Home Range Dynamics and Den Use of Nine-banded Armadillos on Cumberland Island, Georgia

Bobby T. Bond, *Georgia Department of Natural Resources, Wildlife Resources Division, 1945 Highway 199 South, East Dublin, GA 31027*

Martin I. Nelson, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Robert J. Warren, *Daniel B. Warnell School of Forest Resources, University of Georgia, Athens, GA 30602*

Abstract: We implanted radio transmitters in 11 armadillos *(Dasypus novemcinctus)* on Cumberland Island, Georgia, and monitored them seasonally from July 1987 through May 1988. Six individuals survived (S) the entire study: 5 died (D) between 1–4 months post-implantatin. Home range sizes for S individuals did not differ significantly between sexes ($N=6$; 3 males and 3 females). Mean overall home range size was significantly smaller for S compared to D armadillos for both the minimum convex polygon (MCP) (S = 6.55 ha, D = 11.55 ha; F = 12.49, df = 1, $P < 0.002$) and adaptive kernel (AK) (S = 9.47 ha, D = 18.81 ha; F = 11.07, df = 1, $P = 0.003$) methods. Mean home range sizes for S armadillos differed among seasons for both the MCP (summer = 5.34 ha, fall = 5.23 ha, winter = 1.65 ha, spring = 3.95 ha; F = 6.58, df = 3, $P < 0.003$) and AK (summer = 10.26 ha, fall = 8.75 ha, winter = 3.70 ha, spring = 6.02 ha; F = 5.29, df = 3, $P < 0.008$) methods. The S armadillos were located at dens significantly (F = 19.46, df = 1, $P < 0.001$) more frequently in winter (64.7%) compared to summer (29.7%), and they used significantly (F = 9.28, df = 1, $P < 0.001$) fewer different dens in winter (0.24 dens/day) compared to summer (0.66 dens/day). The average number of different dens used by the S individuals during our entire study was 10.9. Dens were typically in burrows, but aboveground nests were also used. About 75% of all dens were under saw palmetto *(Serenoa repens).*

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Historically, the nine-banded armadillo *(Dasypus novemcinctus)* was present in south-central North America, Central America, and most of South America, but today it is distributed widely in the United States (Taulman and Robbins 1996). Armadillos are solitary foragers that occupy the same area for relatively long periods of time; therefore, home range is a helpful concept in understanding their movement behavior (Galbreath 1982). Early studies on armadillo home ranges were based on daylight observations (Clark 1951, Fitch et al. 1952, Layne and Glover 1977, Breece and Dusi 1985). Radiotelemetry, which includes diurnal and nocturnal tracking periods, provides a more comprehensive understanding of movement behavior than daylight observations. Preliminary radiotelemetry data for the nine-banded armadillo are available (Zimmerman 1990, Herbst and Redford 1991), but seasonal studies of home ranges and den use of armadillos are lacking.

Armadillos dig numerous burrows that function as dens, escape refuges, and possibly insect traps (Taber 1945, Clark 1951). Armadillos share dens simultaneously with offspring, litter mates, and/or their mate, but only rarely with another adult of the same sex (Galbreath 1982). Armadillo also have been reported to share their dens with other species (Taber 1945). Burrow sustems in Texas and Oklahoma usually have only 1 entrance, but may have up to 4, and are typically located in thick vegetation or other thick cover (Clark 1951, Zimmerman 1990). In addition to denning in burrows, armadillos occasionally construct surface nests in leaf piles or thick brush (Clark 1951, Galbreath 1982, Layne and Waggener 1984). We hypothesized that there would be seasonal differences in home range size, amount of time spent in dens, and in the number of dens used by armadillos because of seasonal changes in climate and the armadillo's poor body thermoregulation (McNab 1980, 1985). Therefore, our objectives were to determine seasonal home ranges and patterns of den use for nine-banded armadillos on Cumberland Island, Georgia.

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Methods

Study Site

Cumberland Island is the southernmost and largest of Georgia's barrier islands. It is located in Camden County about 2 km from the mainland. The 9,416-ha island is approximately 28.2 km long by 4.8 km wide, narrowing to 0.8 km on its southern end. In 1972, the National Park Service acquired most of the island and established Cumberland Island National Seashore.

