Articles

Distribution and limiting factors of edentates in the Paraguayan Chaco

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Abstract

Data were collected for one year in the Paraguayan Chaco to: (1) report new geographic localities, range extensions, and habitat associations for edentates of the Paraguayan Chaco; and (2) investigate the effects that seasonality, abiotic factors, and temporal allocation have on shaping edentate species composition. Eight new localities, six range extensions, and three Dpto. records were reported. Additionally, two potentially new habitat associations were recorded. Species richness and activity did not change from season to season, or between wet and dry seasons. Neither individual abiotic factors, or a suite of abiotic factors seem to be significant in structuring the assemblage as a whole, although *Euphractus* correlated positively with temperature, rainfall, and weather activity. Preliminary analyses suggest that temporal allocation is not significant in determining assemblage composition.

Introduction

Studies involving sympatric assemblages of edentates are relatively few and far between. Topics at the assemblage level have ranged from variation of species burrows (Carter & Encarnação, 1983) to variation in diet (Redford, 1985), and have taken place primarily in Brazil. The results of collecting expeditions in Paraguay (Wetzel & Lovett, 1974; Myers & Wetzel, 1979) comprise most of the work done on edentates in this region, reporting distribution, habitat association, and notes on taxonomy.

The first objective of this study is to describe potentially new geographic localities, range extensions, and habitat associations for edentates of the Paraguayan Chaco. The second objective is to investigate composition determinants in an edentate assemblage. Seasonality, abiotic factors (weather conditions), and temporal allocation may all contribute to composition of any assemblage in ecological time.

Different seasons yield increased or decreased productivity, resulting in varying quantities of resources. These in turn may influence edentate richness during a particular season. As productivity increases, both increases (Brown & Davidson, 1976) and decreases (Rosenzwieg, 1971) in species richness might result as species move into or out of an area. How abiotic factors determine species abundance may provide insight into the role (Willig & Moulton, 1989) that stochastic events have in molding assemblages. Presence and absence of sympatric guild members also might contribute to niche allocation within an edentate assemblage. In evolutionary time, size assortment (Case & Sidell, 1983) is the situation where the probability of persistence of a species is diminished by presence of morphologically similar species. Ecological separation (Seidensticker, 1976) describes how sympatric species occupying the same guild partition resources in ecological time. Allocation of temporal components may influence species composition on an ecological scale. The chance for similarly sized, sympatric guild members to coexist simultaneously on a month-to-month scale should diminish if shared resources are temporally allocated.

Although there exists a high diversity of edentates in the Paraguayan Chaco, factors determining edentate composition have not been investigated within any Chacoan community. Thus, this study addresses the effects that seasonality, abiotic factors, and temporal allocation have on shaping species composition in a Neotropical xeric-dwelling edentate assemblage. The results will hopefully provide insight towards how a suite of factors contribute to composition of a diverse assemblage of edentates in a sub-tropical environment, which is virtually as species rich (Redford *et al.*, 1990), if not more so (Mares, 1992), as some of the most productive rainforests in the New World.

Methods

Distribution and Habitat Association

This study took place from August 1989 to August 1990. Hereafter, each locality (or group of localities) listed in Figure 1 is followed parenthetically by the month (for long-term sampling periods) or time of month (for short-term sampling periods) when the

