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Burrow characteristics and habitat associations of armadillos in Brazil and the United States of America

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Abstract: We censused and measured armadillo burrows in ten 10 m x 40 m plots in each of four habitat types at a study site in northern Florida and one in the Atlantic coastal rainforest of Brazil. The nine-banded armadillo (*Dasypus novemcinctus*) was the only species of armadillo found in Florida, but several additional species were present in Brazil. Burrows were more numerous but smaller in Brazil than in the U. S., probably due to the inclusion of burrows dug by the smaller congener *D. septemcinctus*. In Brazil, burrows were larger and more numerous in swamp and forest habitats than in grassland or disturbed areas, suggesting that *D. novemcinctus* is found primarily in forests and swamps while *D. septemcinctus* is located in the other areas. This was supported by data from sightings of live animals. In Florida, burrows were more numerous in hardwood hammocks than in wetlands, fields or upland pine areas, but burrow dimensions did not vary across habitat types. In Florida, armadillos were seen more frequently than expected in hammocks and wetlands and less frequently than expected in fields and upland pine areas. There were also age (juvenile versus adult), sex, and yearly differences in habitat use in Florida. Biomass, abundance, and species diversity of terrestrial invertebrates did not vary significantly between habitat types in Florida, suggesting that habitat associations of armadillos were not influenced by prey availability.

Key words: *Dasypus*, armadillos, Brazil, United States, burrows, habitat usage

Landscapes are mosaics of different habitat types (Forman and Godron 1986, Pickett and Cadenasso 1995) and animals are expected to vary in their use of these habitats. For example, more individuals should be found in areas with abundant resources than in areas where resources are scarce (Sutherland 1996). However, determining habitat usage can be difficult for many species of mammals. For example, the nine-banded armadillo (*Dasypus novemcinctus*) is found throughout the southeastern United States (Humphrey 1974, Wetzel 1985, Taulman and Robbins 1996), but there are few quantitative data on which habitats these animals occupy within this broad geographic range. This is probably due to the fact that *D. novemcinctus* is relatively nocturnal and asocial (Galbreath 1982, McBee and Baker 1982), so obtaining large numbers of observations on individuals in different habitats is extremely time consuming. However, *D. novemcinctus* digs burrows (Newman 1913, Kalmbach 1943, Taber 1945, Clark 1951, Talmage and Buchanan 1954, Zimmerman 1990). As has been done with numerous species of burrowing animals, (e.g., King 1955, Schaller 1983, Burke 1989, Breininger *et al.* 1994, Moller *et al.* 1997), censusing burrows can provide data on population density and, if censused across different habitat types, habitat use. Caution is required though, as sole reliance on burrow counts can provide misleading data about population density (Hoogland 1981, Burke 1989, Vanhorne *et al.* 1997). In addition, animals may construct refuges in one area but travel to other areas to feed, so that presence of burrows may not accurately reflect the extent of habitat utilization. Consequently, observations of live animals are needed to confirm patterns of habitat usage and population size derived from burrow counts.

Burrow dimensions can be diagnostic of particular species of armadillos (Carter and Encarnaçao 1983). In the United States, where *D. novemcinctus* is the only armadillo present, differences in burrow dimensions would presumably reflect age differences, because juveniles might construct smaller burrows than adults due to their smaller body size. Thus, differences in burrow dimensions between habitat types could provide evidence about habitat usage by different age groups of armadillos. Along the same lines, knowing the dimensions of *D. novemcinctus* burrows in one habitat might allow identification of *D. novemcinctus* burrows in other habitats where other burrowing animals (such as other species of armadillos) may occur (Guyer and Hermann 1997).

In this study, we censused and measured armadillo burrows in each of four different habitat types in two different locales: one in northern Florida and one in the Atlantic coastal rainforest of Brazil. We used these data to compare burrow densities and dimensions between locales and between habitats within locales. In addition, because habitat types were similar in the two locales, we were able to compare burrow characteristics between matching habitat types. These data provided some insight into patterns of habitat usage by nine-banded armadillos. We used data from sightings of live animals to confirm these patterns and to examine age, sex, and yearly differences in the use of habitats. Finally, we measured resource availability (*i.e.*, terrestrial invertebrates) in the four habitat types in Florida to examine the relationship between habitat usage and resource distribution.

