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Dietary specialization and variation in two mammalian myrmecophages (variation in mammalian myrmecophagy)

Especialización dietaria y variación en dos mamíferos mirmecófagos (variación en la mirmecofagia de mamíferos)

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ABSTRACT

This paper compares dietary variation in an opportunistic myrmecophage, *Dasypus novemcinctus,* and an obligate myrmecophage, *Myrmecophaga tridactyla.* The diet of the common long-nosed armadillo, *D. novemcintus,* consists of a broad range of invertebrate as well as vertebrates and plant material. In the United States, ants and termites are less important as a food source than they are in South America. The diet of the giant anteater. *M. tridactyla,* consists almost entirely of ants and termites. In some areas giant anteaters consume more ants whereas in others termites are a larger part of their diet. Much of the variation in the diet of these two myrmecophages can be explained by geographical and ecological variation in the abundance of prey. However, some variation may be due to individual differences as well.

Key words: *Dasypus novemcinctus, Myrmecophaga tridactyla, Tamandua,* food habits, armadillo, giant anteater, ants, termites.

RESUMEN

En este trabajo se compara la variación dietaria entre un mirmecófago oportunista, *Dasypus novemcinctus,* y uno obligado, *Myrmecophaga tridactyla.* La dieta del armadillo común, *D. novemcinctus,* incluye un amplio rango de invertebrados así como vertebrados y materia vegetal. En los Estados Unidos, hormigas y termites son menos importantes como recurso alimenticio de los armadillos, de lo que son en Sudamérica. La dieta del hormiguero gigante, *M. tridactyla,* está compuesta casi enteramente por hormigas y termites. En algunas áreas el hormiguero gigante consume más hormigas que termites, en tanto que en otras las termites forman la parte más importante de su dieta. Mucho de la variación dietaria en estos dos mirmecófagos puede explicarse por variación geográfica y ecológica en la abundancia de presas. Sin embargo, alguna variación puede deberse a diferencias individuales entre los mirmecófagos.

Palabras claves: *Dasypus novemcinctus, Myrmecophaga tridactyla, Tamandua,* hábitos alimenticios, armadillo, hormiguero gigante, hormigas, termites.

INTRODUCTION

A great number and variety of ants and termites provide food for a variety of mammals. These ant and termite-eating mammals or myrmecophages are found on all tropical continents and include opportunistic myrmecophages such as mongooses, and obligate myrmecophages such as aardvarks (Redford in press a). In this paper I compare two South American mammals, the common long-nosed armadillo, *Dasypus novemcinctus,* an opportunistic myrmecophage, and the giant anteater, *Myrmecophaga tridactyla*, an obligate myrmecophage.

This comparison elucidates some of the factors governing dietary variation in invertebrate-eating mammals. The dietary importance of social insects as a group and of ants versus termites varies for both of these species geographically, ecologically, and individually. I will relate this variation to the differing availabilities of prey and the extent of myrmecophagy.

ANTS AND TERMITES AS FOOD

In many parts of the world ants and termites provide a large base of potential prey for mammalian predators. Both ant

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and termite faunas are most diverse in tropical latitudes with species diversity dropping off sharply with increasing latitude (Kusnezov 1957, Wilson 1971, Wood & Sands 1978, Mill 1982a). Single habitats in tropical Brazil have over 40 species of termites (Mill 1982b) whereas there are only 13 species in the entire state of Florida (Snyder 1954). The pattern is similar for ants with 455 species found in North America, north of Mexico (Wilson 1971), compared with 222 species known from the Brazilian state of São Paulo alone (Kusnezov 1957).

There are few data from the Neotropics allowing quantification of the importance of ants and termites (Pisarski 1978). One rough estimate provided by Fittkau & Klinge (1973) based on their extensive work in the Amazon forest indicated that ants and termites composed over 30% of the total animal biomass and about 75% of the total insect biomass. It is possible to compare this with the termite biomass calculated from three different studies. Lubin *et al.* (1977) estimated that termites of the genus *Nasutitermes* had a biomass of 12.8 kg/ha in a Panamanian forest. The biomass of all termites in the top five cm of soil in an Amazonian forest averaged 4.3 kg/ha (Bandeira 1979) whereas in the Brazilian cerrado four species of termites averaged 33.3 kg/ha (Redford 1984).