The natural history and ecology of the island have been described by Hillestad et al. (1975). Armadillos first arrived on Cumberland Island by unknown means in 1971 (Hillestad et al. 1975). The absence of hunters and large predators, limited motor vehicle traffic, and favorable habitat conditions and climate on Cumberland Island were conducive to armadillo survival and population growth.

We examined the seasonal variation in armadillo home ranges and den use in 2 areas of Cumberland Island that were separated by about 1.2 km. One area was near Plum Orchard and the other was near Ashley Pond. The primary forest types in both areas were live oak-saw palmetto *(Quercus virginana-Serenoa repens)* and oak-pine *(Quercus* spp.-*Pinus* spp.*)* communities. Palmetto comprised 10%–50% of the understory coverage at both localities.

Capture and Implantation

We captured armadillos with a long-handled dip net. We retained only 11 individuals that weighed >3.0 kg, on the assumption that they were >1-year-old adults (McNab 1980). Each animal was numbered on the carapace with enamel paint, and a numbered stainless steel tag was affixed through a hole drilled in the ventrolateral pectoral shield to permit identification in case of transmitter failure. Following sedation via an intramuscular injection of a mixture of xylazine hydrochloride (0.5 mg/kg) and ketamine hydrochloride (3.5 mg/kg), a 2.5-cm incision was made in the ventrolateral abdominal wall and a 25-g radiotransmitter was inserted intraperitoneally (Davis et al. 1984, Nelson and Warren 1987). We used implantable transmitters because the body shape and behavior of armadillos, like other burrowing animals, precludes the use of collars (Smith and Whitney 1977, Davis et al. 1984, Eagle et al. 1984). Armadillos were released at their capture sites about 18 hours post-surgery when they had fully recovered from anesthesia. Our research was conducted before institutional animal care and use requirements were established in 1990; nonetheless, our procedures complied with scientifically acceptable field methods (Am. Soc. Mammal. 1987).

Radiotelemetry

We monitored armadillos seasonally: summer = August 1987 (13 days), fall = September and November 1987 (17 days), winter = January 1988 (8 days), and spring = March and May 1988 (16 days). We ran continuous workshifts during each monitoring period (3 8-hour workshifts/24 hours) and attempted to locate each armadillo about 6 times daily. A single observer determined all armadillo locations during a particular workshift. Locations were estimated by triangulation of compass bearings and with visual observations. Telemetry stations were georeferenced from a map using geographical features, such as roads, trails, and their intersections. We used 2–3 bearings per location with an angle of intersection between 45°-135° from the telemetry stations to minimize telemetry error. Telemetry error also was minimized because most of our locations were ≤300 m of each armadillo. Telemetry stations were separated by 167 m and a maximum of 15 minutes elapsed between all bearings. All bearings were entered in program LOCATE (Kie et al. 1996) to derive Universal Transverse Mercator (UTM) coordinates for armadillo locations.

Home Range Data

We entered armadillo locations (UTM coordinates) into program CALHOME to compute home range sizes for both 95% minimum convex polygon (MCP) and 95% adaptive kernel (AK) methods (Kie et al. 1996). Each seasonal home range and the overall home range were computed separately. We included the MCP method so we could compare our results with past studies. We used the AK as a nonparametric estimation procedure because it is applicable to a variety of home range estimation problems where the assumptions of a parametric model, such as bivariate normal distribution, may not be met (Worton 1989, 1995). It also is not as sensitive to grid size as the harmonic mean (Kie et al. 1996), and has been useful for analyzing data on home range space use (Worton 1989, 1995).

We analyzed home range data with Statistical Analysis System (SAS Inst. 1990). Prior to analysis, all data were tested to ensure normality of distribution and homogeneity of variances to meet the assumptions of analysis of variance (ANOVA). We separately analyzed telemetry data from S armadillos to describe seasonal home range characteristics. We then examined differences in overall home range data between S and D armadillos. Home range data for S armadillos were analyzed using a repeated measures ANOVA model (Cody and Smith 1991) to determine the significance ($P < 0.05$) of sex, season, and sex-by-season interactions. Home range data for S and D armadillos were analyzed using a general linear model (PROC GLM) ANOVA to test for the significance of sex, season, survivorship, sex-by-season, sex-by-survivorship, season-by-survivorship, and sex-by-season-by-survivorship interactions. Only the summer, fall, and winter seasons were analyzed between S and D armadillos, because all of the D individuals had died by spring. Significant seasonal effects in the analysis of home range data were further analyzed post hoc with the Duncan's New Multiple Range Test (Cody and Smith 1991) to determine significant differences among seasonal means.

