Artículo

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SAREM

ANT DIVERSITY IN THE DIET OF GIANT ANTEATERS, *Myrmecophaga tridactyla* (PILOSA: MYRMECOPHAGIDAE), IN THE IBERÁ NATURE RESERVE, ARGENTINA

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ABSTRACT. The giant anteater, *Myrmecophaga tridactyla,* globally categorized as a vulnerable species, has disappeared in several regions of its original distribution in Argentina. A program to reintroduce the species has been conducted in the Iberá Nature Reserve in Corrientes province since 2006. The diet of released giant anteaters was studied to determine the identity of their prey, and establish whether they have preference for ants or termites or, rather, prefer certain feeding habitats (e. g., open or closed). Twenty two fecal samples were randomly collected during 2008-2013, and heads and mesosomes were recovered. We identified 12 taxa of ants and only one taxon of termites. Observed taxa represent around 80% of the taxa expected to be eaten by anteaters. *Camponotus* was the most common ant genus, and *Acromyrmex* and *Solenopsis* were the numerically most abundant genera. The ant taxa ingested by *M. tridactyla* were reflective of their natural availablility in the area, suggesting that giant anteaters had no preference for any particular prey. They mainly consumed ant species of the genera *Solenopsis*, *Camponotus* and *Acromyrmex* with conspicuous nests that occur mostly in open habitats of the reserve and not in the most preferred habitat (forest). One possible explanation is that anteaters reduce their foraging search time, and consequently the time they are out in open habitat, so avoiding predation risk and thermal injuries. Thus, conservation of both open and closed habitats would be essential for maintaining the reintroduced populations of giant anteaters.

RESUMEN. Diversidad de hormigas en la dieta del oso hormiguero gigante, *Myrmecophaga tridactyla* (Pilosa: Myrmecophagidae), en la Reserva Natural Iberá, Argentina. El oso hormiguero gigante, *Myrmecophaga tridactyla*, es una especie catalogada como vulnerable tanto a nivel mundial como en Argentina, donde desapareció en varias regiones de su distribución nativa. Un programa de reintroducción de especies se lleva a cabo desde 2006 en la Reserva Natural Iberá en Corrientes. Se estudió la dieta de los osos hormigueros gigantes liberados para determinar la identidad de sus presas y conocer si poseen preferencia por hormigas o termitas o por sitios de alimentación (abiertos o cerrados). Se colectaron 22 muestras de heces entre 2008-2013, recuperándose cabezas y mesosomas. Estos tagmas fueron identificados en 12 taxones de hormigas y uno de termitas. Los taxones observados representaron el 80% de lo esperado a ser ingerido por los osos. *Camponotus* fue el género más común, y *Acromyrmex* y *Solenopsis* los más abundantes numéricamente. Los taxones ingeridos por *M. tridactyla* se relacionaron positivamente con la disponibilidad del área, sugiriendo que los osos no tienen preferencia por presas en particular. Principalmente consumieron hormigas con nidos conspicuos de *Solenopsis*, *Camponotus* y *Acromyrmex* que se encuentran mayormente en áreas abiertas de la reserva y no en el bosque,

hábitat preferido. Creemos que debido a la alta disponibilidad de esas presas, los osos reducen su tiempo de búsqueda de forrajeo, y por ende, su tiempo de permanencia en áreas abiertas, evitando así riesgos de prelación y daños térmicos. La conservación de ambos hábitats, abiertos y cerrados, sería esencial para el mantenimiento de la población reintroducida de osos hormigueros gigantes.

Key words: conservation, diet preference, feces, prey availability, wild anteaters.

Palabras claves: conservación, disponibilidad de presas, heces, oso hormiguero salvaje, preferencia

INTRODUCTION

The giant anteater (*Myrmecophaga tridactyla* Linnaeus, 1758) is a large insectivorous mammal (Pilosa: Myrmecophagidae) native to Central and South America. This species is considered highly vulnerable in its homeland as a consequence of road kills, deforestation (mostly for agriculture), grassland burning, and hunting (International Union for Conservation of Nature 2013). Anteater is a common name for the four extant mammal species of the suborder Vermilingua (meaning "worm tongue") that almost exclusively eat ants (Hymenoptera: Formicidae) and termites (Isoptera). The other three species are the silky anteater *Cyclopes didactylus* (Cyclopedidae) and two Myrmecophagidae: the southern collared *Tamandua tetradactyla* and the northern collared *Tamandua mexicana*.