MATERIALS AND METHODS

Study sites: Data were collected during the summers (June-August) of 1992-1995 and 1997 at the Tall Timbers Research Station located just north of Tallahassee, Florida, and during the austral summer (January-June) of 1996 at the Poço das Antas Federal Biological Reserve, located approximately 100 km north of Rio de Janiero in Brazil (see Loughry and McDonough 1997, 1998a). Poço das Antas is 5200 ha in size and consists primarily of steep hills separated by narrow valleys. There are four main habitat types (Camargo 1996, Dietz *et al.* 1997): (1) mata, or Atlantic coastal rainforest; (2) grassland, consisting primarily of *Imperata brasiliensis* and/or *Melinus minultiflora*; (3) disturbed woodland ("corridors" in Dietz *et al.* 1997), which contains some grass but is primarily dominated by the tree *Gouchimatia polimorpha*; and (4) swamp, which may have standing water during wet portions of the year, but not year round. The first three habitats are found on the slopes of hills while swamps comprise most of the valleys (Dietz *et al.* 1997).

The nine-banded armadillo is the most abundant species of armadillo at Poço das Antas, but its smaller congener, the seven-banded armadillo (*D. septemcinctus*) is also present, as is the southern naked-tailed armadillo (*Cabassous unicinctus*; Loughry and McDonough 1997). The yellow armadillo (*Euphractus sexcinctus*) used to occur but may now be locally extinct (Loughry and McDonough 1997). All of these species dig burrows and the possibility exists of misclassifying burrows constructed by the similarly-sized *D. novemcinctus* and *C. unicinctus*. However, this may not be a large problem because *C. unicinctus* was very rare at

Poço das Antas (2 individuals sighted over the course of the study, Loughry and McDonough 1997) and, at least sometimes, appears to bury itself in the ground in a new location each night (Carter and Encarnaçao 1983, Eisenberg 1989, Emmons 1990, Redford and Eisenberg 1992), thus not producing a detectable burrow.

D. novemcinctus is the only species of armadillo found at Tall Timbers Research Station (Humphrey 1974, Stevenson and Crawford 1974, Wetzel 1982, 1985, Taulman and Robbins 1996). Tall Timbers is 1600 ha in size and is situated along the north shore of Lake Iamonia. Brennan *et al.* (1998) identified three main habitat types at Tall Timbers: (1) hammocks, consisting primarily of hardwoods such as oak (*Quercus* spp.), American beech (*Fagus grandifolia*), and southern magnolia (*Magnolia grandiflora*), (2) fields, which were plowed annually and planted with corn (*Zea mays*), clover (*Trifolium* spp.), and browntop millet (*Brachiaria ramosa*), and (3) upland pine areas, consisting of loblolly (*Pinus taeda*), shortleaf (*Pinus echinata*) and some longleaf (*Pinus palustris*) pines. In addition, we included (4) wetlands, defined as areas within 25 m of permanent water and thus having the potential to be flooded at certain times during the year. These four habitat types were roughly similar to the habitat types found in Brazil, *e.g.*, hammocks and rainforest were both characterized by a closed canopy of hardwoods with little understory, fields and grasslands were open areas with thick ground cover, upland pine and disturbed areas were open woodlands with considerable ground cover in the form of grasses and shrubs, and swamps and wetlands were both areas that could potentially be under water during certain times of the year.

Burrow characteristics: All data on burrows were collected during February 1996 at Poço das Antas and late June to early July, 1997 at Tall Timbers. At each locale we set up ten 10 m x 40 m plots in each of the four habitat types. The location of each plot was determined using a random numbers table to select x and y coordinates from a topographic map of each study site. Each plot was set up along polar coordinates; on hillsides, the long axis of the plot was oriented up the hill slope, in swamp/wetland plots, the long axis of the plot ran parallel to the edge of the water. In each plot, we counted all of the potential armadillo burrows we could find that looked large enough to contain at least a juvenile armadillo. To distinguish burrows from depressions created by armadillos while foraging (cf. Zimmerman 1990), burrows were defined as having a minimum depth of 25 cm. Other species of burrowing animals occur at Poço das Antas (e.g., paca, *Agouti paca*, and red-rumped agouti, *Dasyprocta agouti*) and it is possible that burrows dug by these animals could have been mistakenly classified as armadillo burrows. We feel this was not a large problem because we specifically avoided censusing areas where these species were known to dig burrows (*e.g.*, in the sides of banks, Emmons 1990).