Den Use

When triangulation suggested that an armadillo might be in a den, we used homing to locate and verify den locations each day. Dens used by the radio-equipped animals were marked to facilitate relocation, mapped, and had adjacent cover characteristics recorded.

Den Use Data Analysis

We analyzed data from S individuals to determine den site characteristics and seasonal patterns of den use. We divided the number of times the armadillos were located in a den during each monitoring period by the number of times the armadillos were located for that period. As an index of the number of different dens used seasonally (i.e., den use index), we divided the number of different dens by the number of days each armadillo was observed in a den (maximum value = 1.0) during each season. The relative amount of time per monitoring period each armadillo was located in a den and the den use index were analyzed in a repeated measures ANOVA model to determine the significance ($P < 0.05$) of sex, season, and sex-by-season interaction. Significant seasonal effects were further analyzed post hoc with the Duncan's New Multiple Range Test to determine significant differences among seasonal means.

We also were interested in estimating the total number (i.e., population) of dens used in each season. We used the Schnabel multiple census method to estimate the total number of dens used by armadillos (Ricker 1975, Johnson et al. 1976, Davis and Winstead 1980):

$$\text{Total dens} = \frac{\Sigma(\text{total dens}_{\text{(used in each sampling period)}} \times \text{total dens}_{\text{(used previously)}})}{\text{total dens reused}}$$

This estimate provided a different measure of armadillo movement behavior than the den use index because it was not influenced by the time the armadillos spent in dens.

Results

Study Animals

We implanted 10 armadillos (5 females and 5 males) with transmitters in July 1987; 1 additional armadillo (female) was implanted in September 1987. Six of the originally implanted armadillos survived (S) the entire study; the other 5 armadillos (including the 1 implanted in September) died (D) between 1–4 months post-implantation. We assumed none of these 5 individuals died of capture/implantation mortality because they died >1 month post-implantation.

Home Range

In the analysis of S vs. D individuals, home range size did not differ significantly ($P > 0.05$) between sexes of either MCP or AK methods; thus, sexes are not reported separately. The S individuals had significantly smaller overall home range sizes than the D armadillos for both MCP ($F = 12.49$, $df = 1$, $P < 0.002$) and AK ($F = 11.07$, $df = 1$, $P = 0.003$) methods (Table 1). These differences between S and D individuals were not an artifact of a difference in the number of radiotelemetry locations for D armadillos, because the number of locations was similar for S and D armadillos (Table 1).

Significant seasonal differences ($P < 0.05$) in home range sizes occurred for the S individuals, whereas there were no significant seasonal differences ($P > 0.05$) in home range sizes for the D individuals (Table 1). The significant seasonal differences observed for S individuals occurred for both MCP ($F = 6.58$, $df = 3$, $P < 0.003$) and AK ($F = 5.29$, $df = 3$, $P < 0.008$) methods (Table 1). For the MCP method, winter home range size for S individuals was significantly smaller than for all other seasons (Table 1). For the AK method, home range size for S individuals was significantly smaller during winter than summer and fall, and significantly smaller during spring than summer (Table 1).

For S individuals, the winter and summer seasons differed the most in home range sizes (Table 1). A graphical overlay of the 95% MCP home ranges revealed that the smaller winter home range occurred within the core of each armadillo's larger summer home range. Therefore, the seasonal differences in winter and summer home ranges we observed resulted from an expansion and reduction in the size of the area occupied rather than because of a seasonal shift to a different area.

Table 1. Seasonal home range sizes based on number of locations for the 95% minimum convex polygon (MCP) and 95% adaptive kernal (AK) methods for 2 survivorship classes of nine-banded armadillos on Cumberland Island, Georgia, summer 1987 through winter 1988.