For ants, the data are more scarce. Levings & Franks (1982) and Levings & Windsor (1982), calculated an average of 663 ant colonies/ha in the Panamanian rainforest and found that half of all of the individual forest litter arthropods collected over 30 months were ants. Based on many years of work in Peruvian forests, Erwin (1983, p. 14) stated that: "It is also clear that ants constitute the greatest number of individuals and biomass in the canopy as well as on the ground". This conclusion is supported by Adis *et al.* (1984) who found that ants accounted for between one-quarter and one-half of the total arthropod biomass obtained from the canopy of a Brazilian forest.

There are few data available to allow comparison of the relative abundances of ants and termites in single habitats. Ants are distributed over a much greater latitudinal range than termites and unlike termites, can be dominant elements in temperate arthropod faunas (Kusnezov 1957, Wilson 1971, Petal 1978). The percent contribution that ants make to invertebrate faunas increases with an increase in the dryness of a habitat (Pisarski 1978). Termites, on the other hand, have a primarily tropical and sub-tropical distribution due to their low mobility, their reliance on cellulose for food, and their susceptibility to dessication. The termite species which are found in temperate latitudes are frequently confined to the buffered environment of dead wood (Wilson 1971, Wood & Sands 1978).

When compared with other arthropods, ants and termites are good food. Redford and Dorea (1984) have shown that although lower in fat and higher in ash content than some other invertebrates, termites and ants have equivalent total nitrogen contents. What makes these insects particularly suitable as a source of food is their colonial habit and the consequent concentration of potential food.

MAMMALIAN MYRMECOPHAGES

Dasypus novemcinctus

The long-nosed armadillo (*Dasypus novemcinctus*), an opportunistic myrmecophage, is found not only in areas where ants and termites are common but also where they are scarce. The food habits of this species are well known in the United States because armadillos were at one time suspected of eating the eggs of game birds. As a result, the stomachs of hundreds of animals were painstakingly examined. Table 1 summarizes the results of the three largest published studies of *D. novemcinctus* food habits in the United States.

In Texas, where the largest study was done (Kalmbach 1944) armadillos ate mostly beetles and beetle larvae. Other major foods included Orthoptera, centipedes and millipedes, and Diptera. Hymenoptera equalled 14.1% volumetrically, with the great majority being ants of 44 different species. Termites of the genus *Reticulitermes* ocurred in 75% of the stomachs, although composing only 4.5% by volume. Armadillos also consumed small amounts of earthworms, crayfish, carrion, amphibians, reptiles, small mammals, fruit and mushrooms.

TABLE 1

Relative composition of *Dasypus novemcinctus* diets, expressed as percent of total stomach volume
Composición relativa de la dieta de *Dasypus novemcinctus*, expresada como porcentaje del volumen de la ingesta en el estómago

Food Type	Texas (n=169) Kalmbach 1944	Louisiana (n=104) Fitch et al. 1952	Florida (n =172) Nesbitt et al. 1977
Hymenoptera	14.7	3.9	14.7
Isoptera	4.7	1.2	0.1
Coleoptera	43.5	44.6	29.0
Orthoptera	6.5	8.5	10.2
Lepidoptera	8.2	4.7	9
Other insects	2.6	5.8	13.5
Myriapoda	6.5	8.5	7.9
Other invertebrates	8.3	8.5	11.0
Amphibia & Reptilia	1.3	4.5	1.8
Other vertebrates	0.5	0	1.9
Plant material	2.2	9.8	0.8

In Louisiana (Fitch *et al.* 1952), beetles comprised an even larger proportion of the diet with ants comprising only 3.9%, and termites 1.2%. Plant material, including seeds, berries and fungi comprised 9.8%. In Florida (Nesbitt *et al.* 1977) approximately one third by volume of armadillos' diet was beetles with ants comprising 15.1%, and termites 0.1%. Crayfish, small amphibians, reptiles, and mammals such as nestling cotton rats *(Sigmodon),* were also consumed.

In summary, in the United States *D. novemcinctus* is omnivorous, though primarily entomophagous, with beetles and their larvae comprising the largest single dietary item. The percent of ants and termites in the diet varies from a low of 5.1% in Louisiana to a high of about 18% in Texas. In all three samples ants were a much more important food than termites. Despite the fairly low representation of ants and termites, all authors have commented that, when available, ants and or termites comprise one of the favored foods of *D. novemcinctus* and many of the stomachs examined contained thousands of ants and their coccons or termites and their nymphs. In fact in some smaller samples (Newmann 1913) ants were said to be the most common prey encountered in the stomachs.