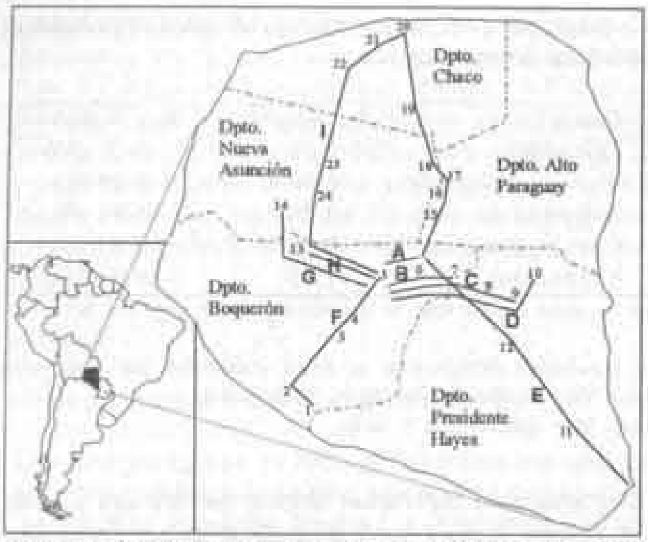

Figure 1. Road transects (A-H) and localities in the study area. Localities: 1) Est. Madregadda, 2) Est. Ferrer, 3) Felix Zaracho, 4) La Pirizei, 5) Est. Fort. Toledo, 6) Filadelfia, 7) Loma Plata, 8) Lag. Pora, 9) Est. Amalia, 10) Lag. Capitan, 11) Rio Negro & Ruta T.C., 12) Fort Zalazar, 13) Mscl. Estigarribia, 14) Tte. Ochoa, 15) 60 km N of Fernheim, 16) Fort. Carlos A. Lopez, 17) W of Lag. Frente Dos, 18) Tte. Martinez, 19) Cerro Leon, 20) Est. San Jose, 21) Palmar de las Islas, 22) Capt. Pablo La Gerenza, 23) Tte. Picco, 24) 23 km S Tte. Picco.

areas were surveyed, as follows: 1-4 (late September, 1989); 5-6 (September 1989 to August 1990, see below); 7 and 11-14 (periodically from August 1989 to August 1990); 8-9 (mid September, late October, and mid November 1989); 10 (late April); 15-24 (early July, 1990).

Data were collected by driving along road transects (Fig. 1) of varying lengths and adjacent to various habitats, complemented with walking along transects or through areas (of varying extent) impassable by vehicle, to log recordings of live specimens, road kills, or identifiable tracks. Carcasses other than road kills were omitted, as they may have been translocated and deposited in an area by hunters. More surveys were done in the morning and during daylight hours than during the night.

Even though biased estimates may arise if individuals of a species increase or decrease activity due to metabolic constraints or other reasons, the transect method allows consistent data collection, as there was only one person collecting data and the periods during which data were collected remained consistent throughout the study, thus reducing the variability among separate estimates. Attraction to or avoidance of roads can be additional problems which may cause bias from transect sampling, which perhaps can be counterweighted by complementing road-driven transects with walking through areas which are impassable by vehicle. Although transect surveys do not provide precise data on mammalian densities, they are the most feasible method for estimating relative abundance or activity over time (Emmons, 1984).

New localities and Dpto. records were identified by overlaying a reduction of Figure 1 onto the maps in Redford & Eisenberg (1992), and cross-referencing following Wetzel & Lovett (1974) and Myers & Wetzel (1979). For each species, range increases in this study comprised those localities beyond the previously documented distributions within the Chaco, as determined by the enclosed polygon of known localities. Habitat associations were noted for each specimen.

Habitats

Short's (1975) classification of Chacoan habitats as water habitats, treeless terrestrial habitats, and woodlands is followed. Water habitats contain permanent surface water and include rivers (localities 1, 2, and 11; Figure 1) and flooded swamps (localities 8 and 9). Treeless terrestrial habitats include grasslands (locality 5) and pasture (localities 5-7). Most of the woodland habitats are dry, including: algarrobo (localities 13, 14, 23, and 24), palo santo-quebracho (localities 12 and 22), and quebracho (localities 3-5, 15-18); other woodland types include pantanal (localities 20-22) and gallery forest (localities 1, 2, and 11). Two additional habitat types which were not indicated by Short (1975) include salinated lagoon (locality 10), and rolling hills (locality 19), perhaps similar to foothills of the Bolivian Andes. The latter region is typified by dwarf palo santo-quebracho woodland, perhaps due to its higher altitude.

