

Spatio-temporal trends in armadillo diurnal activity and road-kills in central Florida

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Abstract Armadillos (*Dasypus novemcinctus*) are one of the mammals most commonly found dead along Florida highways. Thus, they may serve as a model to study which factors are affecting wildlife road-kills. Armadillo diurnal activity and road-kills were examined along a 168.9-km stretch of the Ronald Reagan Turnpike in Florida. We conducted 49 surveys during a 13-month period (3–5 surveys/month), with 143 road-kill incidents and 173 observations of active armadillos. Activity and road-kills were spatially and temporally correlated with several factors. Rate of armadillo road-kill was from interactions among temperature, vegetation coverage, and traffic volume. During winter (November–March), armadillos are more diurnal and generally less active, thus they are less likely to be killed by vehicles. Armadillo activity in these months was concentrated near habitat with dense woodlands. In summer, armadillos are predominantly nocturnal and apparently more active. Consequently, their road-kill rates nearly doubled and were highly correlated with traffic volume, but not with vegetation. Of all the traffic-volume data sets, mean nighttime traffic generated the only significant correlation with road-kills. Traffic did not affect armadillo diurnal activity. Our study demonstrated how the relative importance of the factors affecting road-kill changed temporally. Spatial analyses suggested that armadillos are more dispersed during summer.

Key words armadillo, diurnal activity, Florida, road-kills

The rapid expansion of roads and the increase in traffic volume create a serious human-wildlife conflict worldwide. This conflict causes hundreds of human casualties and multibillion-dollar damage costs annually. Wildlife populations may be severely affected by road-kill losses and habitat fragmentation (Mader 1984, Drews 1995, Groot Bruinderink and Hazebroek 1996). It also was suggested that vehicles and road infrastructure could accelerate the evolution 2-dimensionality in vertebrates (Yom-Tov 1997). Wildlife road-kills may be affected by several factors, such as speed limits, traffic volume, right-of-way structure, weather conditions, the nature of surrounding habitat, and vegetation cov-

erage. Species-specific biological and ecological traits also may contribute to road-kill rates. Phenology (diel, seasonal, and annual) of feeding activity, breeding, dispersal, and migration may affect the chance of collisions with vehicles (Carbaugh et al. 1975, Case 1978, Fahrig et al. 1995). Therefore, the relative importance of each of these factors on road-kills of particular wildlife species often varies.

Road-kills are a frequent cause of mortality of endangered species in Florida. For example, nearly half of the reported deaths of the Florida panther (*Puma concolor coryi*) are from collisions with vehicles (Foster and Humphrey 1995). The armadillo

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(*Dasypus novemcinctus*) is one of the most common mammals found dead along Florida highways (Galbreath 1982, Cristoffer 1991) and thus may serve as a model to study factors associated with wildlife road-kills. Their frequent road-kills may be related to their tendency to jump upward when suddenly alarmed. Even if not hit by the wheels, they may die by hitting the undercarriage of the vehicle (Kalmbach 1944). In addition, because armadillos do not generate eyeshine, drivers may not spot them in time to avoid a collision (W. J. Loughry, Valdosta State University, Valdosta, Georgia, personal communication). This study examined the relative importance of and interactions among several biotic and abiotic factors that may be associated with armadillo road-kills in central Florida and how they change temporally. These factors included vegetation coverage, soil pH, weather, and traffic volume. Because armadillo activity is influenced by weather conditions such as cloud cover, temperature, wind speed, precipitation, and relative humidity (McDonough and Loughry 1997), we hypothesized that weather-related behavior would interact with habitat characteristics and traffic to affect incidence of road-kills.

The common long-nosed (nine-banded) armadillo (*Dasypus novemcinctus*) is the only member of the family *Dasypodidae* found in the United States. Since it first invaded southern Texas in the middle of the eighteenth century, the armadillo has extended its range into the southeastern United States, where it occupies many habitats (Humphrey 1974, Taulman and Robbins 1996). Armadillos that probably escaped from captivity were first reported in Florida in the early 1920s (Neill 1952). Despite their abundance throughout Florida, excluding the Everglades (Taulman and Robbins 1996), little is known about their ecology (Layne and Glover 1985, McDonough and Loughry 1997).