Dasypus novemcinctus unfortunately, has been much less studied in Central and South America where both ants and termites are more common than in the United States. The two available samples of *D. novemcinctus* stomachs from the southern part of its range show a different picture from the results discussed before. Mathews (1977) analyzed two *D. novemcinctus* stomachs from western Brazil. One of the stomachs contained 90% termites of several species with the remaining 10% containing ants, termites, beetles and scorpions. The second stomach contained a large quantity of what he guessed to be fruit with the rest consisting of mostly termites. Similar results were encountered in a sample of five *D. novemcinctus* stomachs from central Brazil (Redford unpubl. data). These stomachs were found to contain an average of 69% ants and termites with the remainder beetles and millipedes. Another five stomachs from the same locality analyzed with a different methodology showed ants to comprise 17% by volume, termites 15%, and beetles and beetle larvae 41%. One of the stomachs contained 65% fruit by volume, supporting Mathews (1977) observation. Several small vertebrates including a worm lizard and two skinks were also encountered.

Other Dasypus

The observation of increased consumption of ants and termites by *D. novemcinctus* in South America is supported by examining the few data available for other species in the genus *Dasypus.* One *D. kappleri* stomach from Colombia (Barreto *et al.* 1985) had 19% ants and 10% termites. One *D. sabanicola* stomach from Colombia contained 10% ants and 88% termites (Barreto *et al.* 1985). Although a larger sample of the same species from the llanos of Venezuela (Ferguson-Laguna 1984) contained mostly beetles and only 7.3% ants and termites, other *D. sabanicola* stomachs from Venezuela (Pacheco & Naranjo 1978) had 45% termites, 22% ants and only 18% beetles. Finally, one *D. hybridus* stomach from Uruguay (Barlow 1965) contained 49% ants and 9% termites, other assorted invertebrates and the remains of several nestling mice.

In summary, it is clear that despite small sample sizes there is a strong suggestion of geographical variation in the consumption of ants and termites both within *D. novemcinctus,* and within the genus *Dasypus* as a

whole (Fig. 1). The general pattern appears to be a greater consumption of both ants and termites in tropical areas. More ants than termites are consumed in temperate areas such as the United States and Uruguay, and in areas which are otherwise unsuitable for terrestrial termites such as the seasonally flooded llanos of Venezuela.

Myrmecophaga tridactyla

The second edentate is the giant anteater, *Myrmecophaga tridactyla,* an obligate myrmecophage. Although the data consist of few samples, this species appears to consume virtually nothing but ants and termites. However, as in the long-nosed armadillo, there is geographical variation in the diet (Table 2, Redford 1985). In the Venezuelan llanos ants comprise virtually the entire diet whereas in northern Brazil the entire diet seems to consist of termites. Within a much smaller spectrum of prey types it appears that the giant anteater, like the long-nosed armadillo, is also an opportunist.

TABLE 2

Food habits of *Myrmecophaga tridactyla* based on stomach contents, feces and observations (from Redford 1985)

Hábitos alimenticios de *Myrmecophaga tridactyla,* basado en contenidos estomacales, fecas y observaciones directas (tomado de Redford 1985)

Location	% Ants	% Termites
Paraguay	100	0
Ceara, Brazil	100	0
N.E. Brazil	100	0
Llanos of Venezuela	99	1
Minas Gerais, Brazil	88	12
Brasilia, Brazil	15	85
Goias, Brazil	11	89
Amapa, Brazil	0	100

There have not been any detailed studies on variation in the diet of *Myrmecophaga,* but this species will take prey other than ants and termites. One stomach from Bolivia contained only beetle larvae (Krieg 1939), whereas examination of feces from southern Brazil showed consumption of millipedes (Shaw *et al.* In press) Anteaters in a U.S. zoo consumed nestling cottontail rabbits (MacNamara pers. comm.), and young mice offered to captive giant anteaters were consumed with great relish (Redford 1983).

Tamandua

The genus *Myrmecophaga* is monotypic so congeneric comparisons are impossible, but food habits of two species in a closely related genus, *Tamandua,* may be examined. As with the giant anteater, tamanduas show geographical variation in diet with some stomachs reported to contain only ants and others only termites (Redford 1983). Individual differences in feeding by *Tamandua* contribute to variation in patterns of myrmecophagy (Montgomery & Lubin 1977). For example, two *T. tetradactyla* from Venezuela consistently spent very different amounts of time foraging for termites at nests versus in wood (Lubin & Montgomery 1981). They also demonstrated differences in feeding bouts with one animal spending 90% on termites and the other only 24% (Lubin & Montgomery unpubl.). Similarly, two *T. mexicana* individuals fed for different amounts of time on the same prey types (Montgomery & Lubin 1977).