FACTORS DETERMINING COMPOSITION

Species included in this study (Table 1; latin names provided in species accounts, below) were those found within a 35 km radius from the centerpoint of Estancia Fortin Toledo proper (hereafter, referred as Estancia Toledo) (22°33' S, 60°30' W), Dpto. Boqueron, located 35 km W of the Mennonite Colony, Filadelfia. This area, representative of the Central Paraguayan Chaco, was cleared for cattle production more than other areas of the Paraguayan Chaco (Benirschke *et al.*, 1989). The secondary growth habitat in the vicinity of Estancia Toledo is a mosaic of quebracho woodland and grassland, characterized by thorny bushes, shrubs, and cacti, with scattered trees up to 13 m high. *Prosopis ruscifolia*, a thorny legume, and *Opuntia* sp. cactus are the dominant species (Lopez et al., 1987). Isolated tracts of thick, impenetrable, thorny forest are sometimes left when land is being cleared for agrarian purposes in the central Chaco. The forest's primary understory consists of thorny *Bromelia serra* and *Cleistocactus baumanii* (Stabler, 1985).

Table 1. Sizes (based upon principal component scores) of species present at Estancia Toledo, ranked from least to most active.

Common Name	Genus	Activity*	Size Value
Lesser Anteater	*Tamandua*	0.08	-0.02 (M)
Giant Anteater	*Myrmecophaga*	0.16	1.19 (L)
Three-banded Armadillo	*Tolypeutes*	0.75	-1.81 (S)
Hairy Armadillo	*Chaetophractus*	0.75	-1.81 (S)+
Yellow Armadillo	*Euphractus*	1.00	-0.61 (M)

* Activity is ranked from least to most active and is the annual mean relative activity for each species.

+ Due to confusion regarding taxonomic designation of hairy armadillo, the size value assigned (-1.81) was based upon that of the similar-sized *Tolypeutes*.

- Key for size classes: S = small; M = medium; L = large.

Monthly road transect surveys extended 9.3 km through western Estancia Toledo. Weekly surveys were 70 km round-trip, through eastern Estancia Toledo to Filadelfia and back. In addition, an average of 1.75 km of transect was walked daily. Data on activity were obtained from observations and recordings of live specimens, road kills, or identifiable tracks. Relative activity was rated numerically on a monthly basis using the following scale: not seen (0), rare (1), uncommon (2), common (3), or abundant (4); activity values (annual means of relative activity) are provided in Table 1. Temperature was recorded using a standard high-low Celsius thermometer, rainfall was recorded in millimeters using a standard rain gauge, cloud cover (clear=1 , partly cloudy=3, cloudy=5, overcast=7, or rainy=9) and relative wind velocity (stagnant=1, occasional light breeze=3, consistent light wind=5, or windy=7) were recorded several times during daylight hours, primarily between 14:00-18:00 hours. Monthly means were obtained for temperature, cloud cover, and relative wind velocity; a monthly total was obtained for rainfall. An intercorrelated suite of these four abiotic factors was computed with principal component analysis (PCA) using Pearson product-moment correlations, using the computer program, SYSTAT (Wilkinson, 1986). PCA scores for each month were calculated using the first principle component which accounted for 55% of the total variation among the four variables. The relationships among these abiotic variables are shown in Table 2, which provides Pearson product-moment and Spearman rank correlations.

Austral seasons were defined as follows: Spring (September to November), Summer (December to February), Fall (March to May), and Winter (June to July). Whether these seasons were characterized by changes in abiotic factors, a suite of abiotic factors, or seasonal variation in species richness was tested using analysis of variance (ANOVA), or corresponding Kruskal-Wallis tests if statistical assumptions were violated, using the computer program STATGRAPHICS (STSC, 1986).

The effects of individual abiotic factors and a suite of abiotic factors were measured using Spearman rank correlations, again using STATGRAPHICS (STSC, 1986), pairing each abiotic variable with each species across time. If all five species (100%) correlate significantly with individual abiotic factors or with a suite of all abiotic factors, they were judged to be significant in structuring the assemblage.

Presently, there is no practical way to test patterns of temporal allocation without using a randomization model, which is currently in progress. To measure temporal allocation, guild members were first divided into one of three size classes (small, medium, and large) using the following methods. Five morphometric measurements (total, head and body, hind foot, and ear lengths [mm]; cubed root of mass [g]) obtained from Redford & Eisenberg (1992) were used to compute principle components, using a covariance matrix of the log-transformed data. Table 1 provides scores

Table 2. Pearson product-moment (upper matrix) and Spearman rank (lower matrix) correlations between paired abiotic variables.