Methods

We conducted the research in central Florida along the Ronald Reagan Turnpike between Interstate 95 (milepost 154) near Fort Pierce north to Interstate 4 (milepost 259) near Orlando (Figure 1). The reach spanned 168.9 km within St. Lucie, Indian River, Okeechobee, Osceola, and Orange counties. This portion of the turnpike serves as a main connector between southeast Florida (Miami area) and central Florida. The highway was 4 lanes with an enforced speed limit of 112.6 km/hour.

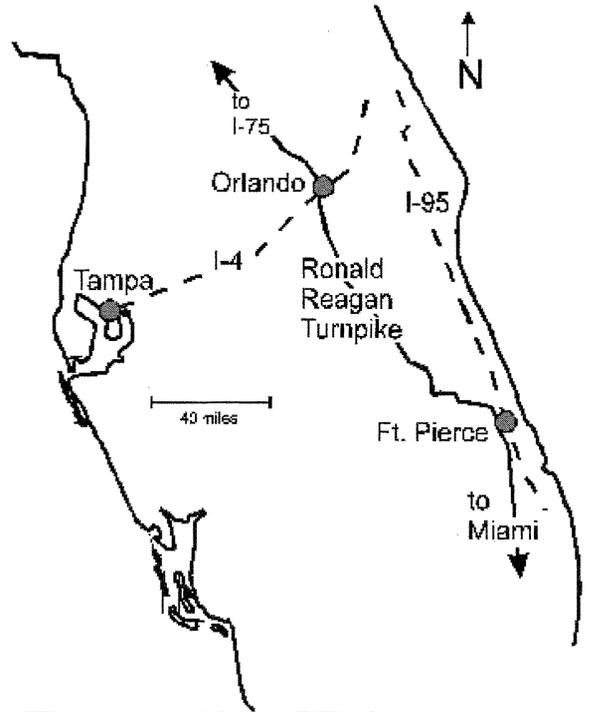


Figure 1. Area of the study to examine armadillo road-kills in central Florida extended along the Ronald Reagan Turnpike between Interstate 95 in the south near Fort Pierce and Interstate 4 near Orlando in the north.

Topography along the highway was flat with frequent creeks, bridges, and water culverts. The surrounding habitat varied between citrus groves (St. Lucie and Indian River counties in the south), prairie-type grassland that was improved to pasture land, suburban areas (mainly in Orange county toward I-4), and relatively undisturbed woodlands. The woodlands were composed of a natural mosaic of flatwoods, hardwoods, and intermediate scrubby communities. Dominant trees were slash pine (*Pinus elliottii*) on higher elevations and bald cypress (*Taxodium distichum*) scattered in isolated stands in lower areas. The shrub vegetation was greatly variable; saw palmetto (*Serenoa repens*) and scrub live oak (*Quercus geminata*) were among the dominants. Common grasses on the right-of-way were bahia grass (*Paspalum notatum*) and caesar weed (*Urena lobata*). Brazilian pepper (*Schinus terebinthifolius*), paper tree (*Melaleuca quinquenervia*), and willows (*Salix sp.*) were often found near the edge of the right-of-way, mostly in roadside ditches.

We conducted 49 surveys (3–5 surveys/month) from January 1996 through January 1997. We per-

formed surveys from Orlando to Ft. Pierce between 0700 and 1000 hours, and from Ft. Pierce to Orlando between 1400 and 1700 hours. Highway maintenance crews keep vegetation in the right-of-way low by frequent mowing, enabling easy observation of active armadillos while driving. We recorded time and location of active armadillos on the grassy right-of-way, and road-kills. We defined location using the survey vehicle odometer (± 80 m), eliminating the problem of re-counting the same (dead) individual in the next survey. Counts of live and road-killed armadillos within each mile were pooled before analyses.

