nocturnal (Layne and Glover 1985). In addition, repeated visual observations may alter armadillo behavior (Robertson et al. 2000). Radiotelemetry can overcome these problems, but studies that have used this method have generally had small sample sizes or inadequately described methods (Thomas 1980, Zimmerman 1982, Herbst and Redford 1991, Schnell 1994, Bond et al. 2000 but see Jacobs 1979). Because armadillos are solitary, primarily nocturnal, occupy thickly vegetated habitats, and difficult to mark permanently (Loughry et al. 2005), research on their space use using radiotelemetry could provide more reliable estimates than available with previous studies.

**THESIS FORMAT**

This thesis will report the results of 2 radiotelemetry studies (Chapters 2 and 3) that were conducted from 2005-2006. It is written in manuscript format. Chapter 2 describes home range and habitat use of resident armadillos within a longleaf pine (*Pinus palustris*) ecosystem, and, based on the results, provides management recommendations for reducing armadillo populations within that system. Chapter 3 explores the effects of translocation (a common method of removing nuisance animals in urban and suburban areas) on armadillos and compares the movements of translocated animals to their resident counterparts. Both of these chapters will be submitted to the *Journal of Wildlife Management* for publication. The final chapter (Chapter 4) reports the summary and conclusions.

The remainder of this chapter is a literature review that provides a background on armadillos in the United States, describes the types of conflicts that occur between armadillos and humans, and summarizes what is currently known about their space use patterns.
HISTORY OF THE ARMADILLO’S RANGE EXPANSION

Compared to other pioneering mammals, the range expansion of the armadillo in the United States has been well documented (Fitch et al. 1952, Humphrey 1974, Taulman and Robbins 1996). Their unique appearance, apparent lack of awareness when approached, ease of being captured or shot, and frequency as road-kill, have greatly facilitated the documentation of their range expansion (Layne 2003). Audubon and Bachman (1854) were the first to describe the armadillo in the United States. They defined its distribution as confined to the lower Rio Grande Valley in southern Texas. During the subsequent years, armadillos began expanding their range to the north and east and colonies were reported in Louisiana (Strecker 1926), Oklahoma (Blair 1936), Arkansas (Black 1944), and Mississippi and Alabama (Fitch et al. 1952). By 1972, armadillos had reached extreme western Florida (Humphrey 1974).

Although human translocations of armadillos have probably occurred “hundreds of times” (Fitch et al. 1952), their spread from Texas has largely been through natural dispersal, facilitated through a number of environmental changes caused by man. Elimination of large carnivores (Fitch et al. 1952), conversion of native grasslands to woody species through fire suppression (Taulman and Robbins 1996), and construction of features such as bridges, levees, and elevated roadbeds that provide corridors for movement through unsuitable habitats (Layne 2003) likely combined to create conditions favorable for the spread of armadillos.

It is probable that armadillos would have eventually spread throughout Florida via natural dispersal, but at least 3 different purposeful or accidental introductions occurred between 1920 and 1936 (Talmage and Buchanan 1954). The Florida population has since merged with the naturally expanding population from the west, and currently armadillos are present throughout all of the coastal southeastern states, in addition to parts of Kansas, Missouri, and Tennessee.
While the western limit of expansion has probably been reached, further expansion northward in the center of their range and along the East coast is expected to about 41° N latitude (including parts of Georgia, South Carolina, Tennessee, and Virginia), where temperature and precipitation constraints will likely become limiting (Taulman and Robbins 1996). It is worth noting, however, that armadillos have spread beyond several previously predicted range limits (e.g., Bailey 1905, Newman 1913, Taber 1945), and their ability to adapt to novel environments is well known. For example, in coastal environments, armadillos have expanded their diet to include beach-nesting turtle eggs, which is thought to be a learned behavior (USDA 2002).

ARMADILLO-HUMAN CONFLICT

Considered by some to be an innocuous novelty and by others to be a nuisance, the armadillo has long held a controversial position in public opinion (Kalmbach 1944, Clark 1951, Chamberlain 1980). In fact, because their range expansion has been the result of both natural dispersal and human-facilitated introductions, there is even disagreement as to whether armadillos should be regarded as native or exotic species in certain locales. Galbreath (1982) summarized this dilemma by describing the armadillo as exemplifying a “philosophical problem.” That is, even though armadillos have the potential to alter ecosystems, should humans attempt to eradicate them, simply because they were originally absent?

These arguments notwithstanding, armadillos are a species of intense concern among landowners, both in rural and urban situations. For example, Mengak (2003) found that armadillo-related inquiries to Georgia county extension agents made up 10.1 % of the total number of inquiries for all agents across the state, even more than white-tailed deer (*Odocoileus virginianus*). As evidenced by recent sightings in Nebraska (Freeman and Genoways 1998), Kansas (Kamler and Gibson 2000), and South Carolina (Platt and Snyder 1995), the distribution
of the armadillo is continuing to expand, and conflicts between landowners and armadillos are likely to increase.

Armadillos come into conflict with humans in both urban/suburban and rural areas, but the types of conflicts generally differ between the two areas, although there is some overlap. In urban and suburban situations, complaints are primarily about property damage. Most damage to property is a result of their feeding habits; armadillos dig shallow holes, 3-8 cm deep and 8-13 cm long, while searching for soil invertebrates (Hawthorne 1994). Armadillo “rooting” damages lawns, gardens, flowerbeds, and golf courses in a manner similar to feral hogs (Sus scrofa). They also may damage structural foundations, driveways, and tree root systems by their habit of burrowing (Chamberlain 1980, Hawthorne 1994, Schaefer and Hostetler 2003).

In rural situations, property damage is also bothersome, but the more important concerns are ecological. Nonindigenous (e.g., alien or exotic) species are one of the primary causes of biodiversity loss worldwide (Sala et al. 2000, Sakai et al. 2001), so the potential for an exotic species such as the armadillo, which can reach very high densities in some areas, to impact native fauna through predation is not merely an academic concern.

As mentioned above, several extensive studies of armadillo diets have been conducted, often in an effort to determine their impact on ground-nesting birds. These studies have occurred throughout their range in Alabama (Breece and Dusi 1985), Louisiana (Fitch et al. 1952), Texas (Kalmbach 1944), Georgia (Osborn et al. 2000), Arkansas (Sikes et al. 1990), and Florida (Wirtz et al. 1985). While many land managers would disagree, based on these studies, the general consensus among the scientific community has been that egg predation is infrequent. However, Breece and Causey (1973) cautioned that if armadillos merely break eggs open and lick out the contents, little evidence would remain in their stomachs, making detection of egg predation
through stomach contents analysis almost impossible. This behavior has recently been documented in wild armadillos, using miniature video-surveillance cameras set up on northern bobwhite (*Colinus virginianus*) nests (Staller et al. 2005). In that study, armadillos were the second most important mammalian nest predator. Armadillos may indeed be more significant northern bobwhite predators than previously accepted. Armadillos are also known to excavate the nests of gopher tortoises (*Gopherus polyphemus*) (L. Smith, J.W. Jones Ecological Research Center, personal communication) and several species of threatened or endangered marine turtles (Drennen et al. 1989, Engeman et al. 2003).

Armadillos also pose a threat to several rare or endangered amphibians and reptiles, especially during the winter months when mobility of these prey is limited (Layne 1997). Similar to feral hogs, their “rooting” may disrupt forest soils and soil invertebrates as well (Carr 1982).

**CONTROL OPTIONS**

No repellents or toxicants are registered for use with armadillos and exclusion typically does not work well because they are adept burrowers and can even climb fences (Chamberlain 1980, Hawthorne 1994). Habitat modification (i.e., large-scale vegetation alteration) in urban and suburban environments also is impractical (Chamberlain 1980). Consequently, the only recourses for many landowners often are shooting and live-capture.

In rural areas, the preferred control method is probably shooting because rural residents tend to have a more utilitarian perspective towards wildlife than residents of urban areas (Conover 2002). Armadillos can be killed easily using a .22 caliber rifle as they are relatively easy to stalk within rifle range. This is effective for removing individual animals, but as is the
case with most abundant nuisance animals, it is not feasible on a large scale and must be repeated through time to maintain populations at desired levels (Conover 2002).

