Armadillo Diets Among Seasons and Between Habitats on Cumberland Island, Georgia

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Abstract: In the 1970s, the nine-banded armadillo (*Dasypus novemcinctus*) invaded Cumberland Island, Georgia, which includes a federally designated wilderness area where native flora and fauna are protected by the National Park Service. Because of concerns about the potential ecological effects of this exotic mammal on the island's protected ecosystems, we collected 171 armadillos to determine their diets by stomach content analysis. We measured relative amounts of each food on a seasonal basis for a sub-sample of armadillos from oak-palmetto ($N=44$) versus oak-pine ($N=43$) habitats. Food habits of these armadillos were similar to those reported for armadillos from other temperate environments. They primarily ate invertebrates, but 60 (35%) and 62 (36%) armadillos also ate fruits and vertebrates, respectively, during certain seasons. When combined across seasons and habitats, 8 orders of invertebrates represented 85% of the dry weight of foods consumed. Consumption of Diplopoda (millipedes) and Arachnida (spiders and scorpions) varied among seasons and between habitats. Consumption of Chilopoda (centipedes), Diptera (flies), and Orthoptera (crickets, roaches, and grasshoppers) varied among seasons but not between habitats. Consumption of Hymenoptera (ants and wasps), Coleoptera (beetles), Lepidoptera (butterflies and moths), and fruits was inconsistent (i.e., a season x habitat interaction) and varied depending on habitat and season. Our results provide baseline food habits data that can be used in future ecological assessments involving armadillos on this protected Atlantic coastal barrier island.

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Although historically present in south-central North America, Central America, and most of South America, the nine-banded armadillo *(Dasypus novemcinctus)* is now distributed widely in the United States (Taulman and Robbins 1996). It colonized much of Florida's eastern coast by 1951, including some Atlantic coastal islands

(Neill 1952). Although absent from Georgia's eastern coast in 1962 (Golley 1962), it was observed on Cumberland Island (CUIS) in 1973 (Hillestad et al. 1975) and now is abundant in most of the island's upland habitats.

About 80% of CUIS is designated a national seashore, which is managed by the National Park Service (NPS) for outdoor recreation and protection of native plant and animal communities. Therefore, exotic mammal ecology is of concern and has been the focus of previous research (Warren and Ford 1997, Goodloe et al. 2000). However, diet selection by this population of armadillos is unknown. Furthermore, diets of armadillos in Georgia, on an Atlantic coastal island, and from different but adjacent habitats within a geographical area are unreported. The objectives of our study were to (1) examine armadillo diets on CUIS (2) compare diets among seasons, and (3) compare diets between 2 distinct but adjacent habitats.

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Methods

Study Area

Cumberland Island is Georgia's largest (9,400 ha) and southernmost Atlantic barrier island. It is separated from mainland marshes by 1–2 km of open estuary. Major plant communities include salt marshes, barren dunes, shrub thickets, interdune meadows, and various forest associations. Live oak-palmetto *(Quercus virginiana-Serenoa repens)* and oak-pine (*Quercus* spp.-*Pinus* spp.) habitats comprise 74% of the island's upland forests (Hillestad et al. 1975). Live oak is the dominant tree in oak-palmetto habitat, whereas various oaks and pines are co-dominant in oak-pine habitat. Saw palmetto is the most common woody understory species in oak-palmetto habitat, whereas bamboo-briar *(Smilax auriculata),* muscadine grape *(Vitis rotundifolia),* and bayberry *(Myrica cerifera)* are most common in oak-pine habitat (Hillestad et al. 1975).

Field Collections

We collected 171 armadillos during 1–6 November 1986 (NOV), 27 December 1986 to 7 January 1987 (JAN), 22–28 March 1987 (MAR), 11–15 June 1987 (JUN), 27–30 August 1987 (AUG), and 13–16 December 1987 (DEC) from oak-palmetto and oak-pine habitats. Distribution of collection dates was selected based on logistical constraints (e.g., class and work schedules) and perceived seasonal differences in plant phenology and food availability. Armadillos were collected in daylight during cold weather and at night during hot weather to coincide with periods of their greatest activity (Layne and Glover 1985).