Season	Survivorship class[e]	Locations			MCP (ha)[a, b]		AK (ha)[c, d]	
		N	$\bar{x}$	SE	$\bar{x}$	Range	$\bar{x}$	Range
Summer	S	6	31.5	1.3	5.34A[f]	2.33–7.10	10.26A	4.30–14.66
	D	3	33.0	1.5	10.61	3.73–17.91	18.51	6.75–33.23
Fall	S	6	68.2	1.9	5.23A	3.23–8.05	8.75AB	4.63–13.34
	D	4	65.0	2.6	8.80	6.08–10.69	16.19	11.79–20.70
Winter	S	6	35.5	0.7	1.65B	1.35–2.24	3.70C	2.34–5.60
	D	4	32.8	3.0	3.72	2.48–4.54	8.04	4.10–10.71
Spring	S	6	71.7	2.9	3.95A	2.30–7.43	6.02BC	3.50–12.31
	D[g]	-	-	-	-	-	-	-
Overall	S-4[h]	6	206.7	5.0	6.49	4.66–9.43	9.24	6.36–12.76
	S-3[h]	6	135.0	3.8	6.55	4.79–8.50	9.47	6.69–12.99
	D	5	99.4	18.6	11.55	5.05–24.70	18.81	9.13–38.38

a. Season main effect; $P < 0.003$.

b. Survivorship main effect; $P < 0.002$.

c. Season main effect; $P < 0.008$.

d. Survivorship main effect; $P = 0.003$.

e. S = armadillos that survived the entire 1-year study; D = armadillos that did not survive through until the spring season.

f. *Seasonal means for S armadillos with dissimilar letters are significantly different ($P < 0.05$; Duncan's New Multiple Range Test).*

g. All D armadillos died by spring.

h. S-4 = overall home range for S armadillos calculated using telemetry data from all 4 seasons; S-3 = overall home range for S armadillos calculated using telemetry data for 3 seasons (summer, fall, and winter) to compare with D armadillos.

Den Use

We recorded use of 164 different dens for all study animals. Of these, 73.8% were in palmetto thickets and 17.6% were under fallen logs or at the base of trees or stumps. Among S individuals (excluding 1 individual whose home range was in an open pasture where there was no palmetto), 85.9% of dens were under palmettos. Only 1 burrow entrance occurred without cover located overhead or immediately adjacent. Twelve surface nests were observed in warm weather; other dens may not

Table 2. Seasonal variation in percentage of locations of individuals in dens and in number of dens used by nine-banded armadillos ($N = 6$; 3 males and 3 females) that survived the entire 1-year study on Cumberland Island, Georgia, summer 1987 through spring 1988.

Season	% of locations in dens		Dens use index (N dens/day)	
	$\bar{x}$	Range	$\bar{x}$	Range
Summer	29.7A[a]	25.0–37.5	0.66A	0.43–0.78
Fall	33.0A	19.4–56.8	0.40B	0.14–0.80
Winter	64.7B	50.0–79.0	0.24B	0.13–0.38
Spring	47.2C	37.8–56.8	0.30B	0.13–0.57

a. Means with dissimilar letters are significantly different ($P < 0.05$; Duncan's New Multiple Range Test).

have been detected, because they were typically located in dense cover and hidden by leaf litter, as were burrow entrances. We observed no simultaneous den sharing, but there were 7 cases of different radio-marked armadillos using the same den at different times. All of these instances were between an S and D individual.

For S armadillos there was a significant seasonal effect for both percentage of locations in dens ($F = 18.08$, $df = 3$, $P < 0.001$) and the den use index per season ($F = 9.04$, $df = 3$, $P < 0.001$) (Table 2). Armadillos spent more time in dens and used fewer different dens during winter than summer. Neither a significant sex nor sex-by-season interaction occurred in den use. The 6 S individuals used an average of 10.9 different dens. The Schnabel calculation yielded an estimate of 18–38 dens/armadillos ($\bar{x} = 29.3$) over the 10-month study period.

Discussion

Mean overall home range size for D armadillos was about twice as large as for S armadillos, and D armadillos showed no seasonal change in home range (Table 1). We hypothesize that the D armadillos were transient individuals that never established a home range. However, we did not visually observe any interactions between S and D armadillos. Intraspecific aggression has been observed in armadillos of both sexes. This aggression may help armadillos defend territories with favorable resources, maintain breeding exclusivity, or promote dispersal of young (McDonough 1994). McDonough (1994) reported male armadillos are aggressive towards younger males during the breeding season; females are aggressive towards young individuals (male or female) and adult females during the period associated with late pregnancy and lactation. Male aggression occurs to exclude other males from receptive females, which leads to suppression of reproduction in the excluded males (Bronson 1989, McDonough 1994); female aggression occurs in defense of their litters and to promote the dispersal of last year's young (McDonough 1994). Aggression consists of chases and fights that result in the displacement of the "loser"; however, the displacement is often temporary because the loser usually returns to the same area (McDonough 1994). The displaced losers may be subdominant individuals, or they may be transient armadillos that lack a true home range or are in the process of home range delimitation (Galbreath 1982, McDonough 1994). The idea of territoriality in armadillos conflicts with reports by Taber (1945) and Clark (1951). Future research of radio-equipped armadillos along with visual observations of interactions among them may reveal the effects of aggression on home range size and overlap, and add more insight into their behavioral ecology.