As in the giant anteater, anteaters of the genus *Tamandua* are capable of eating prey other than ants and termites. One zoo-researcher (Parker pers. comm.) reported tamanduas killing and consuming iguanine lizards housed in the same cage.

DISCUSSION

Both *Dasypus novemcinctus* and *Myrmecophaga tridactyla* have large geographical ranges within which they are found in extremely diverse habitats ranging from the dry Paraguayan chaco to the wet forests of Amazonia (Fig. 2). *Dasypus novemcinctus* is found both farther north and farther south than the giant anteater; the latter's more limited range may reflect the primarily tropical distribution of extensive populations of ants and termites which form its major diet. The long-nosed armadillo's range is apparently limited by cold temperatures which affect the availability of soil and litter invertebrates (Humphrey 1974, McNab 1980).

These two edentates have diets with very different size distributions. The armadillo does not specialize on particular classes,

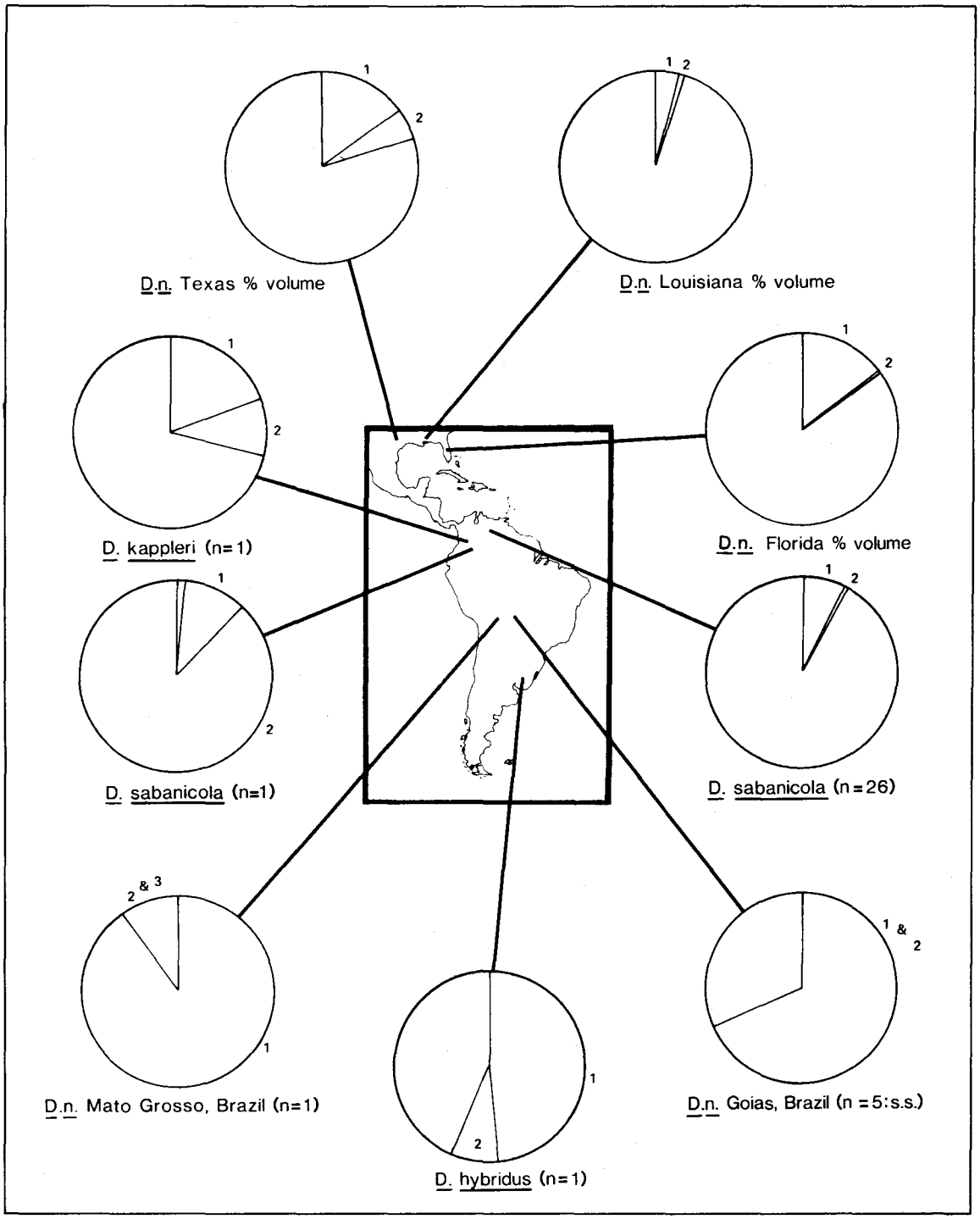

Fig. 1. Summary of the relative consumption of ants and termites by four species of *Dasypus* in various parts of North and South America. *(D.n. = Dasypus novemcinctus)*. The circles represent 100% of the diet, the wedge numbered "1" equals the relative percent of the diet composed of ants, the wedge numbered "2" equals the relative percent composed of termites. The sources of the data are listed in the text.