However, in suburban and urban areas, shooting nuisance wildlife is not practical or desirable for many landowners, so live-capture and translocation is often preferred (Braband and Clark 1992, Craven et al 1998, Conover 2002). As Craven et al. (1998) noted, there is a common perception that translocated animals will “live happily ever after.” No data are available on the frequency of nuisance armadillo translocations, but an estimate in the thousands/year is reasonable. Nuisance armadillos have become such a problem that the USDA’s Wildlife Services program has identified developing effective baits to live-trap armadillos in urban areas as an important research need (APHIS 2001).

However, despite popularity with the general public, there is concern among biologists over the appropriateness of nuisance wildlife translocation (Craven et al. 1998, Conover 2002). Primary concerns include: (1) the spread of disease, (2) humane aspects (e.g., stress and mortality of translocated animals), (3) impacts on residents at release sites, (4) post-release movement of animals to areas where they continue to be a problem, and (5) new animals simply replacing translocated ones so that the problem is not solved (Barnes 1994, cited in Craven et al. 1998, Conover 2002).

**SPACE USE PATTERNS**

**Home range**

At least 13 studies, occurring throughout their geographic range, have reported armadillo home ranges (Table 1.1). However, in general the data are quite limited because studies have been either (1) based on very small sample sizes, (2) mainly daylight observations of marked animals, or (3) of a short duration (mean duration < 8 months).
While the data are limited, it seems clear that armadillos have small home ranges compared to mammals of similar body size (armadillos weigh up to 6 kg), which is thought to be due to the higher biomass per unit area of their primary foods (Layne 2003). And despite problems associated with small samples, some consistent patterns have emerged. Sex differences in home range size have not been reported (generally this has been attributed to their lack of sexual dimorphism), although age and possibly reproductive status influence home range size (McDonough 2000). Older armadillos have larger home ranges than younger armadillos, presumably because home range size reflects resource needs and smaller individuals require fewer resources (McDonough 2000). Breeding males have been found to have larger home ranges than non-breeding males, perhaps to increase overlap with females (McDonough 2000). Armadillos also appear to expand their home ranges during the breeding season (McDonough 2000) and contract them during the winter (Bond et al. 2000).

Previous studies have suggested a relationship between soil moisture and home range size (Layne and Glover 1977, McDonough 2000). Armadillo home ranges tend to be smaller in more mesic areas, presumably because of higher arthropod abundances and therefore reduced foraging costs. However, small sample sizes make generalizing patterns about home range size and environmental factors difficult (Layne 2003). In addition, Herbst and Redford (1991) found that female armadillos with larger home ranges had similar body condition scores to females with smaller home ranges, suggesting that resource availability may not be a determinant of home range size. Clearly, additional research is necessary to understand the environmental factors that influence armadillo home range size.
Habitat use

Much less is known about habitat use in armadillos. Given their wide geographic distribution, it is likely that armadillos as a species are quite flexible in their habitat requirements, although in general, armadillos are associated with bottomland hardwood forests (Inbar and Mayer 1999, McDonough 2000). Studies of habitat selection within individual populations of armadillos (the level at which management decisions will be based), however, are virtually nonexistent.

In one study where armadillo habitat use was assessed by sightings of animals in different habitats, McDonough et al. (2000) found non-random use of habitats in Florida, with armadillos being found more often than expected in hardwood hammocks and wetlands and less often than expected in upland pine forest and agricultural fields. Interestingly, they found no difference in prey availability between preferred and avoided habitat types, although prey availability has often been suggested to influence armadillo habitat use. Limited, but inconclusive evidence was found for sex and seasonal differences. Inbar and Mayer (1999) found evidence of seasonal differences in habitat use, as road-kills locations were associated with dense vegetation during the winter but not during the summer, when road kill locations were not associated with any vegetation characteristics.

Notably, habitat use has not been assessed in any radiotelemetry study, although Bond et al. (2000) examined seasonal variation in den use. In that study, armadillos used fewer dens during the winter than during the summer, likely because of decreased home range sizes during the winter.
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<table>
<thead>
<tr>
<th>Study</th>
<th>State</th>
<th>n&lt;sup&gt;1&lt;/sup&gt;</th>
<th>HR size (ha)&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Length of study (months)</th>
<th>Method of location&lt;sup&gt;3&lt;/sup&gt;</th>
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<td>VO</td>
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<td>1.9</td>
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<td>12</td>
<td>RT-implant</td>
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</tbody>
</table>

<sup>1</sup>Number of animals monitored

<sup>2</sup>Minimum convex polygons were used except for Fitch et al. (1952) who used the area of a circle, using the greatest distance observed apart as the diameter

<sup>3</sup>RT-radiotelemetry, VO-visual observation

<sup>4</sup>Individuals with < 10 locations were not included in calculations

*Information not available
CHAPTER 2
HOME RANGE AND HABITAT SELECTION OF NINE-BANDED ARMADILLOS IN A LONGLEAF PINE ECOSYSTEM

Abstract: Nine-banded armadillos (*Dasypus novemcinctus*) have greatly expanded their range within the last 150 years and are now abundant throughout the southeastern United States, where they may have negative effects on the fauna of sensitive ecosystems such as longleaf pine (*Pinus palustris*) forests. Because of a lack of reliable data on their space use patterns, we used radiotelemetry to determine home range (n = 27) and habitat use (n = 30) of armadillos on a site managed for longleaf pine conservation in southwestern Georgia from June 2005 to June 2006. Mean home ranges did not differ (P = 0.674) between males (9.66 ha ± 1.3; \( \bar{x} \pm s.e \)) and females (7.7 ± 0.6), but home ranges did differ seasonally (P = 0.05), with the largest home ranges occurring during the summer. Large summer home ranges by males (≤ 32.1 ha) indirectly indicate that armadillos in this population were mating polygynously. Armadillos displayed few significant habitat preferences; therefore any negative impacts of armadillos on native fauna are likely to occur in a range of habitat types. However, armadillos avoided mature pine and agriculture habitats, so active conservation and restoration of longleaf pine forests is likely to result in future decreases in armadillo populations.

Key words: armadillo, *Dasypus novemcinctus*, Georgia, habitat selection, home range, longleaf pine, radiotelemetry

INTRODUCTION

Prior to the mid 1800’s, the dominant ecosystem throughout the southeastern Coastal Plain was longleaf pine (*Pinus palustris*) forests. Currently, this ecosystem now occupies only 3% of its former range (Ware et al. 1993); consequently, biodiversity conservation in the remaining patches is a high priority. Because nonindigenous (e.g., alien or exotic) species are one of the primary causes of biodiversity loss worldwide (Sala et al. 2000, Sakai et al. 2001), the
recent invasion of nine-banded armadillos (*Dasypus novemcinctus*) into remaining fragments of this system is cause for concern. Prior to the 1850’s the armadillo’s distribution in the United States was restricted to south Texas, but armadillos are now common throughout the Southeast (Taulman and Robbins 1996), and likely number between 30 and 50 million in the United States (Gilbert 1995). This expansion has been well documented and was caused by a combination of natural dispersal from a contiguous population and hundreds of intentional and accidental human introductions (Fitch et al. 1952, Humphrey 1974, Taulman and Robbins 1996).

Whether one considers armadillos to be naturally invading colonizers or invasive exotics, their potential to impact native ecosystems where they previously were absent is an important consideration for designing land-management strategies. As with most nonindigenous species, however, little is known about the effects of armadillos on native ecosystems, and no studies have evaluated their impacts. Armadillos prey on several rare or endangered reptiles (Layne 1997) and may impact forest soils and soil invertebrates (Carr 1982). Egg predation has long been though to be infrequent based on studies of stomach contents (Kalmbach 1943, Fitch et al. 1952, Breece and Dusi 1985, Wirtz et al. 1985, Sikes et al. 1990), but recently armadillos have been shown to depredate the nests of marine turtles (Drennen et al. 1989, Engeman et al. 2003), northern bobwhites (*Colinus virginianus*) (Staller et al. 2005), and gopher tortoises (*Gopherus polyphemus*) (L. Smith, J.W. Jones Ecological Research Center, personal communication). Northern bobwhites and gopher tortoises are of particular concern within longleaf pine forests.