Our overall estimates of mean home range sized based on radiotelemetry [6.49 ha (MCP method) and 9.24 ha (AK method)] for the 6 S individuals are comparable to other estimates. Clark (1951) visually observed 3 armadillos in Texas and obtained an average home range size of 3.5 ha. Similar visual estimation methods have been used in 3 other studies. Fitch et al. (1952) estimated the home range size of 1 armadillo in Louisiana to be 20.2 ha. In Florida and Alabama, minimum home range sizes of adult armadillos averaged 7.4 ha ($N = 7$) and 3.5 ha ($N = 21$), respectively, and varied seasonally from 0.8 to 13.8 ha; juvenile home range sizes were about half as large as for adults (Layne and Glover 1977, Breece and Dusi 1985). These estimates from past studies may be biased by a lack of nocturnal observations and a large proportion of individuals that were observed infrequently or only in open areas of high visibility. Breece and Dusi (1985) noted that calculated home range size was larger for individuals seen more frequently. Movement data often are most reliably obtained using telemetry, which permits repeated observations of individual animals. The only published study that used radiotransmitters in armadillos to determine home range was Herbst and Redford (1991); however, their reported home range sizes of 3 to 9 ha for non-pregnant females included few details on their methodology and data analysis.

On Cumberland Island, the S armadillos on average used many more dens (10.9) than noted in other studies. In previous research, burrow counts actually may have included mainly inactive burrows, as active dens are typically well concealed and easily overlooked. Fitch et al. (1952) counted 108 burrows on a 20.2-ha area where 13 armadillos had been recorded; most were "used only occasionally." Tabler (1945) found averages of 4.5 and 8.5 burrows/armadillo in 2 areas in Texas. Half of the 26 burrows excavated by Clark (1951) contained nest chambers.

Armadillos probably spend more time in burrows during winter because they are extremely sensitive to cold. They have high thermal conductance, low basal metabolic rate, and low body temperature, all of which prevent overheating in burrows, but confer poor thermoregulatory ability (McNab 1980, 1985). Armadillos survive temperate winters by constructing underground dens insulated with vegetation, and restricting foraging to periods of favorable temperature (Layne and Glover 1985, McCusker 1985). McDonough and Loughry (1997) reported adult armadillos adjusted their activity patterns to weather conditions, but their study only included the summer months from June through August. Inbar and Mayer (1999) reported that armadillos in Florida were more diurnal and less active during winter, whereas they were predominantly nocturnal and more active during summer. Thus, armadillos would be expected to be more sedentary during periods of cold temperatures. We postulate that our armadillos selected dens that offered the best insulation against cold temperatures during winter. We observed the fewest number of different dens (0.24 dens per day) and the greatest percentage of locations in dens (64.7%) and smallest mean home range sizes (MCP = 1.65 ha and AK = 3.70 ha) during winter. Conversely, we observed the greatest number of different dens (0.66 dens per day) and the lowest percentage of locations in dens (29.7%) during summer, most likely as a consequence of the increase in their mean home range size (MCP = 5.34 ha and AK = 10.26 ha). Also, the only time surface nests were observed was during summer.

In conclusion, our radio-marked armadillos decreased their movements and spent the greatest amount of time in dens during the coldest time of the year, which resulted in a reduction of home range size during winter. Armadillos did not shift their home range in winter, but simply decreased their home range from summer. Therefore, we conclude that primarily temperature and reproductive activity influenced seasonal variation in home ranges and den use of armadillos on Cumberland Island.

Management Implications

The National Park Service is mandated by Congress to minimize the ecological effects of exotic species on the public lands it manages. The armadillo is a recently introduced species on Cumberland Island. Chamberlain (1980) and Layne (1997) have reported the ecological impacts of this invading species. Managers wishing to implement armadillo control programs should consider the seasonal variations in movements we documented. Control programs may be most successful if implemented during summer months when armadillos are more active and move over larger areas.

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