The giant anteater is the largest extant Xenarthra, reaching up to two meters of total body length, including the tail, and weighting 40 kg in adulthood (Drumond 1992). *Myrmecophaga tridactyla* is a solitary species that does not show strong sexual dimorphism (Camilo-Alves 2003). Because of its low metabolic rate and body temperature (27-33°C), anteaters are very susceptible to extreme temperatures (McNab 1984). In consequence, their daily activity pattern changes from diurnal in the colder seasons to nocturnal in the warmer periods of the year (Camilo-Alves & Mourão 2006; Di Blanco et al. 2012, 2016). The giant anteater has home ranges between 2 and 25 km² (Medri & Mourâo 2005). Their home ranges contain open areas where they spend most of the time feeding, and forested areas, closed scrubs or high grasslands that they use as anti-predatory and thermal shelter (Camilo-Alves & Mourão 2006; Mourão & Medri 2007; Di Blanco et al. 2015, 2017).

Myrmecophaga tridactyla is one of the most specialized mammalian predators that eats almost exclusively ants and termites (Redford 1985; Rodrigues et al. 2008), for which they have extremely long tongues and powerful claws adapted to destroy anthills and termite mounds. Early studies established that giant anteaters feed mainly on ants, and occasionally on termites (Montgomery 1985; Redford 1985, and references therein). Several studies have been additionally conducted on the diet of wild and captive giant anteaters in central (Cunha et al. 2015), southwestern (Medri et al. 2003) and central eastern (Shaw et al. 1987; Drummond 1992) Brazil and Colombia (Sandoval-Gómez et al. 2012). However, hardly anything is known from Argentina, the southern limit of their distribution, with exception of a recent study conducted by Gallo et al. (2017) in the Chaco ecoregion, northwestern Argentina. This work provides novel information on the presence of ants found in feces of wild giant anteaters, although relative abundances are not reported.

The wide geographical distribution of *M. tridactyla* ranges from southern Mexico to northern Argentina (Chebez & Cirignoli 2008). However, it is considered vulnerable in Argentina (Superina et al. 2012), where it disappeared in the provinces of Tucumán and Córdoba, and presumably also in Corrientes since around the middle of the twentieth century (Chebez & Cirignoli 2008), due to the fragmentation of its habitat by urbanization, spread of agriculture and other factors like direct mortality by bulldozer clearing, fire, fights with domestic

dogs and their owners, road kills and deliberate hunting (Jiménez-Peréz 2013), a process also observed in Brazil (Diniz & Brito 2013).

A multispecies reintroduction program to restore a large ecosystem in Corrientes was initiated in the Iberá Nature Reserve (INR) in 2007 (Zamboni et al. 2017). This ambitious program started with the reintroduction of giant anteaters in the INR, where deforestation and traditional cattle management may have caused the local extinction of the species (Di Blanco 2015; Jiménez-Peréz et al. 2016). From 2007 to 2015, 47 individuals were released successfully in two locations of the INR, and it is believed that at least 28 anteaters were born there (Jiménez-Peréz et al. 2016; The Conservation Land Trust 2017). All anteaters released were monitored to assess, among other things, their habitat use, home ranges (Di Blanco 2015; Di Blanco et al. 2012, 2015, 2017) and activity patterns (Di Blanco 2015; Di Blanco et al. 2016), although nothing is known about their local diet.

Food and habitat are the most common foci in resource selection studies (Manly et al. 2002), and the distribution of food is often one of the most important factors defining spatial characteristics of a given species. Open savannas at INR showed more ant species, individuals, biomass, and functional groups of ants than other habitats (Calcaterra et al. 2010a). Giant anteaters spend most of their time feeding in open areas (Camilo-Alves & Mourão 2006; Mourão & Medri 2007). However, this habitat type was avoided by anteaters in the INR, probably because the vegetation cover had a buffering effect from extreme temperatures and the trees acted as a refuge, decreasing risk of predation (Di Blanco et al. 2015). Still, there is no clear evidence of the presence of potential predators (e. g., jaguar and cougar) in the INR during the last decades, with the only exception of a cougar that was recorded several times by camera traps in 2008 (Di Bitetti et al. 2010). However, there were no records of anteaters being either damaged or killed by the cougar after those records. In spite of this, it has been hypothesized that food availability may not be the main factor affecting habitat use of reintroduced giant anteaters (Di Blanco et al. 2015). If avoiding risk of predation and seeking protection from extreme temperatures are more important than prey availability, it would be expected that giant anteaters in the INR would consume a higher abundance of forest prey species than open savanna prey species.