Data on traffic volume were provided by the Turnpike Authority through URS Consultants, Inc., Tallahassee, Florida. Data were collected hourly during the year, but were not available for February 1996. Mean monthly traffic volumes on the southbound and northbound lanes were similar (Paired $t=0.004$, $df=11$, $P=0.97$) and were therefore pooled. We used 3 scales of traffic volume: average daily traffic, ADT; average hourly daytime traffic, AHLT (0600–1800 hours); and average hourly nighttime traffic, AHNT (1800–0600 hours). Mean monthly AHLT was 43% greater than AHNT (Paired $t=18.5$, $df=11$, $P<0.01$). When we analyzed road-kills on a per-survey basis, they were correlated with traffic volume during the intervals between rides.

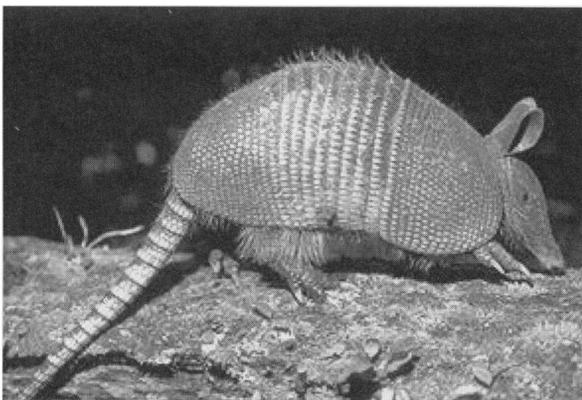
Vegetation cover ranking of the area within approximately 100 m of the right-of-way edge was determined perpendicularly away from each milepost. Ranking was the mean of the values obtained for the northbound and southbound sides of the road and was based on a 0–5 scale, where 0=habitat covered only with grasses (mainly pasture land) without bushes or trees; 1=grassy habitat with

infrequent bushes or trees that covered up to 10% of the area; 2=grassy habitat with trees and bushes covering 10–40% of the area; 3=tree coverage without lower vegetation of bushes and grasses, i.e., citrus groves; 4=mixed vegetation of trees and bushes covering 40–80% of the area; and 5=fully developed stands of hardwood and flatwoods with a dense shrub layer covering 80–100% of the examined area.

Armadillos feed on invertebrates, which they find by digging in the top 10 cm of the soil (Wirtz et al. 1985). Most soil-dwelling arthropods avoid extreme acidic or alkaline habitats (e.g., van Straalen and Verhoef 1997), thus pH was used to evaluate soil quality. On 17 January 1997, 2 soil core samples were taken to a depth of approximately 5 cm from the grassy right-of-way, 4 m from each milepost. Soil was sealed in 30-ml plastic cups. We mixed 25 ml of deionized water with 25 g of soil in 90-ml vials. Samples were stirred vigorously and allowed to sit for 30 minutes and then stirred again. After an additional 30 minutes, pH was determined using a Corning 350 pH-ion analyzer.

Daily temperatures (mean, minimum, and maximum), rainfall, relative humidity, wind speed, and barometric pressure data were provided by the Southwestern Regional Climate Center from data collected at the Orlando International Airport, located near the northern edge of the study site. Road-kills were correlated with the mean climatic data recorded during the intervals between surveys; diurnal activity was correlated with the climatic data on the same survey day.

We used multiple regression and correlation analyses (Sokal and Rohlf 1981) to test effects of spatial and temporal factors on armadillo activity and road-kills. Numbers of road-killed and active armadillos were normalized using a square-root transformation before analyses. We estimated the degree of clumping of diurnal activity and road-kills by the index of dispersion (ID, Ludwig and Reynolds 1988), $ID=S^2/\bar{x}$, where \bar{x} and S^2 are the mean and variance, respectively, of the frequency distribution of active and killed individuals within each mile. ID was compared to a Poisson series for randomness using the d statistic for large sample size ($n \geq 30$). Green's index (GI), which estimates clumping independent of sample size (n), was calculated as $(ID-1)/(n-1)$. $GI=0$ indicates complete randomness, and $GI=1$ is maximum clumping. As a measure of armadillo distribution along the high-