Collections were conducted from a vehicle driven slowly along low-use earthen roads. Armadillos were shot with a .22-caliber rifle. We noted the exact collection location for each armadillo on a habitat map. Carcasses were iced immediately, and dissected within 18 hours. We removed the stomachs and stored them frozen.

Diet Analysis

We incised thawed armadillo stomachs (*N* =171) and sorted their contents by size. We used a wet sieving and flotation process to separate various sizes of organic matter and sand. Contents remaining in the largest-mesh sieve were rinsed into a shallow basin of 1–3 cm water to facilitate sorting and identification. We identified insects to order and other invertebrates to class; vertebrates and fruits were identified to species. When possible, adult beetles were categorized to family. Using these data (*N*=171), we calculated frequency of occurrence (i.e., percentage of stomachs containing a food) for each food by season (i.e., seasonal frequency of occurrence; SFO) and for all seasons (i.e., total frequency of occurrence; TFO).

We also examined the quantity of foods consumed by a sub-sample of 87 armadillos collected from distinct oak-palmetto (*N*=44) and oak-pine (*N*=43) habitats. We selected these armadillos because they were collected ≥200m from habitat ecotones, thereby minimizing the chances that their home ranges overlapped habitats. We selected this buffer distance because armadillos on CUIS have average seasonal home ranges of 1.7 to 5.3 ha (Bond et al. 2000).

For the sub-sample of armadillos, we weighed foods retained by the largest-mesh sieve, and collected the small and fragmented organic matter (i.e., fine organic matter) from the smaller-mesh sieves. We viewed a sub-sample (5%–10% of the aggregate) of the fine organic matter under a 7–15× dissecting microscope to identify potential foods. Then, to estimate amounts of these foods, we removed and weighed the largest components of fine organic matter (small ants and larger fragments) until only unidentifiable fragments remained. We combined dead leaves, woody debris, and humus with unidentifiable fragments and classified this mixture as miscellaneous debris.

We oven-dried the sorted foods, sand, and miscellaneous debris at 55–60 C until weights stabilized (1–14 days). Then, we measured dry weights for each food in each stomach to the nearest 0.01 g. Foods present in quantities <0.02 g were recorded as trace items and added to miscellaneous debris before it was weighed. For each armadillo (*N*=87), we calculated percent dry weight (%DW) for each food by dividing the weight of the food by the summed weight of all foods and multiplying this quotient by 100.

We used SFO, TFO, and %DW data to characterize armadillo diets. We cannot address food preferences because we did not measure food availability. However, we acknowledge that food availability might have varied among habitats, which is why we stratified our collections by habitat.

Statistical Analysis

To test hypotheses regarding seasonal (i.e., collection month) and habitat-related differences in diets, we treated armadillos as replicates and compared %DW of foods with a 2-way ANOVA (SAS Inst. 1985). We included habitat-type as a factor in the model because of potential differences in food availability between habitats. We did not include sex or age as factors in our model because our primary objectives were to identify seasonally based differences in diets, rather than to test sex- or age-related sources of variation. Percent dry weights were arcsine-transformed before analysis. Tukey's studentized range test was used to identify pair-wise differences among season means. When the 2-way analysis revealed a significant season x habitat interaction for a food, we reanalyzed those data and tested for seasonal effects within each habitat with a 1-way ANOVA. Again, Tukey's test was used to identify pair-wise differences among season means. For all tests, significance was accepted at $P < 0.05$.

Results

Stomach Contents

We identified 18 armadillo foods. The SFO data for foods (Table 1) varied from 0% (i.e., not consumed during that season) to 100% (i.e., consumed by all armadillos during that season). In contrast, when combined across seasons, TFO data of foods varied from 3% (5 of 171) for Dermaptera (earwigs) to 99% (169 of 171) for Coleoptera (beetles) larvae and Hymenoptera (ants and wasps) eggs, pupae, and adults. Although we did not sort beetle larvae by family, we generally observed that white

Table 1. Seasonal frequency of occurrence (%) for foods within the stomachs of 171 armadillos collected from oak-palmetto and oak-pine habitats on Cumberland Island, Georgia during November 1986–December 1987.