The main objective of this study was to determine the relative abundance and richness of ants and termites in the diet of *M. tridactyla* released into the INR, and secondarily, to determine whether giant anteaters show preferences in their diet and habitat use. We aim at answering questions such as: 1) do anteaters consume taxa in proportion to their natural abundance?; 2) do they prefer ants above termites?; 3) do they select prey on the basis of their size?; and 4) do they preferentially feed in closed, forested areas or in open habitats, such as open savannas?

MATERIALS AND METHODS

Study area

The Iberá Natural Reserve (INR) is located in the center of the province of Corrientes, Argentina, and comprises 13 000 km^2 that protect varied landscapes, including wetlands, temporary freshwater lakes, grasslands, open and closed savannas, and hygrophilous forests (Canziani et al. 2003). The climate is subtropical with average temperatures of around 15-16 °C, and absolute minimum temperature of -2 °C in winter; summer temperatures average 27-28 °C, with an absolute maximum temperature of 44 °C. Mean annual rainfall is around 1500-1800 mm (Neiff & Poi de Neiff 2006).

Collection and preservation of samples

From October 2007 to December 2013, 31 giant anteaters (17 males and 14 females) were released in El Rincón del Socorro (RS, the first reintroduction site), a private ranch that is part of the INR, next to the town of Carlos Pellegrini (Di Blanco et al. 2012, 2015; Jiménez-Pérez 2013). All anteaters released were fitted with harnesses equipped with very high frequency transmitters (Telonics, Mesa, Arizona). Released animals were of different ages (**Table 1**) and originated from the Argentine Chaco region (Jiménez-Pérez 2013). Animals were located by "homing in", following the radio signal until the animal was actually seen or heard, and then

Table 1
Name, sex, age and release date of anteaters released in the Iberá Natural Reserve and collection date and season of their feces. F = Female, M = Male, U = Unidentified anteater, A = Autumn, S = Summer, Sp = Spring, W = Winter.

Sample	Name	Sex	Age (months)	Release date	Collection date of feces (season)
1	Arandú	M	17	15/08/2008	26/09/2008 (Sp)
2					30/09/2008 (Sp)
3					26/08/2009 (W)
4					27/09/2010 (Sp)
5	Mishky	F	35	09/01/2009	10/09/2009 (W)
6					13/09/2009 (W)
7					09/10/2009 (Sp)
8					25/08/2013 (W)
9	Tota	F	75	15/08/2008	05/10/2008 (Sp)
10					09/06/2011 (A)
11					05/08/2011 (W)
12	Hatá	M	>48	01/07/2010	26/07/2010 (W)
13	Ivoty Porá	F	30	17/10/2007	27/01/2008 (S)
14	Machetero	M	13	14/05/2009	14/06/2009 (A)
15	Olivia	F	12	02/02/2012	12/07/2012 (W)
16	Panchita	F	19	14/10/2010	25/01/2011 (S)
17	Preto	M	30	17/10/2007	27/01/2008 (S)
18	Scarface	M	>38	13/08/2011	22/08/2011 (W)
19	U1	-	-	-	02/01/2008 (S)
20	U2	-	-	-	03/01/2008 (S)
21	U3	-	-	-	01/02/2008 (S)
22	U4	-	-	-	02/02/2012 (S)

followed for varying periods of time (Di Blanco et al. 2012, 2015).

To assess the diet of anteaters, their feces were randomly collected in 21 opportunities between January 2008 and August 2013 during animal tracking or monitoring, in habitats with high visibility or open understory grass layers in savannas and forests in RS. A total of 22 samples belonging to 10 (32%) identified (5 of each sex) and four unidentified anteaters of the 31 released giant anteaters were collected (**Table 1**) and preserved in 70 and 96% alcohol vials.