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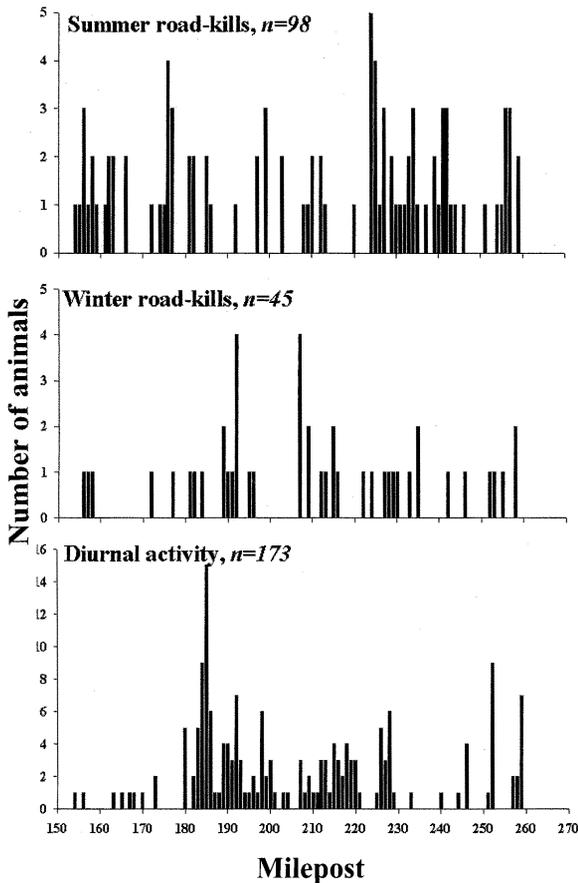


Figure 2. Spatial distribution of diurnally active and road-killed armadillos along the survey route. Data are described per milepost to maintain the association with the actual habitat along the highway.

way, Levins' formula of Niche breadth (B) was calculated (Ludwig and Reynolds 1988), $B = 1 / \sum P_i^2 \times S$, where P_i is the proportion of individuals reported in milepost i and S is the number of mileposts ($S=106$). $B=1$ indicates maximal distribution along all habitat units (mileposts).

Results

We observed 143 road-killed and 173 diurnally active armadillos during the study. Active and dead armadillos were recorded along 89 different mileposts distributed throughout the route, indicating that they are widely distributed throughout the area (Figure 2). More than 71% of the active armadillos were alone (no other animals were recorded within a 100-m strip of right-of-way), 19.5% were groups of 2, 7% were groups of 3, and in one case (1.7%) there was a group of 4 (possibly

siblings because armadillos give birth to quadruplets). In 2 incidents, 2 armadillos were found dead less than 100 m apart (in the same survey); the rest were scattered individuals.

Temporal distribution

Seasonal activity was observed from November through March (winter), with a peak in January and February (Figure 3c). Excluding one observation in April, no active animals were observed in the right-of-way in summer (April–October). Mean monthly maximum (data not shown) and minimum temperatures (Figure 3a) were negatively correlated with mean monthly diurnal activity ($r=-0.89$, -0.88 , $P<0.01$, respectively). Only 6 of the 173 active armadillos were observed during the cool morning hours between 0700 and 1000 hours ($\chi^2=146.1$, $df=1$, $P<0.01$). On a survey basis, diurnal activity was correlated with the climatic factors, but not with traffic (Table 1, $R^2=65.0$, $F_{10,34}=9.26$, $P<0.01$). Thus, traffic volume did not affect diurnal activity.

Mean monthly road-kills displayed an opposite trend. Road-kills were more frequent during summer (3.7 dead/survey) compared with winter (1.95 dead/survey, Mann-Whitney U test $Z=2.24$, $P=0.024$). Road-kills peaked in midsummer (June–August) and declined in September (Figure 3d). ADT (average daily traffic) was greatest in December, March, and June–August and sharply decreased by 30% in September (Figure 3b). Mean monthly road-kills were correlated positively with mean monthly temperatures ($r=0.56$, $P=0.023$), but were not correlated with mean monthly ADT ($r=0.32$, $P=0.31$). On a survey basis analysis, multiple regression indicated ($R^2=39.0$, $F_{8,40}=3.4$, $P=0.004$) that road-kills were correlated positively with temperatures, but not with other climatic variables (Table 1). AHNT was the only traffic data set that was correlated significantly with total road-kills (Table 1).