In addition to counting the number of burrows per plot, we obtained data on the following characteristics of individual burrows: (1) height was the maximum vertical size (in cm) of the burrow opening; (2) width was the maximum horizontal size of the burrow opening; (3) length was the mininum length of the burrow as determined by the insertion of a flexible rod as far into the burrow as possible; (4) burrows were characterized as active (= 1) or inactive (= 2) on the basis of a visual assessment of the recency of burrow occupation, *e.g.*, a burrow that was filled with leaves or had spider webs across the entrance was classified as inactive, while one with fresh diggings was classified as active; and (5) the visibility of the burrow was ranked on a 3 point scale with 1 = a burrow that was clearly visible and conspicuous from a distance of several meters, 2 = a partially visible burrow, and 3 = a burrow that was hidden by foliage, debris, etc. We also noted the type of soil found in each plot but, because almost all plots had the same soil classification, these data are not presented here.

Population differences in burrow characteristics (pooled across habitat types) were analyzed with t-tests. In addition, we used t-tests to compare burrows between matching habitat types (*e.g.*, hammock versus rainforest, grassland versus field, etc). Variation in burrow characteristics between habitat types within each locale was analyzed with ANOVA.

Habitat use: Burrow densities in different habitat types provided some indication of habitat usage by armadillos. We sought to confirm this using data from sightings of live animals (cf. Loughry and McDonough 1998a). At both sites we censused the study areas during both daylight and evening hours (250 days for a total of 2 967 person-hours of field time in the U.S., in Brazil, 108 days and 958 person-hours). A daily census typically lasted 4-6 h and was conducted by walking or driving along trails or roads on each property. Spotlights and miner's lamps were used to observe animals after dark. The total linear distance censused was approximately 25 km at both sites. Cenuses at both sites passed through all habitat types. A rotating schedule of observations was used, such that a portion of the entire sampling area was censused each night, followed by another portion the next night, and so on until the entire area had been sampled. This schedule was then repeated for the duration of the field season.

We recorded the habitat in which every animal observed during these censuses was located. In many cases, we subsequently caught and marked these animals (for details, see McDonough and Loughry 1997a, Loughry and McDonough 1998a, b) so we were able to examine age (juvenile, *i.e.*, young of the year, versus adult) and sex differences in habitat usage. We were able to assign individuals that were observed but not caught to age categories on the basis of body size and, if the genitalia were visible, we could classify the individual by sex as well. In some cases, we were unable to obtain any information on the identity of an animal. These individuals were included in the total count of animals observed in each habitat type, but were excluded from analyses of age or sex differences. Animals that were caught were marked with reflective tape for long-range identification. To avoid pseudoreplication, resightings of these animals on the same day were ignored. Although we tried to avoid sampling the same areas repeatedly on the same night, we can not be sure that all of our sightings of unmarked animals represented different individuals, so our estimates of habitat usage may be slightly inflated. In Brazil, we also noted the species of each animal sighted. However, adult *D. septemcinctus* are about the same size as juvenile *D. novemcinctus* (Wetzel 1985), so visual identification from a distance is difficult. In this study, we only included animals that we could positively identify.

We did not sample all four habitats at either site with equal frequency. To analyze habitat usage, we first determined the percentage of each habitat type found along our census routes. This was done by recording at 20 m intervals the type of habitat(s) found along each side of the road or path being sampled. These percentages allowed us to calculate the expected number of armadillos in each habitat type (total number of individuals observed across all habitats x proportion of entire study area comprised of that particular habitat), assuming the animals were distributed randomly. Comparisons of the overall distribution of armadillos observed with these expected values were analyzed with contingency tables, while comparisons between observed and expected frequencies for a particular habitat were analyzed by calculating Z scores (Bhattacharyya and Johnson 1977). In Florida, where we had a much larger sample to work with (see below), we further analyzed distributions of animals for each age/sex group separately and for each year of the study.