Food	Nov 1986 (N=30)	Jan 1987 (N=28)	Mar 1987 (N=29)	Jun 1987 (N=26)	Aug 1987 (N=29)	Dec 1987 (N=29)
Ants, wasps	100	93	100	100	100	100
Beetle adults	100	100	97	92	97	97
Beetle larvae	100	96	100	96	100	100
Butterfly and moth larvae and pupae	100	93	100	100	86	100
Centipedes	100	26	93	65	97	97
Cicadas	20	12	21	31	14	14
Crabs	10	2	4	0	0	4
Crickets, roaches, grasshoppers	83	13	59	88	93	86
Earthworms	53	17	69	0	24	59
Earwigs	10	0	0	4	4	0
Fly larvae	90	28	100	46	52	97
Fruits	37	29	10	4	93	35
Millipedes	97	26	97	73	93	93
Slugs, snails	20	16	48	42	14	31
Sowbugs	17	12	45	35	14	17
Spiders, scorpions	67	23	76	88	41	90
Termites	13	7	41	6	17	21
Vertebrates	13	9	41	65	35	35

Table 2. Mean percent dry weight (%DW) of foods comprising >1.0% of the seasonal stomach contents of 87 armadillos collected from oak-palmetto and oak-pine habitats on Cumberland Island, Georgia, during November 1986–December 1987.

	November 1986				January 1987				March 1987				June 1987				August 1987				December 1987			
	Oak-palmetto (N=8)		Oak-pine (N=6)		Oak-palmetto (N=6)		Oak-pine (N=6)		Oak-palmetto (N=8)		Oak-pine (N=7)		Oak-palmetto (N=7)		Oak-pine (N=8)		Oak-palmetto (N=9)		Oak-pine (N=7)		Oak-palmetto (N=6)		Oak-pine (N=9)	
Food	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE	%DW	SE
Ants, wasps[a]	11.9	4.2	9.7	2.9	6.3	4.2	3.1	1.9	11.9	2.6	26.7	6.4	45.0	7.4	34.9	7.9	6.9	2.1	10.0	1.9	17.7	4.5	1.4	0.4
Beetle adults[b]	8.5	3.4	10.7	3.0	2.5	1.0	6.8	3.6	3.9	0.7	9.0	2.9	20.6	7.5	13.6	3.5	4.5	1.5	24.6	9.1	7.8	2.7	6.1	1.7
Beetle larvae[c]	25.5	6.4	39.0	6.1	27.2	9.8	6.3	2.2	41.9	8.8	13.6	1.6	8.1	2.8	19.3	7.8	16.0	3.3	22.2	4.7	10.6	4.0	19.8	7.8
Butterfly, moth larvae and pupae[d]	4.3	1.9	8.0	3.0	6.0	1.0	51.7	13.9	4.6	1.7	5.9	0.8	10.1	1.2	23.4	2.6	0.6	0.2	9.2	3.9	10.7	4.2	48.4	13.0
Centipedes[e]	6.6	2.6	6.3	2.0	3.5	1.6	5.9	2.5	2.4	0.6	6.4	1.2	1.6	0.9	0.7	0.2	1.2	0.2	3.5	1.5	5.3	2.2	7.0	1.9
Crickets, roaches, grasshoppers[f]	4.1	1.6	5.7	4.2	0.4	0.3	0.9	0.9	0.4	0.2	1.7	1.3	2.5	0.5	5.7	2.1	3.6	1.7	2.0	0.9	10.4	3.8	4.4	2.0
Earthworms	0.8	0.3	0.1	0.1	1.5	0.4	2.2	1.9	2.2	1.7	2.1	1.0	0.0	0.0	0.0	0.0	0.1	0.1	0.2	0.2	5.3	3.2	0.7	0.3
Fly larvae[g]	0.8	0.2	0.9	0.2	2.3	0.9	4.1	2.3	4.8	2.6	3.2	0.6	0.4	0.3	0.2	0.1	0.1	0.0	0.3	0.1	1.6	0.4	0.8	0.2
Fruits[h]	12.7	6.6	11.1	9.6	15.7	15.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	55.4	8.2	14.9	8.1	3.4	1.9	0.0	0.0
Millipedes[i]	11.6	5.3	6.6	2.3	30.7	8.2	8.6	2.8	23.0	6.6	18.3	6.3	7.0	1.7	0.3	0.1	11.4	3.1	11.9	5.8	18.0	5.5	3.0	1.0
Spider, scorpions[j]	1.2	0.9	0.2	0.1	1.3	0.5	3.5	1.0	0.2	0.1	2.6	1.2	1.3	0.6	1.4	0.6	0.1	0.1	0.4	0.1	2.5	0.9	5.5	1.7
Vertebrates	5.3	5.3	0.1	0.1	1.7	1.1	6.2	4.7	1.8	1.6	1.5	1.3	2.0	0.7	0.3	0.2	0.0	0.0	0.5	0.3	6.0	2.4	2.6	2.0