Spatial distribution

Because of the sharp seasonal shift in armadillo diurnal activity, the road-kill data were arranged according to summer and winter and re-analyzed. Summer and winter road-kills differed in many aspects and were not correlated spatially ($r=0.087$, $P=0.44$, Figure 2). Winter road-kills were correlated spatially with diurnal activity ($r=0.25$, $P<0.01$) and vegetation coverage (Table 1), but were not correlated temporally with either the climate or traffic factors measured (Table 1). In contrast, summer road-kills were not correlated spatially with diurnal

Table 1. Temporal and spatial factors associated with diurnal activity and road-killed armadillos presented as Pearson's correlation coefficient.

Factors	Diurnally active (n=173)	Total road-killed (n=143)	Summer road-killed (n=98)	Winter road-killed (n=45)
Temporal^a				
Temp. (max.)	-0.84 ***	0.43 ***	0.51 **	0.17
Temp. (mean)	-0.85 ***	0.42 ***	0.42 ***	0.15
Temp. (min.)	-0.84 ***	0.41 ***	0.41 *	0.13
ADT	-0.23	0.21	0.41 *	-0.13
AHNT	-0.14	0.33 *	0.38 *	-0.09
AHLT	-0.32	0.19	0.44 *	-0.09
Rainfall	-0.26	0.07	-0.001	-0.03
Relative Humidity	-0.49 **	-0.06	-0.01	-0.07
Wind speed	0.37 ***	-0.02	0.039	0.17
Barometric pressure	0.51***	0.12	0.18	-0.08
Spatial^b				
Soil pH	-0.01	0.01	-0.03	0.18
Vegetation rank	0.41 ***	0.09	-0.05	0.24 *

^a Conducted on a per survey basis.

^b Conducted on a mile-post basis (n=106 mile-posts).

*=P<0.05; **=P<0.01; ***=P<0.001; no *=not significant, P>0.5.

(winter) activity (r=-0.169, P=0.11) or vegetation coverage, but were temporally correlated positively with traffic volume and temperature (Table 1).

Mean soil pH along the right-of-way was 7.4±0.9 (range 3.8–8.3), but was not correlated with number of live or dead armadillos (Table 1). Multiple regression analyses indicated that diurnal activity was correlated positively with vegetation coverage (R²=18.0, F_{2,101}= 10.32, P<0.01, Table 1), peaking in undisturbed habitats with dense vegetation. The greatest level of diurnal activity was observed within the 180–193 milepost range (Figure 2), which was characterized by undisturbed woodlands and dense scrub community (mean vegetation rank=4.6). Narrower and smaller diurnal activity counts were found in mileposts 252 and 259 (suburban Orlando), near areas with great vegetation rank. Low diurnal activity was associated with low vegetation coverage or managed habitats (pasture and citrus grove). The section between mileposts 230 and 245 had low diurnal activity and 2.4 vegetation coverage rank. The predominantly citrus grove area that stretches between mileposts 159 and 170 deserves special attention. Despite its tree coverage (average rank 3.1), active armadillos were observed only rarely (5 cases), less than expected

by chance (χ²=9.2, df=1, P<0.01, expected diurnal active/mile was 173/106= 1.63).

Neither pH nor vegetation cover was correlated with road-kills (R²=1%, F_{2,101}=0.45, P= 0.63, Figure 1, Table 1). Consequently, there was no correlation between the spatial distributions of live and road-killed (total) armadillos along the highway (r=0.04, P=0.73). Fewer road-kills occurred in the citrus grove area (8 cases) at mileposts 159–170, but this was only significant marginally (χ²=3.07, df=1, P=0.07, expected road-kills/mile was 143/106 =1.35).

Armadillo niche breadth, as measured by the distribution of road-kills, indicated that summer distribution was twice as wide as in winter. Road-kills were scattered along 34 different 1-mile intervals during winter and along 54 1-mile intervals during summer. Road-kills were not clumped as indicated by low GIs. Diurnal activity GI was 4 times greater than those calculated for road-kills, suggesting clumping (Table 2) near areas with great vegetation coverage (Table 1).