There is a potential problem with the above analyses. If armadillos were more detectable in some habitats than others, our results could reflect differences in detectability rather than differences in habitat usage. We consider this unlikely for the following reasons. First, while visibility does vary between habitats (Loughry and McDonough 1998a), armadillos are quite noisy as they forage, making them conspicous even when they are not initially visible. In many cases, we first detected armadillos aurally and followed them until they came into view. Thus, we are reasonably confident that, in all habitats, we were able to detect all armadillos within 25-30 m of the road or trail we were surveying. Second, if detectability was the primary determinant of our results, one would expect the most observations of armadillos in the habitats where they should be most detectable (*e.g.*, open fields). In fact, this was not the case (see below), suggesting that our results can not be due solely to differences in detectability.

Prey availability: Nine-banded armadillos feed primarily on invertebrates they find while digging in the soil (Kalmbach 1943, Clark 1951, Fitch *et al.* 1952, Breece and Dusi 1985, Redford 1985, Sikes *et al.* 1990, White 1992, Lippert 1994). We sought to determine if habitat usage was related to prey availability by sampling terrestrial invertebrates in each of the plots censused for burrows. In each plot, a jar filled with 70% alcohol was placed in the soil and a 12.4 cm diameter funnel was placed on the top of the jar so that the top of the funnel was level with the ground. These pitfall traps were left in the plot for 48 hr and then removed. Trap contents were identified to family for insects and order for non-insects. The total number (*i.e.*, abundance), biomass (in g dry weight), and diversity of invertebrates found in each sample were recorded and compared between habitat types with ANOVA. Species diversity was calculated using the Shannon index (Smith 1992). Pitfall traps were only set out at Tall Timbers, so no data from Brazil were included in these analyses.

RESULTS

Burrow characteristics: Armadillo burrows were more numerous, less visible, less active, and had smaller openings in Brazil than in the U.S. when data from all habitat types were combined (t-tests, all $p < 0.005$, Table 1). The difference in burrow density between Brazil and the U.S. was due to the larger number of inactive burrows per plot in Brazil (mean ± SD = 3.33 ± 3.25 versus 1.12 ± 1.22, $t = 4.01$, $p < 0.0001$, $df = 78$). The proportion of active burrows (number of active burrows per plot divided by the total number of burrows in each plot) was significantly higher at Tall Timbers than at Poço das Antas (0.38 ± 0.35 versus 0.21 ± 0.28, $t = 2.19$, $p = 0.03$, $df = 62$; note that plots containing no burrows were excluded from this analysis).

Comparisons between comparable habitats showed that burrow densities were higher in Brazil in each case except for

TABLE 1

Mean (± SD) densities and characteristics of armadillo burrows found in each of four habitat types in Brazil and the United States

Habitat	Density	Width (cm)	Height (cm)	Length (cm)	Visibility	Activity
Florida						
Field	0.30 (0.68)	20.50 (3.50)	15.33 (5.69)	52.83 (21.10)	2.67 (0.58)	2.00 (0.0)
Wetland	3.30 (2.79)	19.38 (5.96)	15.02 (3.61)	62.79 (32.22)	1.52 (0.67)	1.46 (0.51)
Upland pine	1.70 (1.89)	21.03 (4.57)	15.79 (2.74)	53.00 (19.34)	1.94 (0.56)	1.59 (0.51)
Hammock	2.70 (2.06)	19.00 (4.87)	15.38 (4.28)	55.28 (19.14)	1.78 (0.85)	1.63 (0.49)
Brazil						
Grassland	2.10 (2.23)	15.33 (2.29)	11.74 (2.15)	55.26 (20.81)	2.52 (0.75)	1.81 (0.40)
Swamp	2.90 (3.54)	17.90 (3.90)	14.28 (3.36)	57.57 (21.15)	1.79 (0.82)	1.83 (0.38)
Disturbed	4.40 (3.53)	15.99 (3.75)	12.21 (2.22)	66.00 (32.81)	2.07 (0.73)	1.82 (0.39)
Forest	6.90 (4.36)	18.12 (4.27)	14.30 (2.69)	56.72 (21.78)	1.97 (0.77)	1.81 (0.39)