a. Season effect (P=0.0001) within oak-palmetto habitat; JUN >AUG, DEC, JAN, MAR, and NOV (P<0.05). Season effect (P=0.0001) within oak-pine habitat; JUN >AUG, DEC, JAN and NOV (P <0.05).

b. Season effect (P=0.01) within oak-palmetto habitat; JUN >AUG, JAN, and MAR (P<0.05).

c. Season effect (P=0.005) within oak-palmetto habit; MAR >AUG, DEC, and JUN (P <0.05). Season effect (P=0.04) within oak-pine habitat; NOV >JAN (P <0.05).

d. Season effect (P=0.04) within oak-palmetto habitat; DEC and JUN >AUG (P <0.05). Season effect (P=0.0006) within oak-pine habitat; DEC and JAN >AUG, MAR, and NOV (P<0.05).

e. Season effect (P=0.006); DEC and NOV >JUN (P <0.05).

f. Season effect (P=0.01); DEC>JAN and MAR (P <0.05).

g. Season effect (P=0.001); MAR> AUG, JUN, and NOV (P <0.05).

h. Season effect (P=0.0001) within oak-palmetto habitat; AUG >DEC, JAN, JUN, MAR, and NOV (P <0.05).

i. Season effect (P=0.003); JAN and MAR>JUN (P <0.05). Habitat effect (P=0.002); oak-palmetto>oak-pine (P <0.05).

j. Season effect (P=0.0008); DEC >AUG, MAR, and NOV (P <0.05). Habitat effect (P=0.03); oak-pine>oak-palmetto (P <0.05).

grubs (Scarabaeidae) and wireworms (Elateridae) were the most frequently consumed beetle larvae throughout the year. Adult beetles, mostly click beetles (Elateridae), scarab beetles (Scarabaeidae), and tiger beetles (Cicindelidae) were consumed by 166 armadillos (97% TFO). A total of 165 armadillos (97% TFO) ate Lepidoptera (butterflies and moths) larvae and pupae. Diplopoda (millipedes) were consumed by 137 armadillos (92% TFO), Chilopoda (centipedes, 91% TFO), Diptera (flies, 81% TFO), Orthoptera (crickets, roaches, and grasshoppers, 76% TFO), and Arachnida (spiders and scorpions, 74% TFO) were important foods throughout the year.

In addition to invertebrates, 60 armadillos (35% TFO) ate fruits. Grapes (*Vitis* sp.) and saw palmetto were the most frequently consumed fruits, but fruits of greenbriars (*Smilax* sp.) and Carolina laurelcherry (*Prunus caroliniana)* were also eaten. Sixty-two (36% TFO) armadillos ate Vertebrata (vertebrates) including the eastern spadefoot toad (*Scaphiopus holbrooki),* five-lined skink (*Eumeces fasciatus),* green anole (*Anolis carolinensis),* eastern fence lizard (*Sceloporus undulatus),* rough green snake (*Opheodrys aestivus),* and various lizard and snake eggs.