The potential threat of armadillos to native fauna has resulted in a desire for population reduction in many areas managed for longleaf pine, but mortality-based control strategies (shooting, trapping) are often not feasible on a large scale and must be repeated through time to maintain populations at desired levels (Conover 2002). An alternative strategy is to manipulate
habitats to reduce the availability of key resources. The application of prescribed fire to alter habitats, for example, has been shown to reduce raccoon (*Procyon lotor*) use of areas important to ground-nesting birds and gopher tortoises, of which raccoons are a primary predator (Jones et al. 2004). In order for habitat-manipulation strategies to be implemented for armadillos, however, additional knowledge about their space use patterns, particularly within longleaf-pine ecosystems is needed.

While armadillos are generally associated with hardwood bottoms, only 1 study has examined their habitat use patterns (McDonough et al. 2000). Numerous studies have examined armadillo home ranges but many have been based on opportunistic visual observations of marked animals (Clark 1951, Fitch et al. 1952, Layne and Glover 1977, Breece and Dusi 1985, Suttkus and Jones 1999, McDonough 2000). This method generally limits the opportunity for both multiple relocations of individuals and for nocturnal observations, which are essential for reliable estimates because armadillos are primarily nocturnal (Layne and Glover 1985). In addition, repeated visual observations may alter armadillo behavior (Robertson et al. 2000). Radiotelemetry can overcome these problems, but studies that have used this method have generally had small sample sizes or inadequately described methods (Thomas 1980, Zimmerman 1982, Herbst and Redford 1991, Schnell 1994, Bond et al. 2000 but see Jacobs 1979). Because armadillos are solitary, primarily nocturnal, occupy thickly vegetated habitats, and difficult to permanently mark (Loughry et al. 2005), research on their space use using radiotelemetry could provide more reliable estimates than available with previous studies.

The objectives of this study were to (1) use radiotelemetry to provide estimates of armadillo space use, and (2) use this information to provide habitat-manipulation strategies for reducing armadillo populations in longleaf pine ecosystems.
STUDY AREA

The study was conducted at Ichauway, a plantation operated by the Joseph W. Jones Ecological Research Center (JWJERC). This 11,735-ha research facility is located near Newton, Georgia, in the southeastern Gulf Coastal Plain. Historically, Ichauway was managed as a northern bobwhite hunting preserve, and while hunting still plays a significant role in its management, the main objectives of land management today are: (1) conservation and restoration of the longleaf pine ecosystem; and (2) integrating sustainable land-use practices for wildlife and forest management while conserving biological diversity. Currently, 40% of Ichauway’s land is managed to conserve and restore the natural longleaf pine ecosystem, while the remaining 60% is managed as multiple use zones that integrate wildlife and timber management with agricultural productivity. Land managers at Ichauway conduct prescribed burns on 4,000 to 5,000 ha each year, maintaining the entire property on a 2-year burn rotation. We delineated a 3,610-ha section of Ichauway for our study.

METHODS

Capture and radiotransmitter implantation

From 22 May 2005 to 20 March 2006, we captured armadillos using either long-handled dipnets or un-baited wire cage traps (Hawthorne 1994). Because armadillos may alter their behavior if subjected to repeated surveys (Robertson et al. 2000), we did not search for armadillos in the same areas within a short period of time (< 2 weeks). While this meant that many captures were widely separated spatially, limiting the potential for interaction and home range overlap among radio-tagged individuals, it ensured that individuals were distributed throughout available habitat types within the study area. Captured animals were weighed, sexed, and aged according to criteria established by McDonough (1994). Because we were interested in
determining survival rates and sources of mortality, of which shooting was expected to be a primary source, we did not permanently mark animals (i.e., with fingerling fish tags in their ears or reflective tape on their carapaces), because permanent markings are known to potentially bias hunter behavior (Kaine and Litvaitis 1992). For example, hunters may harvest tagged individuals at higher rates than unmarked individuals because the animals are easier to detect or they may harvest tagged individuals at lower rates because of concern over disrupting the study.

Externally attached transmitters have been used with armadillos (e.g., Jacobs 1979), but prolonged use is impractical due their compact body form, flexible carapace, and burrowing and foraging behaviors (Herbst 1991). Therefore, captured armadillos were held overnight and then received a surgically implanted radiotransmitter (Model M1240, Advanced Telemetry Systems, Isanti, Minnesota) the following day, following procedures adapted from Herbst (1991). Briefly, armadillos were sedated by either (1) gas anesthesia (n = 1), (2) an intramuscular injection of butorphanol (0.1 mg/kg), medatomadine (0.07 mg/kg), and ketamine (15.0 mg/kg) (n = 13), or (3) an intramuscular injection of ketamine (40.0 mg/kg) and xylazine (1.0 mg/kg) (n = 17). Through a 2.5-cm incision centered over the umbilicus, the transmitter was placed in the intraperitoneal cavity and allowed to float freely. The incision was closed with 2 layers of sutures: one for the abdominal muscle layers and one for the subcutaneous tissue. The skin was brought into apposition by the subcutaneous closure, and was closed with surgical glue. All animals received subcutaneous injections of meloxicam (0.1 mg/kg), penicillin (75,000u/kg), and 0.09% saline (40-60 mL). Total surgical time averaged 20 min. All armadillos were handled in compliance with the University of Georgia’s Animal Care and Use Committee (IACUC) project A2004-10138-0.
Most animals (n = 29) were released at their capture sights within 24 hours. Two animals, however, were released 698 and 1,429 m away from their capture sights, respectively. The first escaped from its holding cage while recovering from surgery and the latter was intentionally released away from its capture sight as part of a separate project evaluating the effects of translocation on armadillos. Because both of these animals returned to their capture sights and established home ranges, we include them in the following analyses and treat them as though they were released at their capture sights.

Radiotelemetry

We located armadillos 3-4 times/week using remote triangulation or homing (White and Garrott 1990). Independence of locations was ensured by maintaining a minimum interval of 8 hours between consecutive locations on an individual (White and Garrott 1990). Locations were recorded equally throughout the diel period (i.e., every hour of the day) for each animal.

When remote triangulation was used, bearings were recorded from UTM-located permanent telemetry stations distributed throughout the study area. Triangulation error was minimized by maintaining short distances (< 300 m) from observer to armadillo and by recording sequential bearings quickly (an average of 4.4 min to calculate a location). Because of the short distances between the observer and armadillos, most (87%) observations required only 2 bearings to estimate an animal’s location. However, when 3 or more bearings were recorded, the location of the animal was estimated using the maximum-likelihood method (Lenth 1981). All bearings were entered into a hand-held PDA (Palm m125, Palm, Inc., Santa Clara, California) and animal locations were calculated and verified in the field using the program Locate III (Nams 2006). There were several advantages to using this system, such as eliminating errors associated with recording backbearings or incorrectly identifying telemetry stations, because
visual confirmation of locations occurred on the PDA. Homing was used primarily when animals were located in their underground burrows. We used a hand-held GPS unit (Garmin GPS 60, Garmin International, Inc., Olathe, Kansas) to mark the location of the burrow/animal. All telemetry data were collected by the same observer.

Data analysis

We examined the effects of sex and season on armadillo home range size and habitat selection. Seasons were defined as summer (21 June 2005-20 September 2005), fall (21 September 2005-20 December 2005), winter (21 December 2005-20 March 2006), and spring (21 March 2006-20 June 2006). A biologically relevant seasonal division may have been to separate the year into breeding (June-November) and non-breeding (December-May) seasons (sensu McDonough 2000); however, because up to 83% of breeding occurs during the months of June-August (McDonough 2000) and armadillos have been noted to reduce their activity and home ranges during the winter months (Layne and Glover 1985, Bond et al. 2000), we feel that a calendar-based division of seasons was more appropriate than other seasonal divisions and allowed an examination of meaningful time periods that may affect armadillo space use.

Home ranges.—Seasonal home ranges were estimated in ArcGIS (ESRI 2005) with the program Home Range Tools (Rodgers et al. 2005), using the area added method (White and Garrott 1990) for 95% minimum convex polygons (MCP). With this method, points are removed from the polygon based on the amount of area they add to the home range. It is an iterative process that results in the smallest possible polygon from all possible combinations of remaining points. Seasonal home ranges were estimated only for animals with \( \geq 30 \) locations/season. Composite home ranges (i.e., all locations/animal) were not estimated and analyzed because few individuals were monitored for the same lengths of time over the same seasons.
We used a 2-factor analysis of variance (ANOVA) to examine the effects of sex, season, and their interaction on armadillo home range size, using an armadillo-season as the experimental unit. Home range sizes were found to violate the normality of residuals (tested with the Shapiro-Wilk statistic) and homogeneity of variance (tested with Levene’s test) assumptions of an ANOVA; therefore, the analysis was performed on rank-transformed data, making the test non-parametric (Conover and Iman 1981). In the case of a significant seasonal effect, we used a Tukey multiple range test to differentiate among seasonal means. Statistical significance for all tests was accepted at $\alpha = 0.10$.