swamps versus wetlands (t-tests, all $p < 0.05$; for the swamp-wetland comparison, $p = 0.78$; Table 1). However, burrow dimensions (height, width and length) did not vary between forests and hammocks or between swamps and wetlands (t-tests, all $p > 0.14$; Table 1). Burrows appeared less active in swamps in Brazil than in wetlands in the U.S. ($t = 3.23$, $p = 0.002$), but not in any other comparison (all $p > 0.06$; Table 1). Burrows in grassland and disturbed areas in Brazil had smaller openings (height and width) than those in fields and upland pine areas in the U.S. (t-tests, both $p < 0.04$), but did not differ in any other measure (all $p > 0.13$; Table 1).

Burrow density varied significantly between habitats in Brazil (ANOVA, $F = 3.64$, $p = 0.02$, df = 3, 36; Table 1). Pairwise post-hoc Scheffé tests showed that burrows were more numerous in forest than in grassland. Burrow width ($F = 4.69$, $p = 0.004$, df = 3, 159), height ($F = 9.47$, $p < 0.001$) and visibility ($F = 4.03$, $p = 0.009$) also varied between habitats. Post-hoc Scheffé tests of these analyses showed that burrow entrances were larger and more visible in forests and swamps than in grasslands or disturbed areas.

Burrow densities also varied between habitats at Tall Timbers (ANOVA, $F = 4.29$, $p = 0.01$, df = 3, 36; Table 1). The only significant pair-wise comparison with post-hoc Scheffé tests showed that burrows were more numerous in wetlands than in fields. There were no significant differences in burrow characteristics between habitats (ANOVAs, all $p > 0.22$, df = 3, 76) with the exception of visibility ($F = 3.27$, $p = 0.026$). However, this comparison yielded no significant post-hoc pair-wise comparisons with Scheffé tests.

Habitat use: Nine-banded armadillos were not randomly distributed across habitat types in Brazil ($\chi^2 = 26.7$, $p < 0.0001$, df = 3, Table 2). Instead, they were found more frequently than expected in disturbed woodland and less frequently than expected in grassland (Table 2; distributions did not differ from expected in swamp and forested habitats). There were few confirmed observations of *D. septemcinctus* ($n = 3$), however all sightings were either in grassland or disturbed habitats.

TABLE 2

*Numbers of nine-banded armadillos observed in each of four habitat types in Brazil. Expected numbers of animals, based on the percentage of each habitat type that was censused, are indicated parenthetically. *** Z score comparison, $p < 0.001$.*

Habitat type	Number observed
Forest	42 (35.33)
Disturbed	44 (28.19)***
Swamp	34 (39.81)
Grassland	1 (17.67)***

Habitat use was also non-random in the U.S. ($\chi^2 = 458.1$, $p < 0.0001$, df = 3), with armadillos found more often than expected in hammocks and wetlands and less often than expected in upland pine and fields (Z scores, all $p < 0.01$, Table 3). These results were derived from data pooled across all individuals and all years of the study. However, there were significant differences in habitat usage between adults and juveniles (all years pooled, $\chi^2 = 21.53$, $p < 0.0001$, df = 3) and between years of the study (all ages pooled, $\chi^2 = 27.06$, $p = 0.008$, df = 12). Further examination of these effects showed that habitat usage by adults did not vary between years ($\chi^2 = 14.16$, $p = 0.29$, df = 12), but did for juveniles ($\chi^2 = 50.15$, $p < 0.0001$, df = 12). Consequently, we compared adult and juvenile habitat usage separately.

Adults were not randomly distributed across habitat types when data from all years were pooled ($\chi^2 = 345.3$, $p < 0.0001$, df = 3) or when each year was examined separately (Table 3). Instead, adults were more commonly observed in hammocks and wetlands and less frequently in upland pine (Z scores for data pooled across all years, all $p < 0.0001$, Table 3). There was no significant difference between the observed and expected frequencies of adults in fields ($p = 0.395$, Table 3).