Resumen del consumo relativo de hormigas y termites por parte de cuatro especies de *Dasypus* en varias partes del Norte y Sudamérica. *(D.n. =Dasypus novemcictus)*. Los círculos representan 100% de la dieta; la cuña numerada "1" representa el porcentaje de la dieta que está compuesto por hormigas; la cuña numerada "2" representa el porcentaje de la dieta que está compuesto por termites. Las fuentes bibliográficas de los datos están listadas en el texto.

taking very small prey as well as comparatively large prey. A long-nosed armadillo stomach may be thought of as a Berlese funnel, reflecting, with some biases, the composition of the leaf litter fauna. In South America, where ants and termites are more important components of the ground dwelling invertebrate fauna, they make up a greater percentage of its diet. However, throughout its range this species will eat small vertebrates and fruit when available. *Dasypus novemcinctus'* extensive range reflects a virtually unprecedented ability to utilize whatever foods are locally available (Redford in press b).

Fig. 2. The geographical ranges of the common long-nosed armadillo. *Dasypus novemcinctus* and the giant anteater, *Myrmecophaga tridactyla.*

Los rangos geográficos del armadillo común, *Dasypus novemcinctus,* y del hormiguero gigante, *Myrmecophaga tridactyla.*

The giant anteater on the other hand, consumes mostly small invertebrates, specializing on small arthropods found in dense aggregations (i.e., ants and termites). This strict myrmecophagy is reflected by the highly specialized skull of the giant anteater which severely limits the type of prey that can be ingested. The proportion of ants versus termites in the diet probably reflects the relative availability of each to the anteater and is not based on factors intrinsic to particular prey species. This would allow the giant anteater to range throughout many different habitats with their different tropical social insect communities (Redford 1985).

Both *Dasypus novemcinctus* and *Myrmecophaga tridactyla* respond opportunistically to local availabilities of prey. This opportunism by long-nosed armadillos is illustrated by seasonal trends in prey consumption. In the U.S. some prey such as Orthoptera, reptiles and amphibians are more commonly taken in the colder months when low temperatures slow them down (Kalmbach 1944, Fitch *et al.* 1952, Talmage & Buchanan 1954). Diptera and Lepidoptera larvae are taken in the spring and summer when plentiful (Kalmbach 1944, Fitch *et al.* 1952) whereas earthworms are most common in the diet during the wet season when a high water table forces them up (Kalmbach 1944, Nesbitt *et al.* 1977).

The consumption of ants and termites by *Dasypus* is probably also affected by seasonal factors. In the Florida data (Nesbitt *et al.* unpubl.), the trend is for ants to be taken more frequently in the wet season. This also occurs in the Venezuelan llanos (Ferguson-Laguna 1984). Termites are very responsive to humidity levels and are much more common above ground during the wet season. Therefore, in areas where termites are common, one would expect them to be a more common prey item for surface-foraging armadillos during the rainy season.

The giant anteater also responds to local variation in prey availability. As is the case with *D. novemcinctus* some of this response can be explained by correlations of prey abundance with humidity and rainfall. Ants were reported to compose 100% of the diet in very dry areas where termites would be expected to be rare. The other area where ants comprise a high percentage of the diet is the seasonally flooded Venezuelan llanos which is unsuitable for terrestrial termites.

In conclusion, both *Dasypus novemcinctus* and *Myrmecophaga tridactyla* are opportunistic predators, responding to local availabilities of prey. Their responses are in large part shaped by the degree to

which they have specialized on ants and termites. The available data, summarized in this paper, allow formulation of four hypotheses. First, *Dasypus* armadillos consume a particular prey type in proportion to its availability. Second, over much of the tropical portion of their range the diets of *Dasypus* armadillos will consist largely of ants and termites. Third, in any given habitat *Myrmecophaga* will prefer the most available species of ant or termite. Fourth, individual variation accounts for a significant proportion of the within-population variation in feeding by anteaters.

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