*Habitat selection.*—Armadillo locations and home ranges were entered into ArcGIS (ESRI 2005) and intersected with an annually updated coverage containing 8 habitat types delineated as agriculture/food plot, shrub/scrub, hardwood, pine regeneration, mature pine, mixed-pine hardwood, wetlands, and barren land/urban. We used a distance-based approach (Conner and Plowman 2001, Conner et al. 2003) to assess (1) whether armadillo habitat use was non-random, (2) which habitats were used disproportionately, and (3) whether sex and season influenced armadillo habitat use. This approach is mathematically similar to compositional analysis (Aebischer et al. 1993), but distances between habitats are used as dependent variables in a multivariate analysis of variance (MANOVA) rather than log-ratio differences (Conner and Plowman 2001, Conner et al. 2003).

Habitat analyses were considered at 2 spatial scales: Johnson’s second (selection of a home range) and Johnson’s third (selection within a home range) orders (Johnson 1980). To determine if armadillo habitat use was non-random, distances between random points within an animal’s home range and all habitat types were compared to a null model ($2^{nd}$ order), and distances between animal locations and all habitat types were compared to a null model ($3^{rd}$ order).
order). For each order of selection, the effects of sex and season on habitat selection were tested using a 2-factor MANOVA, using an armadillo-season as the experimental unit. If no significant sex x season interaction was detected, the main effects (sex and season) were examined separately by averaging over the other main effect (Zar 1984), using individual armadillos as the experimental unit. If the MANOVA was significant, univariate \( t \)-tests were performed on each habitat type to determine which were used disproportionately. Ranking matrices using pairwise \( t \)-tests were used to rank habitats in order of preference and to determine which habitats were significantly preferred over others (Conner and Plowman 2001, Conner et al. 2003). Statistical significance for all tests was accepted at \( \alpha = 0.10 \).

RESULTS

Study animals

From 21 June 2005 to 19 June 2006, we obtained 2,913 locations on 31 armadillos (18 F, 13 M). The mean number of locations per individual was 94.0 ± 6.7 (range = 3-144) and the average length of time an individual was monitored was 227.5 ± 16.7 days (range= 5-358). Effects of the surgical procedure on armadillo survival and behavior appeared to be minimal. Only 1 animal (F50), which had apparently sustained severe wounds on her carapace from a predator within days of her capture, failed to survive > 1 month post-implantation.

Home ranges

Two armadillos (F40 and F50) died before they could be located \( \geq 30 \) times each and 2 additional armadillos that also died (F26 and M31) had \( \geq 30 \) locations, but not within any individual season; therefore, we estimated 70 seasonal home ranges for 27 armadillos (12M, 15F). Home ranges varied from 1.3 to 32.1 ha. Sex and season did not interact to affect armadillo home range size (\( F_{1,62} = 0.33, P = 0.806 \)). Males had larger home ranges (9.66 ± 1.3
ha; $\bar{x} \pm s.e$) than females (7.7 ± 0.6 ha), but this difference was not significant ($F_{1, 62} = 0.18, P = 0.674$). Home range sizes differed seasonally ($F_{3, 62} = 2.72, P = 0.05$), with the largest home ranges occurring during the summer season (14.35 ± 1.5 ha) (Table 2.1). The spring, fall, and winter seasons did not differ significantly (all $P > 0.10$) from each other. For comparison with previous studies, the average of all 70 home ranges was 8.7 ± 0.7 ha.

**Habitat selection**

We used 89 armadillo-seasons from 30 (13M, 17F) armadillos in our habitat selection analyses. For second order selection, sex and season did not interact to affect armadillo habitat selection ($\Lambda = 0.9174, P = 1.0$) and selection did not differ by sex ($\Lambda = 0.8958, P = 0.390$) or season ($\Lambda = 0.9372, P = 1.0$). Data were then pooled by sex and season and analyzed for overall habitat selection, using the individual animal as the experimental unit, and non-random habitat selection was detected ($\Lambda = 0.5723, P = 0.087$). For most habitats (agriculture, shrub/scrub, hardwood, pine regeneration, and mixed pine-hardwood), random locations within armadillo home ranges were not significantly closer/further than expected, but they were closer than expected to 3 habitats: mature pine, other/barren, and wetland (Table 2.2). The ranking matrix suggested that these 3 habitats were the most preferred, although none were significantly preferred ($P < 0.10$) over the others, or over remaining habitat types, except for agriculture, which was the least preferred habitat type (Table 2.2).

For third order selection, sex and season did not interact ($\Lambda = 0.7559, P = 0.591$) and season had no effect ($\Lambda = 0.8282, P = 0.929$), but sex-specific differences in selection were detected ($\Lambda = 0.8014, P = 0.0299$). However, when data were pooled across seasons and individual animals used as the experimental unit, sex did not affect habitat selection ($\Lambda = 0.6720, P = 0.305$). Sex was then excluded from the model and data were analyzed for overall habitat
selection, and non-random habitat selection was detected ($A = 0.4154, P = 0.006$). For most habitats (shrub/scrub, hardwood, pine regeneration, mixed-pine hardwood, wetland, and other/barren), armadillos were not found significantly closer/further than expected, but they were farther than expected from agriculture and mature pine habitats (Table 2.2). The ranking matrix indicated that the 2 avoided habitats were less preferred than the top 6 habitats, although they did not differ from each other. The top 6 habitats, in order of preference, were pine regeneration, wetland, shrub/scrub, other/barren, hardwood, and mix. None of the top 6 habitats were significantly preferred over the other (Table 2.2).

**DISCUSSION**

Most recent ecological work on armadillos is from a single population in Florida that was studied extensively from 1992-2003, using mark-recapture (Loughry and McDonough 1996, McDonough and Loughry 1997, Loughry and McDonough 1998a, Loughry and McDonough 1998b, Loughry et al. 1998a, McDonough et al. 2000, Loughry and McDonough 2001, McDonough and Loughry 2005) and genetic techniques (Prodohl et al. 1996, Loughry et al. 1998b, Prodohl et al. 1998). Data were collected on several hundred animals during these studies which provided valuable information about armadillo behavior, social spacing, and population structure. However, home range and habitat use are difficult parameters to measure in mark-recapture studies because most animals are observed only once (e.g., Loughry and McDonough 1998b). Our study provides the largest sample size and longest duration of any radiotelemetry study on armadillos to date, which allowed us to obtain many more observations per individual than previously available. Jacobs (1979) used radiotelemetry to monitor 23 animals, but animals were only monitored for < 1 month on average because externally attached transmitters were used.
Home range

Comparisons between studies should be made with care, as data were collected with different methods over different seasons and in different habitats; nonetheless, the average home range size of armadillos in our study (8.7 ha) is generally comparable to estimates from previous studies. The relatively small home range of armadillos compared to carnivores of similar body mass (armadillos weigh up to 6 kg), is thought to be due to the higher biomass per unit area of their primary foods (Layne 2003).

Bond et al. (2000) found that armadillos on Cumberland Island, Georgia reduced their home range sizes during the winter relative to other seasons. In contrast, winter home ranges for armadillos in our study were similar to those of the other seasons, with the exception of summer. Although armadillos on our study site did reduce their activity during the winter (D. Gammons, personal observation) as has been observed by other authors (Zimmerman 1982, Layne and Glover 1985, Inbar and Mayer 1999), when weather conditions permitted, armadillos were quite active and covered all parts of their home ranges. We suggest that the winter estimate from Bond et al. (2000) is biased low because observations were only made on 8 days during the winter season, likely missing days when armadillos were more active.