Habitat usage by juveniles varied yearly, so we analyzed the distribution of juveniles across habitats separately for each year (except for 1994 when too few juveniles were observed to permit analysis). Juveniles were non-randomly distributed across habitats in 1992 ($\chi^2 = 21.3$, $p < 0.0001$, df = 3), 1993 ($\chi^2 = 77.8$, $p < 0.0001$), and 1995 ($\chi^2 = 55.9$, $p < 0.0001$), but not in 1997 ($\chi^2 = 0.47$, $p = 0.93$; Table 3). In years with significant non-random distribution, juveniles, like adults, were found more frequently than expected in hammocks (Z scores, $p < 0.0001$ in each year) and swamps (ns in 1992, $p < 0.04$ in 1993 and 1995) and less frequently than expected in fields (ns in 1992, $p < 0.05$ in 1993 and 1995) and upland pine areas ($p < 0.003$ each year, Table 3).

TABLE 3

*Numbers of adult and juvenile nine-banded armadillos observed in each of four habitat types in northern Florida in each year of the study. Expected numbers of animals, based on the percentage of each habitat type that was censused, are indicated parenthetically. Chi-square values are from comparisons between expected and observed values within each year for each age group (too few juveniles were observed in 1994 to permit analysis, so this year is left blank). ** p < 0.001, *** p < 0.0001*

		Pine	Hammock	Wetland	Field	χ^2
Juveniles						
	1992	13 (27.6)	45 (27.6)	7 (5.5)	4 (8.3)	21.3***
	1993	0 (23.2)	56 (23.2)	0 (4.6)	2 (7.0)	77.8***
	1994	0 (6.0)	15 (6.0)	0 (1.2)	0 (1.8)	—
	1995	14 (40.8)	68 (40.8)	18 (8.2)	2 (12.2)	55.9***
	1997	10 (11.2)	13 (11.2)	2 (2.2)	3 (3.4)	0.47
Adults						
	1992	31 (75.2)	105 (75.2)	28 (15.0)	24 (22.6)	27.22***
	1993	40 (99.6)	151 (99.6)	35 (19.9)	23 (29.9)	41.09***
	1994	26 (56.4)	81 (56.4)	19 (11.3)	15 (16.9)	17.79**
	1995	42 (121.6)	194 (121.6)	45 (24.3)	23 (36.5)	64.69***
	1997	46 (123.6)	172 (123.6)	43 (24.7)	48 (37.1)	49.76***

While there were significant age differences in habitat usage by armadillos at Tall Timbers, we found little evidence of sex differences (Table 4). When pooled across all years of the study, there was no difference in the distributions of adult males and females across habitat types ($\chi^2 = 4.90$, $p = 0.18$, df = 3). The same was true when each year of the study was examined separately (Table 4). Juvenile males and females did differ in their distributions across habitats when all years were pooled ($\chi^2 = 11.28$, $p = 0.01$). However, separate examination of each year showed that male and female distributions only differed in 1992 (Table 4).

Prey availability: Data from two pitfall traps set out in fields and two in upland pine could not be analyzed. A total of 10 163 specimens were collected from the remaining 36 samples, representing 61 families of insects and 3 orders of other animals (primarily worms and frogs). However, there were no significant differences between habitat types at Tall Timbers and any measure of prey availability (Table 5).

TABLE 4

Numbers of male and female adult and juvenile nine-banded armadillos observed in each of four habitat types in northern Florida in each year of the study. Chi-square values are from comparisons between male and female distributions within each year (years in which too few individuals were observed to permit analysis are left blank). Because this table only includes individuals who could be positively identified as to both sex and age, sample sizes are smaller than those in Table 3. ** $p < 0.01$.