Table 2. Niche breadth (B) and indices of clumping of diurnal active and road-killed armadillos along different mile-posts. Diurnal activity was observed in winter only.

	Diurnal active	Road-killed (winter)	Road-killed (summer)	Road-killed (total)
Niche breadth	0.34	0.21	0.4	0.49
Index of dispersion ^a	3.58	1.34	1.39	6.68
	χ ² =10.1 ***	χ ² =0.52	χ ² =0.24	χ ² =20.1**
Green's index ^b	0.015	0.004	0.003	0.004

^a Significant Index of Dispersion (ID) rejects the agreement with a Poisson random distribution and thus suggests clumping.

^b Green's index (GI): corrects the bias of different sample sizes.

^c**=P<0.01; no *=not significant, P>0.5.

Discussion

A uniformly, widely distributed armadillo activity was found across the studied portion of the highway. Evidently, even Florida's mild winters alter armadillo activity patterns. Right-of-way diurnal activity (before 1700 hours) was restricted to winter. Several studies observed seasonal shifts in armadillo activity which were explained by intolerance of low temperatures (Fitch et al. 1952, Breece and Dusi 1985, Layne and Glover 1985). It should be emphasized that in Florida, armadillo diurnal activity, especially of juveniles, can be observed during summer (McDonough and Loughry 1997; Inbar, personal observations). However, most armadillo activity occurs after 1700 hours in early evenings to sunset (McDonough and Loughry 1997). Layne and Glover (1985) reported that summer armadillo diurnal activity was limited to shaded spots and avoidance of open areas (like the right-of-way). Conversely, sunny patches were preferred during winter.

Calculated niche breadth using summer road-kills was nearly twice as wide as in winter (Table 2). During winter, armadillo activity, as indicated by road-kills and diurnal activity along the right-of-way, was limited to habitats with great vegetation cover and expanded as temperature increased. Similar observations of reduced activity, reduced spatial distributions, and deaths of armadillos during winter have been reported from Alabama (Breece and Dusi 1985), Florida (Layne and Glover 1985), Louisiana (Fitch et al. 1952), and Texas (Clark 1951). Nevertheless, we do not know whether road-kills and right-of-way activity accurately represent armadillo abundance in the surrounding habitats. However, armadillos do prefer habitats consisting of areas with dense woody vegetation coverage and rich, wet soils, whereas open habitats are often avoided (Neill 1952, Layne and Glover 1985, Taulman and Robbins 1996). Taulman and Robbins (1996) argued that the replacement of grassland by woody vegetation in southern Texas might have promoted armadillo invasion from Mexico in the last century. The only study that compared road-kills and actual armadillo populations found that summer road-kills may serve as a general indicator of the population structure, although juveniles and yearlings are not likely to be killed (Loughry and McDonough 1996).

In winter, armadillos are more diurnal and in general less active, with smaller home ranges (reduced movement), reducing the chance of collisions with