The significantly larger home ranges we observed during the summer season were expected, as summer is when the majority of breeding occurs (McDonough 2000). Similarly, McDonough (2000) found that adult home ranges were larger during the breeding (June-November) than non-breeding season (December-May), although there was no difference in home range sizes between the sexes. In fact, no studies have reported sex differences in armadillo home range size, generally attributing this to their lack of sexual dimorphism. Our results support this general pattern. Male and female home ranges were very similar in size for
the spring, fall, and winter seasons. However, male home ranges were 64% larger than female home ranges during the summer season (18.2 ha, and 11.1 ha, respectively), and although this difference was not statistically significant, it is perhaps suggestive of males expanding their home ranges to encompass the home ranges of as many females as possible to maximize breeding opportunities. For example, 2 male armadillos in this study had summer home ranges of 32.1 and 28.1 ha, respectively, which are among the largest home ranges ever reported, whereas the largest female home range was only 16.1 ha. We did not assess the breeding condition of armadillos in this study, but it is possible that these exceptionally large home ranges were from breeding males, which have been found to have larger home ranges than non-breeding males (McDonough 2000). These results are interesting because armadillo social structures are highly variable between populations. Some populations are classified as polygynous (McDonough 2000) and others are not (Loughry et al. 1998b); under some conditions, females may exhibit mutually exclusive home ranges (Layne and Glover 1977, Zimmerman 1982) or they may have overlapping home ranges (Jacobs 1979, Herbst and Redford 1991, McDonough 2000). On our study area, females had overlapping home ranges (D. Gammons, personal observation), so females may be a defendable resource for dominant males (McDonough 2000). Our data, at least indirectly suggests that this is a polygynously mating population, but further work will be required to test this idea. Regardless, plasticity in social structure is undoubtedly one of the characteristics of armadillos that has facilitated their rapid range expansion through the United States.

Radio signals were lost for 13 (5M, 8F) (42%) of the armadillos we monitored before the study ended. Radio signal loss could be due to a variety of factors, including dispersal, transmitter failure, or transmitters may have been destroyed by gunshots, vehicle collisions, or
predators. We feel that destruction of the transmitters is unlikely because: (1) the senior author was generally notified when and where armadillos on the property were killed by hunters, (2) vehicle-struck armadillos would have likely been found while conducting telemetry data collection, and (3) transmitters were not affected in 2 animals that were killed by predators during the study, including 1 killed by an alligator (*Alligator mississippiensis*). While certainly some transmitters may have failed, it is unlikely that all (or even most) missing animals were the result of transmitter failure; thus, we speculate that a majority of the missing animals dispersed.

This hypothesis is supported by several lines of evidence. First, the continued range expansion of armadillos requires considerable dispersal of animals from their present range into new areas. Second, recapture rates in previous studies have been low (e.g., Jacobs 1979, Loughry and McDonough 2001), leading authors to suspect dispersal of a large percentage of the population. For example, Jacobs (1979) captured 115 non-juveniles, but only 15 were known to have survived the winter. Loughry and McDonough (2001), documented that only 258 of 474 animals were seen more than once. Finally, aggression and territoriality have been observed in armadillos, and have generally been directed at younger individuals (McDonough 1994). It is possible that a number of missing animals were driven from their home ranges by dominant individuals, because the missing animals weighed significantly less (3.85 ± 0.27 kg) than animals that survived the study (4.33 ± 0.15) \((t_{22} = -1.53, P = 0.07)\).

**Habitat selection**

While this was the first radiotelemetry study that explicitly examined seasonal variation in armadillo habitat selection, previous evidence indicates that armadillos use habitats differently over time. Inbar and Mayer (1999) found that road-kill locations were associated with dense vegetation during the winter but not during the summer, when road kill locations were not
associated with any vegetation characteristics. McDonough et al. (2000) found that during June-August, juvenile armadillos were found both more often than expected in some habitats (hammocks and wetlands) and as expected, depending on the year.

It is probable that levels of resources required by armadillos vary temporally; in fact, remarking on the frequency of temporal changes in resources, Schooley (1994) stated, “variation in habitat use should be expected for most terrestrial invertebrates.” Therefore we expected armadillos would display seasonal variation in habitat selection, particularly a more pronounced preference for wetland and hardwood habitats during the winter. Instead, we found that habitat selection was similar across all seasons. This result is difficult to explain, but as noted above, armadillos at our study site had similar home range sizes in the winter relative to other seasons (except summer), so it is unlikely that their resource requirements changed during this time. We suggest that although resources, such as the abundance of particular soil dwelling invertebrates (the most widely cited factor for armadillo habitat preferences), may change through time, armadillos are sufficiently adaptable to use alternatives without having to change habitats.

We found no difference in habitat selection between males and females during any season. This result is not surprising considering the overall similarities in home ranges, body sizes and presumably, resource requirements, between the sexes.

Overall, armadillos did not use habitats randomly on our study site. Mature pine ranked as the most preferred (but used in proportion to availability) habitat at the 2nd order and as the least preferred (and strongly avoided) habitat at the 3rd order in our study. This apparently contradictory result, which can occur using either distance-based approaches (Dussault et al. 2005) or classification-based approaches (Conner and Leopold 1996, Conner et al. 2005) to habitat use analysis, can be explained if there is a spatial correlation between preferred and
avoided habitat types. On our study area, distances between random locations distributed across the study area and mature pine were positively correlated ($r = 0.23, P < 0.0001$) with distances between random locations distributed across the study area and wetlands (a highly ranked habitat at 3\textsuperscript{rd} order selection), but negatively correlated with all other habitat types (-0.02 $\geq r \geq -0.29$).

We suggest that armadillo preference for mature pine at the 2\textsuperscript{nd} order is spurious, and a result of the spatial association between isolated wetlands imbedded within the mature pine matrix.

We found armadillos near a variety of habitat types, but mature pine and agriculture habitats were strongly avoided at the third order of selection (agriculture ranked as the least preferred habitat at the second order of selection as well). This result agrees with the findings of McDonough et al. (2000), who also found that armadillos avoided these habitat types.

McDonough et al. (2000) found that prey availability did not vary among habitat types (pine, wetland, hammock, and field), and suggested that instead, armadillos avoid these habitats because of harder soils (which increases foraging costs), lack of fresh water, or perhaps the dense understory increases the conspicuousness of armadillos as they forage.

Other/barren, wetland, shrub/scrub, pine regeneration, mixed-pine hardwood, and hardwood habitats were all consistently among the most preferred habitats, regardless of the order of selection. Whereas these habitats were among the most preferred according to the ranking matrices, none of these habitats were significantly preferred over the others (i.e., no habitat stood out as being superior). This was surprising because while armadillos are recognized to occasionally use other areas (McDonough and Loughry 2005), they are generally associated with bottomland hardwood forests (Inbar and Mayer 1999, McDonough 2000, McDonough and Loughry 2005). Most previous research has not used radiotelemetry and because armadillos are primarily nocturnal, they have generally only been observed during the
daylight hours or within the first few hours after emergence from their burrows, which are generally located in bottomland hardwood forests (McDonough and Loughry 2005). This method of observation would tend to find active armadillos within close proximity to their burrows, which may explain why bottomland hardwoods are described as their preferred habitat. If observations are recorded throughout the night while armadillos are actively foraging, however, they are more likely to be located farther from their burrows and in a variety of habitats. We suspect that we found armadillos closer to a variety of habitats because we obtained observations throughout the diel period. Our findings imply that armadillos may be more habitat generalists than previously suspected, at least with respect to foraging habitats.

While we found armadillos in a variety of habitats, they still may be more or less dependent on hardwoods, if only for burrow construction. In the only study that has evaluated the impacts of land management practices on armadillos, McDonough and Loughry (2005) presented a convincing case that a severe decline in the armadillo population at Tall Timbers Research Station (a property in Florida that—similar to our study site—is managed for the conservation of longleaf pine) was caused by the logging of hardwoods. Our study, coupled with information from McDonough and Loughry (2005), suggests that armadillos may be able to fulfill their energetic requirements by foraging in a variety of habitats, but may ultimately be dependent on hardwoods for their survival.

**MANAGEMENT IMPLICATIONS**

First, by demonstrating that large numbers of individuals can be successfully followed using radiotransmitters, we hope that future researchers will use radiotelemetry to answer questions that were previously difficult to resolve, such as those involving dispersal. The transmitters we used had relatively poor range (< 500 m), which made following dispersing
animals impossible, but as transmitter technologies improve, more study design options will become available.