	Males				Females				
	Pine	Hammock	Wetland	Field	Pine	Hammock	Wetland	Field	χ^2
Juveniles									
1992	8	8	0	1	2	28	3	3	13.66**
1993	0	17	0	2	0	28	0	0	—
1994	0	1	0	0	0	12	0	0	—
1995	1	10	5	2	4	32	6	0	6.92
1997	4	7	0	1	3	3	1	1	2.02
Adults									
1992	7	17	8	8	3	32	4	10	6.91
1993	11	40	11	7	13	36	11	10	0.90
1994	13	19	7	5	5	17	3	2	2.63
1995	14	60	20	7	11	50	12	6	0.67
1997	16	40	17	19	9	31	8	10	1.51

TABLE 5

*Mean biomass (g dry weight, ± SD), abundance (number of individuals, ± SD), and species diversity (Shannon index, ± SD) of terrestrial invertebrates collected from pitfall traps in four habitat types at Tall Timbers Research Station, Florida. * ANOVA with 3, 32 df.*

	Pine	Hammock	Wetland	Field	p*
Biomass	0.43 (0.39)	0.38 (0.25)	0.41 (0.26)	0.61 (0.32)	0.44
Abundance	184.12 (118.0)	297.80 (252.6)	470.20 (702.2)	126.25 (108.0)	0.29
Diversity	2.61 (0.42)	1.89 (0.78)	2.25 (1.04)	2.72 (0.36)	0.09

DISCUSSION

We have shown previously that there are considerable differences in the morphology and behavior of nine-banded armadillos at Poço das Antas and Tall Timbers (Loughry and McDonough 1998a). The present paper shows that there are a number of similarities as well. In both locales, nine-banded armadillos dug burrows of similar dimensions and were found more often in forested habitats than those that were more open. However, burrows were more numerous in Brazil. More detailed analysis of habitat usage in Florida showed some evidence of age, sex, and temporal differences, suggesting that considerable variation may exist in patterns of habitat use. Data from pitfall traps suggest that prey availability may not be one of the more important factors contributing to this variability.

In general, our data are consistent with earlier reports. For example, burrow dimensions from Tall Timbers were similar to those reported from other populations in the U. S. (Clark 1951, Talmage and Buchanan 1954, Layne 1976, Galbreath 1980, Zimmerman 1990, Guyer and Hermann 1997). These studies also found that burrows were most commonly located in hardwood/riparian habitat (Fitch *et al.* 1952, Schaller 1983, Zimmerman 1990, but see Galbreath 1980). Likewise, several studies in which sightings of armadillos were collected indicated a higher abundance in hardwood/riparian habitats (Schaller 1983, Breece and Dusi 1985, Inbar and Mayer in press), just as found in the present study.

Age, sex, and temporal differences in the numbers of armadillos observed in different habitat types at Tall Timbers are difficult to explain. Indeed, the difference between juveniles and adults may be more apparent than real because, in years when juveniles exhibited a significant difference in habitat usage, they exhibited the same pattern as adults (Table 3). Thus, the difference between juveniles and adults is probably due to the fact that, in 1997, juveniles exhibited no bias in habitat usage. It is not obvious why this occurred, but more data from additional years will be required to determine if juveniles consistently differ from adults. Along the same lines, habitat usage differed between juvenile males and females overall but, when each year of the study was examined separately, a significant difference was found only in one year (1992, see Table 4). Consequently, it appears that males and females generally have similar patterns of habitat usage most of the time.

The lack of differences in burrow dimensions across habitat types in Florida may indicate that (a) juveniles occupy burrows dug by adults, or (b) juveniles do not begin digging burrows until they are close to adult size. Comparisons of burrow dimensions between matching habitat types in Brazil and Florida showed no differences between hammocks and forests and between swamps and wetlands. However, burrows in grasslands and disturbed areas in Brazil had smaller openings than those in fields and upland pine areas in the U.S. These findings suggest that *D. novemcinctus* is found primarily in swamps and forests in Brazil, while its smaller congener, *D. septemcinctus*, occupies grasslands and disturbed areas. While we can not exclude the possibility that the smaller burrows found in these latter areas were constructed by juvenile *D. novemcinctus*, this seems unlikely because we found no indication of age-related variation in burrow dimensions in the U.S. It is also possible that *D. septemcinctus* may utilize burrows dug by *D. novemcinctus*, but we have no data to suggest that this occurs. Data from sightings of *D. novemcinctus* in Brazil support the inferences about habitat usage derived from burrows, although more individuals were observed in disturbed habitat than expected (Table 2). This may have occurred because swamp and forest habitats were not continuously connected, forcing the animals to move through disturbed areas to reach additional patches of swamp or forest.