	Temp.	Rainfall	Cloud cover	Wind veloc.
Temperature	-	0.399	0.117	0.256
	-	0.199	0.717	0.423
Rainfall	0.399	-	0.640	0.582
	0.185	-	0.025	0.047
Cloud cover	0.067	0.703	-	0.331
	0.824	0.020	-	0.294
Wind velocity	0.182	0.527	0.296	-
	0.545	0.081	0.326	-

(calculated using the first principle component, which accounted for 88% of the total variation among the five variables) and sizes of each species. Differences between the first principle component scores for each species pair represent size differences (Table 3). If similar-sized guild members were not encountered during the same month for 12 months of the year (100%), this would suggest that temporal allocation occurred.

Results

Distribution and Habitat Association

The first paragraph in each of the following species accounts summarizes habitat association and locality information from the Redford & Eisenberg (1992) synopsis, which summarizes synecological and distributional notes. In situations where localities bordered the Chaco (such as delineating rivers), a range representing minimum and maximum values was given. The second paragraph contains new information on locality records, range increases, and Dpto. records for the Paraguayan Chaco, whereas habitat association records are for the species throughout its range. All information is chronologically ordered by locality, and is generally given as follows: numbers of specimens; condition (live, roadkill, tracks); location (Fig. 1); road transect (Fig. 1), unless specimen was recorded on foot; date; record; and additional information. If species could not be identified with complete certainty (such as the hairy armadillo, *Chaetophractus* sp.), no new information was included.

Greater Anteater: *Myrmecophaga tridactyla*

Found in a variety of habitats from tropical forest to xeric Chaco. Most abundant in open vegetation supporting high densities of ant and termite mounds. There is only one locality, from the northwestern Chaco in Dpto. Nueva Asuncion. Tracks were found once at Estancia Toledo on May 24, 1990, extending the range to the southeast and providing the first record from Dpto. Boqueron. Disturbed termite mounds, which may have been due to this species, were found in September of 1989 at Estancia Toledo.

Lesser Anteater: *Tamandua tetradactlya*

Found in a wide variety of habitats, including tropical forest, dry scrub forest, and open grassland. There are three localities from the Chaco. A roadkill individual was found approximately 30 km northwest of Estancia Toledo along transect H on October 18, 1989, which increases the range to the west and is the first record from Dpto. Boqueron.

Hairy Armadillo: *Chaetophractus* sp.

Due to taxonomic confusion as to whether these individuals were *Chaetophractus vellerosus* or *C. villosus*, no new information was included. It is believed that a contact zone for these two species occurs right in the area of study (C. Yahnke, pers. comm.).

Yellow Armadillo: *Euphractus sexcinctus*

Inhabits savannas and other open-vegetation formations, as well as forest edge. Appears to use higher, drier habitats. There are three localities from the Chaco. A single live adult was found 16 km east of Estancia Amalia along transect C on October 20, 1989, by a lagoon, which may be unusual for this species. Three road kills (two adults and a juvenile) were found 15 km west of Filadelfia along transect A on December 6 and 11, 1989 and March 16, 1990, respectively. The first individual represents the first record from Dpto. Boqueron. Two live adults were found at Estancia Toledo on March 27, and May 20, 1990, which extends the range of this species to the west.

Three-banded Armadillo: *Tolypeutes matacus*

Prefers dry vegetation and is abundant in the most xeric part of the Paraguayan Chaco. There are two localities, both from the northwestern Chaco. Four live individuals were found at Estancia Toledo on September 5, 16, and 27, 1989, and November 16, 1989, which extends the range to the southeast. Two additional specimens were found on July 5, and 7, 1990, at Palmar de las Islas and Estancia San Jose, which extend the range to the northwest and north, respectively. These may be the first records of this species being associated with seasonally inundated palm savannah.

Table 3. Size difference values.

	Lesser Anteater	Yellow Armadillo	Hairy Armadillo	Three-banded Armadillo
Greater Anteater	1.21	1.81	3.00	3.00
Lesser Anteater		0.59	1.79	1.79
Yellow Armadillo			1.19	1.19
Hairy Armadillo				0.00

Factors Determining Composition

Seasonality

Because the variances among samples were found to be heteroscedastic, Kruskal-Wallis tests were used to determine whether temperature, rainfall, cloud cover, wind velocity, the suite of these four abiotic factors, or species richness changed significantly from season to season. Although the abiotic suite changed significantly from season to season (TS=8.436, P=0.038), temperature, rainfall, cloud cover, wind velocity, and species richness did not vary significantly.