Patterns of Food Use

Twelve armadillo foods comprised >1% DW of diets during at least 1 season (Table 2). Preliminary analyses revealed that %DW of 7 of these foods could be tested for season- and habitat-related differences because they lacked significant season x habitat interactions. There was seasonal variation in the consumption of 3 foods (centipedes; crickets, roaches, and grasshoppers; and flies; Table 2). Consumption of millipedes and spiders, and scorpions varied by season and habitat (Table 2). Consumption of earthworms and vertebrates, based on %DW data, did not differ by season or habitat (Table 2).

Preliminary analyses revealed that %DW of 5 foods could be tested for seasonal differences only after being sorted by oak-palmetto or oak-pine habitats. There was seasonal variation in amount of larval beetles consumed from oak-palmetto and oak-pine habitats (Table 2). Ant and wasp consumption varied by season for oak-palmetto and oak-pine habitats (Table 2). Butterfly and moth consumption varied by season for oak-palmetto and oak-pine habitats (Table 2). There was seasonal variation in the consumption of fruits and adult beetles for oak-palmetto habitat, but not for oak-pine habitat (Table 2).

Discussion

The cranial and dental morphology of the nine-banded armadillo suggests adaptations for eating ants and termites, which constitute much of its diet in Central and South America (Redford 1985). However, in the United States, armadillos eat a variety of insects and invertebrates, and some vertebrates and fruits (Kalmbach 1943, Fitch et al. 1952, Nesbitt et al. 1977, Breece and Dusi 1985, Wirtz et al. 1985, Sikes et al. 1990).

The importance of particular foods to armadillos on CUIS varied depending on whether the data were expressed based on occurrence or dry weight. For example, SFO of earthworms and vertebrates in armadillo diets appeared to vary among seasons (Table 1), whereas there was no seasonal variation in these foods when expressed on the basis of %DW (Table 2). This apparent contradiction probably resulted from the higher moisture content of these foods (which was lost during the drying process), as compared to the lower moisture content of invertebrates with exoskeletons. Thus, if we had examined diets only based on %DW, then we would have underestimated the importance of these foods.

Beetles were the most important armadillo food during most seasons on CUIS, based on both SFO (Table 1) and %DW (Table 2) data. Click beetle and scarab beetle larvae were prominent in armadillo stomachs during all seasons and in both habitats. Wirtz et al. (1985) reported similar use of these larvae by armadillos in Florida. Greatest amounts of adult beetles were consumed on CUIS during JUN and AUG, but represented a smaller proportion of the diet than did larvae, perhaps because adult beetles were more mobile than larvae.

Differences in consumption of butterfly and moth larvae and pupae among seasons were much greater for oak-pine than for oak-palmetto habitats (Table 2), which probably caused the significant season x habitat interaction. Armadillos ate far greater amounts of these foods during JAN and DEC, but only within oak-pine habitats (Table 2). Other researchers have reported that armadillos readily consume butterfly and moth larvae and pupae, with estimates ranging from 1.2% to 9.2% of the diet (Nesbitt et al. 1977, Sikes et al. 1990). In our study, 1 armadillo that we collected in an oak-pine forest during DEC contained 188 larvae and pupae of butterflies and moths.

Armadillos ate fruits less frequently than some other foods. However, fruits were seasonally important. Our data support other reports, suggesting that some armadillos eat large amounts of fruits (Hamilton 1946, Fitch et al. 1952, Breece and Dusi 1985). Armadillos in oak-palmetto habitats ate more fruits than did those in oak-pine habitats. During AUG, fruits represented >50% of foods consumed by armadillos collected in oak-palmetto habitats. This result may reflect greater availability of palmetto fruits in oak-palmetto versus oak-pine habitats.