Our home range results likely provide little direct immediate management implications, but future research can use these data as reliable baseline information from which to compare other populations to or to evaluate the impacts of various management activities on armadillo space use. However, an important caveat should be noted: southern Georgia is in the interior of the armadillo’s geographic range and they have been present there for at least 50 years (Fitch et al. 1952). Therefore, their population is probably near the carrying capacity of the landscape. Evidence of dispersal of almost half the animals we monitored (presumably because of intraspecific competition) and the large home ranges of males during the summer months (when females may be a defendable resource) similarly suggest that population density in this area is high. Our data provide some of the most reliable estimates of armadillo space use available, but as noted by other authors (Loughry et al. 1998b), given the plasticity of social structure in this species, caution should be made in generalizing patterns. Different patterns may be found in lower density populations, such as near the edge of the advancing front of their distribution.

Few quantitative data are available concerning the impacts of armadillos on native ecosystems, although armadillos are likely significant predators of ground-nesting birds, including northern bobwhites (Staller et al. 2005), and they may impact sensitive species of reptiles and amphibians (Drennen et al. 1989, Layne 1997, Engeman et al. 2003). We believe there is sufficient cause for concern over negative impacts armadillos may have on native fauna, especially considering that we found armadillos in a wider variety of habitats than previously reported. Their impacts may be more widely distributed as well. Active management of
armadillo populations should be considered where appropriate; the longleaf pine ecosystem is a good example.

Historically, longleaf pine ecosystems were not a monoculture; rather, they were a mosaic of different habitat types interspersed within a matrix of widely spaced pines (Myers 1990). Patches of hardwoods have always existed, but fire suppression has led to severe hardwood encroachment (Varner and Kush 2004). Taulman and Robbins (1996) suggested that the armadillo’s spread through Texas in the 1800’s was facilitated by the conversion of grassland to woody vegetation; similarly, we suggest that the encroachment of hardwoods into longleaf pine forests facilitated the invasion of armadillos into that ecosystem. Armadillos in our study used a variety of habitats within the overall longleaf ecosystem, but avoided mature pine. As land managers attempt to restore mature pine through the removal of hardwoods, armadillo populations are likely to decline, as demonstrated by McDonough and Loughry (2005). Active restoration of longleaf pine may eventually reduce the impacts of this nonindigenous species within this endangered ecosystem.

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Table 2.1. Seasonal home ranges (and standard errors) in hectares of armadillos monitored in southwestern Georgia, 2005-2006. Male and female home ranges did not differ during any season; different letters indicate significant difference ($P < 0.10$) between seasons for pooled animals.

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<th>Spring</th>
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<td>HR</td>
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<tr>
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<td>8.5 (1.9)</td>
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<td>11.1 (1.4)</td>
<td>13</td>
<td>8.1 (1.5)</td>
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<tr>
<td>Pooled</td>
<td>11</td>
<td>14.3 (2.6)A</td>
<td>23</td>
<td>8.3 (1.0)B</td>
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Table 2.2. Habitat type distance ratios for each order of selection for armadillos monitored in southwestern Georgia, 2005-2006. Different letters indicate significant difference ($P < 0.10$) in habitat ranking according to ranking matrices.

<table>
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<tr>
<th>Habitat type</th>
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<th></th>
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<td>$t^2$</td>
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<td>Mean$^1$</td>
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<td>0.5464</td>
<td>2A</td>
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<td>-2.20</td>
<td>0.0356</td>
<td>3A</td>
</tr>
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<td>0.82</td>
<td>0.4174</td>
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<td>-0.92</td>
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<td>-2.13</td>
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<td>Hardwood</td>
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<td>7A,B</td>
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<td>0.0054</td>
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<td>1.38</td>
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<td>Mature pine</td>
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<td>2.52</td>
<td>0.0174</td>
<td>8C</td>
<td>-0.3260</td>
<td>-1.79</td>
<td>0.0840</td>
<td>1A</td>
</tr>
</tbody>
</table>

$^1$Observed distances divided by expected distances. Significant mean ratios < 1 indicate habitat preference, > 1 habitat avoidance.

$^2$Univariate $t$-tests testing ratio difference from a value of 1.

$^3$Mixed pine-hardwood.
CHAPTER 3

FROM THE FIELD: TRANSLOCATION OF NINE-BANDED ARMADILLOS\textsuperscript{1}

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INTRODUCTION

During the last 150 years, nine-banded armadillos (*Dasypus novemcinctus*) have become an abundant and conspicuous member of the fauna in the southeastern United States. Considered by some to be an innocuous novelty and by others to be a nuisance, armadillos have long held a controversial position in public opinion (Clark 1951, Kalmbach 1944, Chamberlain 1980). In fact, while their range expansion has been well-documented (Humphrey 1974, Taulman and Robbins 1996, Fitch et al. 1952), there is even disagreement as to how “natural” this expansion has been (Taulman and Robbins 1996), and therefore whether armadillos should be regarded as a native or exotic species in certain locales. Regardless of their official status, armadillos are a species of intense concern among landowners, both in suburban and urban situations. For example, Mengak (2003) found that armadillo-related inquiries to Georgia county extension agents made up 10.1% of the total number of inquiries for all agents across the state, even more than white-tailed deer (*Odocoileus virginianus*). As evidenced by recent sightings in Nebraska (Freeman and Genoways 1998), Kansas (Kamler and Gibson 2000), and South Carolina (Platt and Snyder 1995), the distribution of the armadillo is continuing to expand, and conflicts between landowners and armadillos are likely to increase.

Most damage to property by armadillos is a result of their feeding habits. Armadillos dig shallow holes, 3-8 cm deep and 8-13 cm long, while searching for soil invertebrates (Hawthorne 1994, Figure 3.1). When foraging, armadillos damage lawns, gardens, flower beds, and golf courses. They may also damage structural foundations, driveways, and tree root systems by their habit of burrowing (Chamberlain 1980, Hawthorne 1994, Schaefer and Hostetler 2003). No repellents or toxicants are registered for use with armadillos, and exclusion typically does not work well because they are adept burrowers and can climb fences (Chamberlain 1980,
Habitat modification (i.e., large-scale vegetation alteration) in urban and suburban environments also is impractical (Chamberlain 1980). Consequently, often the only recourses for landowners are shooting and live-capture. Shooting nuisance wildlife, however, is not practical or desirable for many landowners, so live-capture and translocation is often preferred (Braband and Clark 1992, Craven et al 1998, Conover 2002). As Craven et al. (1998) noted, there is a common perception that translocated animals will “live happily ever after.” No data are available on the frequency of nuisance armadillo translocations, but an estimate in the thousands/year is reasonable. Nuisance armadillos have become such a problem that the USDA’s Wildlife Services program has identified developing effective baits to live-trap armadillos in urban areas as an important research need (APHIS 2001).

Despite popularity with the general public, there is concern among biologists over the appropriateness of nuisance wildlife translocation (Craven et al. 1998, Conover 2002). Primary concerns include: (1) the spread of disease, (2) humane aspects (e.g., stress and mortality of translocated animals), (3) impacts on resident wildlife at release sites, (4) post-release movement of animals to areas where they continue to be a problem, and (5) new animals simply replacing translocated ones so that the problem is not solved (Barnes 1994, cited in Craven et al. 1998, Conover 2002). Because no studies have evaluated armadillo translocations, our objectives were to address some of these questions by comparing the survival and movements (release site fidelity and home ranges) between resident and translocated armadillos.

**STUDY AREA**

We studied armadillos at Ichauway, a plantation operated by the Joseph W. Jones Ecological Research Center. This 11,735-ha research facility is located near Newton, Georgia, in the southeastern Gulf Coastal Plain. Historically, Ichauway was managed as a northern
bobwhite hunting plantation, and while hunting still plays a significant role in its management, the main objectives of land management today are: (1) conservation and restoration of the longleaf pine (*Pinus palustris*) ecosystem; and (2) integrating sustainable land-use practices for wildlife and forest management while conserving biological diversity. Currently, 40% of Ichauway’s land is managed to conserve and restore the natural longleaf pine ecosystem, while the remaining 60% is managed as multiple use zones that integrate wildlife and timber management with agricultural productivity. Land managers at Ichauway conduct prescribed burns on 4,000 to 5,000 ha each year, maintaining the entire property on a 2-year burn rotation.