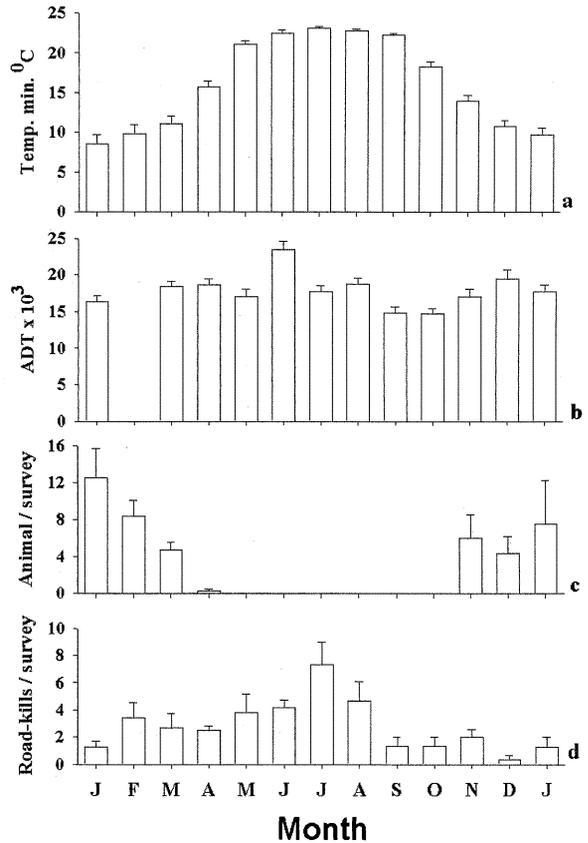


Figure 3. Temporal trends in armadillo abundance and its correlative factors. Mean monthly minimum temperature (a), mean monthly average daily traffic (b), mean monthly diurnally active armadillo/survey (c), and mean monthly number of observed road-kills (d) are given from January 1996 to January 1997 (mean \pm 1 SE), on Ronald Reagan Turnpike in Florida.

vehicles. This study could not clearly distinguish between the temporal and spatial trends in armadillo activity and road-kills. The effect of winter traffic volume was probably masked by temperature-related behavior, whereas in summer, nocturnal activity increased the relative importance of traffic. This trend can be most clearly demonstrated in September and October. Although the animals are still nocturnal, rate of armadillo road-kills fell dramatically in these months, probably from the reduced traffic in the post-tourist season in central Florida (Figure 3). The association with vegetation also may change with season. During winter, armadillo distribution was clumped near the natural very dense woodlands. At that time, road-kills were spatially correlated with diurnal activity. Summer road-kills were scattered across a larger area and were only weakly associated with vegetation coverage. It was unclear why right-of-way winter activity clumped near habitats with developed

vegetation, but this may reflect the availability of soil-dwelling invertebrates (not evaluated in this study).

Occasionally, armadillos may be observed in central Florida citrus groves (Neill 1952, Galbreath 1982). We found that the groves, despite the dense tree coverage, are not favorable habitats for armadillos, especially during winter. The low (though significant) R^2 values obtained in the correlation analyses between armadillo activity and vegetation rank are mainly because of the citrus groves. Pesticide applications and cultural practices may reduce armadillo food, i.e., soil-dwelling invertebrates in the groves. It is likely that lack of the understory vegetation layer in the groves also affects armadillo preference. Frequent grove disking that may destroy armadillo burrows could affect their activity in the groves. Similarly, Smith and Doughty (1984) noted that in Texas, armadillos were rarely seen in citrus groves.

The intuitive assumption that traffic volume directly affects animal road-kills has not been demonstrated in all studies. For example, amphibian (Fahrting et al. 1995) and white-tailed deer (*Odocoileus virginianus*, Allen and McCullough 1976) road-kills were correlated with traffic volume. In contrast, studies on raccoon (*Procyon lotor*, Rolley and Lehman 1992), European roe deer (*Capreolus capreolus*, Groot Bruinderink and Hazebroek 1996), and various other species (Case 1978, Cristoffer 1991) did not find associations between traffic volume and number of road-kills. The magnitude of traffic effects on road-kills may vary among animal species or be masked by other factors. One of the reasons for these ambiguous results may be the scale of traffic-volume data. Road-kills that are correlated with annual or monthly ADT or with data from a single date may not accurately represent the traffic volume the animals actually face (Allen and McCullough 1976). Our study demonstrated the importance of the scale of traffic data used for analysis. Monthly and per-survey ADT were not correlated significantly with armadillo road-kills, whereas per-survey AHNT was highly significant (Table 1). The importance of AHNT was as expected because most of the mammal-vehicle collisions occurred at night. Similarly, Allen and McCullough (1976) found that white-tailed deer road-kills were correlated with nighttime, not daytime, traffic volume.

Although the duration of this study was limited (13 months), some general predictions can be

drawn about where and when armadillo-car collisions will take place. Armadillos are most likely to be killed during summer, when the most dominant factor is nighttime traffic volume. The relatively rarer winter kills tend to occur near habitats with the great vegetation coverage of woodlands, habitats with extensive armadillo (diurnal) activity along the right-of-way.

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