Overall, burrow density was much greater in Brazil than in Florida. This was surprising because the abundance of armadillos (in terms of numbers of animals observed per hour of observation) was much greater in the U.S. (Loughry and McDonough 1998a). However, additional analyses indicated that the difference in burrow density was due to a much larger number of inactive burrows in Brazil and that the proportion of active burrows was actually higher in the U.S. Thus, it appears that the high density of burrows in Brazil may be due to a small number of individuals digging many burrows, many of which then fall into disuse. Such a pattern would be consistent with that reported for other species of armadillos in Brazil (Carter and Encarnaçao 1983). However, it is not obvious why *D. novemcinctus* digs so many more burrows in Brazil than in the U.S. At present, we can identify at least three possibilities. First, armadillos may have more predators (including humans) in Brazil (Loughry and McDonough 1997, 1998a), so they might dig more burrows as possible refuges. Second, because burrows are relatively permanent structures (Guyer and Hermann 1997), it may be that burrow density reflects the length of time armadillos have occupied an area. *D. novemcinctus* colonized Tall Timbers in the early 1970's (Stevenson and Crawford 1974). Armadillos evolved in

South America (Wetzel 1982, 1985) and the Atlantic coastal rainforest represents an ancestral habitat, so presumably armadillos have occupied Poço das Antas for considerably longer than at Tall Timbers. Finally, because armadillos sometimes construct above ground nests (Layne and Waggener 1984), particularly in areas prone to flooding, it is possible that differences in burrow density between our two sites represent differences in the use of above ground nests as alternatives to burrows. This leads to the prediction that above ground nests should be more common at Tall Timbers. However, we have observed very few nests there (pers. observ.). Armadillos at Poço das Antas also use above ground nests (C. Ruiz-Miranda pers. comm.), so it seems unlikely that differential utilization of above ground nests could explain the population differences in burrow density we report. Regardless of the explanation for the difference in burrow density between the two sites, our data do point out serious shortcomings in using burrow densities alone to infer population size (cf. Hoogland 1981, Burke 1989, Breininger *et al.* 1994, Vanhorne *et al.* 1997), although counts of active burrows may be more accurate than counts of all burrows.

Finally, our data provide no insight into why nine-banded armadillos seem to use certain habitats more than others. Individuals seem to spend much of their time above ground foraging (pers. observ.), so prey availability would seem a logical explanation for differences in habitat use. However, we could find no differences in the availability of terrestrial invertebrates between habitat types at Tall Timbers. It is possible that armadillo distributions are influenced by prey that were not adequately sampled by our pitfall traps, *e.g.*, invertebrates found either underneath or above the soil rather than on the surface. The former possibility seems unlikely because, in a pilot study, we took a 30 cm^3 soil sample from each habitat type and found very few potential prey items in these samples. However, the latter hypothesis may have some merit because armadillos do feed on invertebrates found within rotting logs and these prey would not have been sampled by our pitfall traps. Thus, the availability of rotting logs (which presumably would be common in hammocks and wetlands) might influence habitat usage by armadillos. Of course, it is also possible that the quality of available prey is more important than just the quantity of prey. While many of the same families of insects were found in all habitat types, there were some differences in species composition between habitats (P. Q. Le and M. S. Blackmore unpublished data) that could influence armadillo distributions. In addition, it is important to remember that prey availability may not be the sole determinant of habitat usage by armadillos. For example, armadillos might be more frequent in swamps/wetlands because these areas have soil that is easy to dig in (thus lowering foraging costs) or because they provide access to the fresh water that armadillos seem to require (McDonough and Loughry 1997b). Armadillos might occur more often in hammocks/forests because the open understory provides antipredator benefits, perhaps by allowing the detection of predators sooner and from a longer distance (McDonough and Loughry 1995), or by minimizing the conspicuousness of the animals as they move through the environment. These suggestions are necessarily speculative. Additional study will be required to test these ideas and explain why armadillos are not randomly distributed across habitat types.

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