**METHODS**

We captured armadillos using long-handed dipnets and unbaited wire cage traps (Hawthorne 1994). All armadillos were captured and handled in compliance with the University of Georgia’s Animal Care and Use Committee (IACUC) project A2004-10138-0. Captured armadillos were assigned randomly to one of 2 treatments: resident or translocated. Resident animals were released at their capture sites and translocated animals were released within the boundaries of the study site at randomly chosen road intersections > 1,000 m away from the original capture site (mean distance = 3,637 m, range = 1,429-8,052 m). This minimum distance was chosen because it exceeded the longest distance known for armadillos to return to a capture site (Layne and Glover 1977). One exception to this protocol was animal 5M, which was unintentionally released 698 m from his original capture site after he escaped from his holding cage.

All resident animals received surgically implanted transmitters (Model M1240, Advanced Telemetry Systems, Isanti, Minnesota), following procedures adapted from Herbst and Redford (1991). Armadillos were sedated by either (1) gas anesthesia, (2) an intramuscular injection of
butorphanol (0.1 mg/kg), medatomadine (0.07 mg/kg), and ketamine (15.0 mg/kg), or (3) an intramuscular injection of ketamine (40.0 mg/kg) and xylazine (1.0 mg/kg). Through a 2.5 cm incision centered over the umbilicus, the transmitter was placed in the intraperitoneal cavity and allowed to float freely. The incision was closed with 2 layers of sutures: one for the abdominal muscle layers and one for the subcutaneous tissue. The skin was brought into apposition by the subcutaneous closure, and was closed with surgical glue. All animals received subcutaneous injections of meloxicam (0.1 mg/kg), penicillin (75,000u/kg), and 0.09% saline (40-60 mL). Total surgical time averaged 20 min. We also used surgically implanted transmitters for the first 8 armadillos we translocated, but upon finding that 4 of these were never located after their release, we switched to externally attached modified fox squirrel (*Scuirius niger*) or northern bobwhite (*Colinus virginianus*) transmitters on the remaining translocated animals. These transmitters were bolted onto the anterior dorsal shield after animals were sedated.

We monitored armadillos using triangulation and homing (White and Garrott 1990). When triangulation was used, we used the program Locate III (Nams 2006) to estimate the animal’s location using the maximum likelihood method (Lenth 1981). Homing was used primarily when animals were located in their underground burrows; in these instances, we used a hand-held GPS unit (Garmin GPS 60, Garmin International, Inc., Olathe, Kansas) to mark the location of the burrow/animal. Home ranges were estimated in ArcGIS (ESRI 2005) with the program Home Range Tools (Rodgers et al. 2005), using the area added method (White and Garrott 1990) for 95% minimum convex polygons (MCP).

**RESULTS**

Between 26 May 2005 and 22 March 2006 we released 29 (11 M, 18 F) armadillos at their original capture sites (residents) and we translocated 12 armadillos (9M, 3 F). We
monitored animals until 19 June 2006. Effects of the surgical procedure on armadillo survival and behavior appeared to be minimal. Only 1 animal (F50), which had apparently sustained severe wounds on her carapace from a predator within days of her capture, failed to survive > 1 month post-implantation.

**Resident armadillos**

All 29 resident armadillos initially remained near their release sites and maintained stable home ranges. We calculated 95% MCP home ranges for 27 animals with > 30 observations (2 animals died before 30 observations were recorded). The average home range size for these animals was 11.0 ha (range = 3.0-29.7). While initially maintaining stable home ranges, radio signals were eventually lost for 11 animals. Radio signal loss occurred on average 245 days post-release (range = 117-322 days). Of the remaining animals, 6 died and 12 remained within their home ranges until the end of the study.

**Translocated armadillos**

A higher proportion of translocated animals dispersed from their release sites within the first few days after release (11 of 12 = 92%) compared to residents (0 of 29 = 0%; Fisher’s exact test, $P < 0.001$). Because of the relatively poor range (< 500 m) of both our implantable and externally attached transmitters, locating dispersing animals was difficult and we did not obtain post-release observations for 6 animals (4 with implants and 2 with external transmitters). The fate and direction of travel for these animals is unknown. Consequently, we obtained post-release spatial data for 6 translocated animals. Because of this small sample size, general patterns could not be described; therefore, the movements of each translocated individual for which we obtained data are reported separately.
Male # 4.—This animal received an implanted transmitter and was released 1,429 m away from its capture site. For 5 days, it remained in the vicinity of the release site (within 250 m). After this time, however, its location was unknown until it was located 8 days later 404 m from the initial capture site, having moved a distance of over 1,200 m towards its capture site since the previous observation. In moving that distance, it crossed the Ichawaynochaway Creek, which is between 20 and 40 m wide and over 2 m deep in that area. Subsequently, it maintained a 35.6-ha home range (based on 113 observations) in that area for at least 310 days, after which time the signal was lost. It was never located near its release site again. Apparently, it returned to its prior home range (Figure 3.2).

Male # 5.—This animal received an implanted transmitter and was scheduled to be released at its original capture site, but while recovering from surgery it escaped from his holding cage, which was located 698 m from its capture site. The first location obtained after this escape was recorded 5 days later, at which point it had returned to within 128 m of its capture site. Subsequently, it maintained a 15.6-ha home range (based on 144 observations) in that area for at least 358 days, after which time the signal was lost. After apparently returning to its prior home range, it was never located near its release site again (Figure 3.3).

Male # 10.—This animal received an implanted transmitter and was released 5,167 m away from its capture site. For 2 days, it remained in the vicinity of the release site (within 200 m). It was next located 5 days later 1643 m from its release site; however, this movement was not towards its capture site. Nonetheless, it established a new home range of 7.8 ha (based on 17 observations) (Figure 3.4). It was found dead in a burrow 37 days after its release. The cause of death could not be determined, but surgical complications, predation, and shooting were not suspected.
Male # 22.—This individual received a modified fox squirrel transmitter and was released 4,475 m from its capture site. Rather than initially remaining in the vicinity of its release site, it immediately began a long distance movement, but not towards its capture site. Within 3 hours of its release, it traveled over 1,680 m (0.56 km/hr). It was monitored for 4 more days until the transmitter fell off, during which time it moved little.

Male # 27.—This individual received a modified fox squirrel transmitter and was released 2,377 m from its capture site. Upon its release, it apparently made an immediate long-distance movement and we could not record any observations. However, the transmitter was found 10 days after release, having fallen off the animal. It was located 370 m from the release site. The direction of movement was not towards its capture site.

Male # 15.—This individual received an implanted transmitter and was released 8,052 m away from its capture site. In contrast to the previous animals, it made no long distance movement in any particular direction; rather, it appeared to attempt to establish a home range within the area of its release. However, this animal’s home range of 62.3 ha (based on 18 locations) was 6 times larger than the average home range of resident armadillos at this site and twice as large as the largest resident home range. It made several long distance (> 500 m) movements between consecutive observations, which we suspect were because it was avoiding conflict with conspecifics. This hypothesis is supported by the observation of this animal fighting with another individual. This animal was found dead 50 days after its release, having been killed by an unknown predator.

DISCUSSION

The clear difference in initial release site fidelity between resident and translocated armadillos suggests that translocated nuisance armadillos are unlikely to remain at their release
sites. Our data suggest that translocated armadillos will likely either (1) return to the area of capture where they may resume nuisance activities or (2) disperse from the release site to other areas where they might not be desired. Homing in armadillos has not been well-studied, but if only moved a short distance (< 1,500 m), it appears that armadillos can return to their capture sites. Layne and Glover (1977) reported the return of one individual that escaped 930 m from its capture site, although two other animals that escaped 300 and 1,896 m from their capture sites, respectively, settled in their new areas. Longer distance homing has been reported—up to 37 km in one case (Chamberlain 1980)—but this claim was not verified. Given the average home range size of 11.0 ha for resident armadillos at our site, which is similar to the estimates of others (see Table 4 in McDonough 2000), short distance translocations may be within an animal’s home range. In these situations armadillos may be able to navigate back to their capture site via olfactory cues deposited by their paired anal glands (Clark 1951, Jacobs 1979). However, the 2 individuals in which we observed homing behavior appeared to have been released outside their home ranges, as they were never observed near their release sites following their post-release dispersal (Figs. 2.1 and 2.2). Apparently, armadillos can use other environmental cues when homing; this was particularly demonstrated by M4 with its crossing of the Ichawaynochaway Creek to return near its capture site. Incidentally, bodies of water should not be considered barriers to which translocated armadillos will not cross. Frutos and van den Bussche (2002), for example, found that the Paraguay River, in Paraguay, was not a significant barrier to gene flow in that population.