Millipedes and centipedes are important armadillo foods, but they typically represent a small proportion of the annual diet (Fitch et al. 1952, Sikes et al. 1990). During periods of low temperatures, these prey become less mobile, which probably increases their use by armadillos (Fitch et al. 1952, Wirtz et al. 1985). Thus, temperature changes may partially explain the seasonal patterns of use we observed for these foods on CUIS. Consumption of millipedes and centipedes was similar to that reported from Alabama (Breece and Dusi 1985). Our data suggest that the abundance of millipedes on CUIS, and their potential use, may differ among habitats. However, we did not quantify their abundance in either habitat.

Armadillos frequently ate ants, with peak usage occurring during JUN. Ants were prominent in diets of armadillos from oak-palmetto habitats during all seasons. We agree with Wirtz et al. (1985) that in temperate environments, the importance of ants to armadillos may be less than researchers once thought. Consumption of ants apparently varies greatly among geographical locations and among individual armadillos

(Breece and Dusi 1985, Wirtz et al. 1985, Sikes et al. 1990). Some armadillos on CUIS ate few ants, whereas others ate thousands. This might be expected because ant colonies vary greatly in size, containing from a dozen to many thousands of ants (Borror et al. 1981).

Armadillos ate greatest amounts of fly larvae during JAN and MAR (Table 2); similar seasonal trends have been reported for other locations (Nesbitt et al. 1977, Sikes et al. 1990). As in Florida (Wirtz et al. 1985), armadillos on CUIS frequently ate crickets, roaches, and grasshoppers, with peak consumption in DEC. Greatest amounts of spiders were consumed in DEC and JAN (Table 2), which was similar to reports from other locations (Fitch et al. 1952, Breece and Dusi 1985, Sikes et al. 1990).

Reptiles and their eggs and amphibians were the only vertebrates observed in the stomachs of armadillos on CUIS. Seasonal consumption of these foods agreed with the reports of others (Kalmbach 1943, Fitch et al. 1952, Breece and Dusi 1985, Wirtz et al. 1985). We found no evidence to support concerns that armadillos eat the eggs of ground-nesting birds. However, Breece and Causey (1973) stated that armadillos might break bird eggs to consume their contents without ingesting shells, thereby leaving little evidence in stomach contents. Recent video-surveillance research of bobwhite quail *(Colinus virginianus)* nest predation in northern Florida has further confirmed this feeding behavior by armadillos (J. P. Carroll, Univ. Ga., pers. commun.). Although not documented in our study, there is anecdotal evidence that armadillos on CUIS might occasionally eat the buried eggs of sea turtles (J. Bjork, NPS, pers. commun.).

In conclusion, our results agree with the report by Redford (1985) that the nine-banded armadillo is primarily insectivorous, but that in temperate environments its food habits may lie somewhere between those of other armadillo genera that are carnivorous-omnivorous *(Zaedyus, Euphractus,* and *Chaetophractus)* or ant-termite specialists *(Cabassous, Tolypeutes,* and *Priodontes).* Although its physical adaptations are best suited for insectivory, the nine-banded armadillo eats any foods that it can catch. Comparisons of armadillo diets among states, without regard to habitat-related variability, may be of little value. Abundance and diversity of invertebrates and their larvae probably differ among plant communities, and are influenced by physical factors including soil temperature and moisture, soil type, etc. (Breece and Dusi 1985, Barbosa and Wagner 1989). In addition, grapes, saw palmetto, and other fruit-producing plants often are characteristic of specific plant communities. For these reasons, future armadillo food habits studies must pay close attention to characteristics of specific habitats.

Management Implications

Invasion of CUIS by armadillos provides additional opportunities for visitors to view wildlife. However, armadillos are an exotic species that feed on invertebrates, vertebrates, and fruits, which may affect native animal and plant communities. Armadillo feeding activity (e.g., removing soil arthropods, disturbing the soil surface, aerating the soil, etc.) may be adverse or beneficial to these communities. Our results provide baseline data for future research, which should examine the importance of these foods to native wildlife on CUIS, and thus determine the ecological effects of armadillos.

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