Abiotic Factors

Abiotic factors of temperature, rainfall, cloud cover, wind velocity, and the abiotic suite of these four factors were each paired with relative abundance of a given species over the course of one year, to determine whether any significant relationships existed. When species were paired with cloud cover or wind velocity, no significant correlations were found. Only *Euphractus* correlated positively with temperature (n=12, r=0.631, P=0.036), rainfall (n=12, r=0.691, P=0.022), and the abiotic suite (n=12, r=0.591, P=0.050).

Temporal Allocation

The guild is comprised of one large, two medium, and two small size class guild members. Similar-sized myrmecophages were not encountered simultaneously for 10 months of the year (83%).

Discussion

Distribution and Habitat Association

Eight new localities were recorded for four species, six range extensions were recorded for four species, and three Dpto. records were tallied for three species. Two potentially new habitat associations were recorded for two species.

In addition to the edentates reported herein, Wetzel & Lovett (1974) recorded a giant armadillo (*Priodontes maximus*) and some nine-banded armadillos (*Dasypus novemcinctus*) during the late winter and early spring of 1972, primarily from localities 12 (Zalazar) and 14 (Tte. Ochoa) of Figure 1, remarking on localities, new records, habitats, rare species documentation, and taxonomy. Myers & Wetzel (1979) reported on specimens of *Chaetophractus vellerosus* and *C. villosus* and added an additional species, the greater fairy armadillo (*Burmeisteria retusa*), to the known edentate fauna of the Paraguayan Chaco. Redford & Eisenberg (1992) summarized information on the occurrence of brown-throated three-toed sloths (*Bradypus variegatus*) and Chacoan naked-tailed armadillos (*Cabassous chacoensis*) in the Paraguayan Chaco, bringing the total number of edentate species occurring within this biome to eleven.

Factors Determining Composition

Seasonality

The results of this study suggest that austral seasons are not characterized by individual changes in temperature, rainfall, cloud cover, or wind velocity, but rather by a correlated suite of all four of these factors. Mammalian species richness did not change from season to season.

However, because there appeared to be a distinct wet season (summer and fall) and dry season (winter and spring), Kruskal-Wallis tests were used to determine whether variation in species richness occurred between wet versus dry seasons. Although rainfall (TS=6.587, P=0.010), cloud cover (TS=5.115, P=0.024), and the suite of all four factors (T.S.=8.3078, P=0.004) were significantly different between wet and dry seasons, species richness did not change seasonally. Moreover, species activities characterized by seasonal changes were tested separately for each individual species, and again none of the results were significant.

Abiotic Factors

Since only one species (20%) correlated significantly with individual abiotic factors, this would suggest that individual abiotic factors were not significant in structuring the assemblage as a whole. Similarly, only one species (20%) correlated significantly with the suite of abiotic factors, suggesting that a combination of these factors was also not significant in structuring the assemblage as a whole. The fact that no significant correlations were found with cloud cover or relative wind velocity suggests that these factors are not as deterministic in structuring the assemblage as are temperature, rainfall, and all abiotic factors combined.

However, results suggest that *Euphractus* increase activity with increased temperatures, rainfall, and weather activity. This suggests that activity of this species may be largely influenced by abiotic elements. It is likely that increased temperatures and rainfall supplies an abundance of resources in the form of prey. Similar patterns have been noted in other species of edentates, where activity in a concentrated area increases during periods of higher rainfall in response to an abundant prey base (I. Santos, pers. comm.).

Temporal Allocation

A randomization model is needed to properly test patterns of temporal allocation. However, preliminary results suggest that temporal allocation is not significant in determining assemblage composition, as similar-sized myrmecophages were not encountered simultaneously for only 10 months of the year as opposed to 12 months. Had myrmecophages not been temporally sympatric for 11 months of the year, this would have approached significance at the 92% level.

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