In practice, it is likely that nuisance armadillos will be translocated a sufficient distance to prevent homing, so the more important concern may be their movement away from release sites to other areas where they may cause further nuisance problems. In addition, post-release
dispersal may increase the spread of diseases such as leprosy and Chagas’ disease—armadillos are known reservoirs of the causative organisms for these diseases (Walsh et al. 1986, Yaeger 1988, Paige et al. 2002). Extensive post-release movements have been reported in a number of translocated nuisance animals ranging from raccoons (*Procyon lotor*) (Rosatte and MacInnes 1989, Mosillo et al. 1999) and black bears (*Ursus americanus*) (Harger 1970 and McCollum 1974, both cited in Rogers 1986) to even relatively sedentary gila monsters (*Heloderma suspectum*) (Sullivan et al. 2004), so it is not surprising that armadillos in this study behaved similarly. Possible reasons for the immediate dispersal of translocated animals from their release sites include competition with resident animals or disorientation and attempted homing (Mosillo et al. 1999). We found evidence for both of these factors. Competition with resident animals was hypothesized as the reason for the abnormal behavior of M15 (although his behavior could not be classified as “dispersing”), and competition and/or attempted homing may explain the movements of the other translocated animals.

Six (20.1%) of the resident animals died during the study, although the fate of 11 residents was unknown because of radio signal loss. Aggression and territoriality is generally directed at younger individuals (McDonough 1994) and since the animals we lost signals for weighed less (3.69 ± 0.29 kg) than animals that remained in their home ranges (4.33 ± 0.15) (*t* = 2.03, *P* = 0.03), we suspect the majority of the animals we lost signals for dispersed under pressure from conspecifics. Two (16.7%) of the translocated animals died, while the fate of the 10 others was unknown. Because of the high rate of unknown fates for both treatment groups, we cannot determine if translocated armadillos had similar survival rates to those of residents. Because during the last 150 years numerous populations of armadillos have been established through hundreds of purposeful and accidental introductions (Fitch et al. 1952, Humphrey 1974,
Taulman and Robbins 1996), one might assume that translocated armadillos may be able to quickly adapt to local conditions and experience high survival rates. It is important to remember, however, that most of these introductions probably occurred in areas where few or no other armadillos were present, and therefore translocated individuals historically encountered low levels of intraspecific competition and high levels of resources. Survival rates may be lower when translocating individuals into areas where populations are already established, as will generally be the case when translocating nuisance animals today. Certainly it is difficult to imagine a scenario where a nuisance animal would knowingly be released into unoccupied habitat. Additionally, the immediate post-release movements of most of the translocated animals predispose them to higher risks of mortality. For example, when dispersing from a release site, translocated armadillos are more likely to cross roads, which are a significant source of mortality (Loughry and McDonough 1996, Inbar and Mayer 1999).

The high rate of emigration among resident armadillos that we observed is consistent with observations of other researchers. The emerging picture of armadillo population dynamics is that they have quite fluid populations, with some animals remaining within their home range for a number of years, but up to half of the population appears to emigrate each year (Jacobs 1979, Loughry and McDonough 2001). This pattern is to be expected for a population that is continuing to expand its range. It should also be expected that emigrating resident armadillos will likely enter into vacant territories previously occupied by translocated animals and nuisance activities will resume. Conover (2002) noted that when nuisance behavior is exhibited by most members of a population (as is the case with armadillos), problems are likely to reoccur as soon as the translocated animals are replaced.

Management implications
In conclusion, we recommend against translocating nuisance armadillos in most cases because (1) translocated animals are unlikely to remain at their release site—this will likely simply transfer the problem elsewhere, increase the risk of the spread of disease, and increase mortality rates because of an increased risk of exposure to mortality agents, and (2) resident armadillos are highly dispersive and will likely quickly fill vacated territories formerly occupied by translocated animals. In addition, negative ecological impacts of additional armadillos in an area should be considered. Armadillos pose a threat to a number of native fauna including several rare or endangered reptiles (Layne 1997), soil invertebrates (Carr 1982), marine turtles and gopher tortoises (Gopherus polyphemus) (Drennen et al. 1989, L. Smith, J.W. Jones Ecological Research Center, personal communication), and ground-nesting birds, such as northern bobwhite (Staller et al. 2005).

If shooting is not a desired or practical management option for removing nuisance armadillos within certain localities, they should be trapped and then humanely euthanized. It is important to remember, however, that until a more permanent solution is found to keep armadillos away from areas where they are unwanted, whatever removal techniques landowners choose to use will likely need to be continuously applied.

ACKNOWLEDGEMENTS

We thank the wildlife lab at the Jones Center and numerous volunteers for assistance with data collection, particularly J. Keenan and D. Temple. J. Brock assisted with analysis of spatial data. This work was supported with funding from the Jack H. Berryman Institute, the J.W. Jones Ecological Research Center, and the University of Georgia.
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Figure 3.1. Armadillos forage by digging shallow holes in the ground.
Figure 3.2. Locations for male armadillo #4 at Ichauway, Georgia.
Figure 3.3. Locations for male armadillo #5 at Ichauway, Georgia.
Figure 3.4. Locations for male armadillo #10 at Ichauway, Georgia.
CHAPTER 4

SUMMARY AND CONCLUSIONS
Nine-banded armadillos (Dasypus novemcinctus) are a species of intense concern among landowners in urban and rural situations (Mengak 2003). As their range continues to expand, conflicts between armadillos and humans are likely to increase, so there is a need to better understand their space use patterns so that management practices can be developed. Prior to this study, little reliable data have been available on armadillo space use patterns, as radiotelemetry has been rarely employed and when it has been used, sample sizes have generally been low or methods poorly explained (Thomas 1980, Zimmerman 1982, Herbst and Redford 1991, Schnell 1994, Bond et al. 2000 but see Jacobs 1979). Our study provides the largest sample size and longest duration of any radiotelemetry study on armadillos to date, which allowed us to obtain many more observations per individual than previously available, making for a more robust data set. In addition, this study compared movements of resident and translocated armadillos, which is a vital step for determining the appropriateness of nuisance armadillo translocation (Craven et al. 1998), but a step that up until this point has not been performed.

Based on our study, we provide recommendations for dealing with unwanted armadillos for both the urban and the rural landowner. In rural areas, lethally based control strategies (shooting and trapping) are likely to be ineffective (Conover 2002). Our data suggest that populations may be reduced, however, through habitat manipulation, as has been found by McDonough and Loughry (2005). Hardwood removal has dual benefits of assisting in the restoration of the long-leaf pine (Pinus palustris) ecosystem and likely having negative effects on armadillo populations—a rare case of a “win-win” scenario.

In urban areas, habitat manipulation is unlikely to occur on a large scale and often, landowners desire to have nuisance animals translocated, hoping they will “live happily ever after” (Craven et al. 1998). However, our data suggest that translocation of nuisance armadillos
should be minimized whenever possible, because (1) translocated animals are unlikely to remain at their release site—this will likely simply transfer the problem elsewhere, increase the risk of the spread of disease, and increase mortality rates because of an increased risk of exposure to mortality agents, and (2) resident armadillos are highly dispersive and will likely quickly fill vacated territories formerly occupied by translocated animals.

Unfortunately, these recommendations are difficult to implement. Large-scale hardwood removal is compatible with other land-use objectives in areas managed for the conservation of long-leaf pine, but similar habitat manipulation may not be as desirable in other parts of the armadillo’s range or on lands managed for other purposes. And, despite the ecological concerns of biologists, translocation of armadillos and other nuisance animals is likely to continue on a large scale simply because of its popularity with the public (Craven et al. 1998). Clearly, more effective management strategies are needed, not just for minimizing human-armadillo conflict, but for reducing armadillo populations as a whole. The most compelling argument for reducing armadillo populations is that armadillos are exotic animals in many parts of their range and have the potential to disrupt ecological communities (Carr 1982, Drennen et al. 1989, Layne 1997, Staller et al. 2005).

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