Sample examination

A subsample of 5 grams (dry weight) of feces was taken from each container. Samples were washed and shredded under a dissecting microscope in order to extract all recognizable cuticular structures of ants and termites (Medri et al. 2003; Sandoval-Gomez et al. 2012; Gallo et al. 2017). Once separated, structures were preserved in 70% ethyl alcohol for subsequent identification. Different identified tagmata (heads, mesosomes, and gasters) were stored in separate vials for identification to the lowest possible taxonomic level (species, genus or subfamily) using available keys (Kusnezov 1978; Palacio & Fernández 2003; Bolton 2013; and other keys and photographic material available in Antweb: https://www.antweb.org/). The number of structures (heads and mesosomes) of each taxon in each sample was counted. Samples were deposited in the Fundación para el Estudio de Especies Invasivas (FuEDEI) entomological collection.

Data analysis

Richness was estimated using EstimateS 9.1.0 software (Colwell 2013) with a presence-absence matrix. Sample-based taxon accumulation curves (genera and subfamilies for ants, and orders for termites) were used to compare density of taxa (number of taxa per sampling unit using both heads and mesosomes) as an indicator of sampling efficacy. Curves were obtained after 100 randomizations. Three nonparametric indexes (Chao 1, ACE and Bootstrap) were used to estimate the total number of taxa expected to occur in the diet of the giant anteaters.

Nonmetric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix with presence-absence of grouped head and mesosome data were used to compare similarity patterns in ant and termite taxa consumed by *M. tridactyla* per season (22 samples) and sex (18 samples). The ordinations were performed with taxa that occurred in four or more samples. Thus, only eight of the 13 taxa (*Acromyrmex*, *Atta*, *Camponotus*, *Crematogaster*, Dolichoderinae, *Pheidole*, *Solenopsis*, Isoptera) were used in both analyses. These analyses were tested statistically using an analysis of similarity (ANOSIM and post hoc Bonferroni pairwise comparisons; Clarke & Green 1988) based on 1000 permutations in the Past 3.16 software (Hammer et al. 2001). The Sörensen similarity index was also used to compare the similarity in taxon composition between seasons and sexes with the same matrix, using in NMDS. As there was a large unbalance in the number of samples per year, analysis and comparisons between years were not carried out.

Abundance of each taxon in the diet of anteaters was calculated on the basis of the two most informative types of structures (heads and mesosomes). The mean number of structures and taxa found in each season and sex was compared using one-way analysis of variances (ANOVA) with InfoStat software (Di Rienzo et al. 2015). Spearman's correlation between the number of heads and mesosomes was also calculated, in order to determine if both structures are similarly recovered using Past 3.16 software (Hammer et al. 2001).

The presence and relative abundance of ant taxa found in the feces of *M. tridactyla* were related to the presence and relative abundance of the ant species previously found in the INR by Calcaterra et al. (2010b, 2014) at a large (~14 000 ha) and small (~500 ha) spatial scales, respectively. On a large scale, ants were sampled in (grazed and non-grazed) savannas and grasslands, while on a small scale, sampling was carried out in (burned and unburned) grasslands and open and closed savannas, plus (unburned) forests. However, only ants found in undisturbed (non-grazed and unburned) habitats were used in the analysis. The small scale corresponds to the area where the first anteater individuals were released and established (Di Blanco et al. 2012, 2015, 2016). In both cases, samplings were conducted using five unbaited pitfall traps every 10 meters along one transect in each site; traps were exposed for 48 hours (Calcaterra et al. 2010b, 2014). A lineal regression was calculated using InfoStat software (Di Rienzo et al. 2015) between the relative abundance of ants obtained in the feces and the overall availability of ants found in each one of these two spatial scales (grouping ants from all habitats), that is, without discriminating by habitat type usually used by anteaters (Di Blanco et al. 2012, 2015, 2017) because it is impossible to know in which habitat/s anteaters ate before defecating.

RESULTS

Taxon richness

A total of 13 taxa were identified from the feces of giant anteaters; 12 taxa of ants (species, genera or subfamily) and one taxon of termites (subfamily). Accumulation curves of estimated taxa did not reach the asymptote, indicating that more taxa are expected to occur in the diet of the anteaters (**Fig. 1**). According to two nonparametric richness estimators (Chao 1 and ACE) and an extrapolation of 200 samples, an average of 18.3 taxa was expected to occur, whereas, using a Bootstrap estimator, only 14.5 taxa were expected. Thus, the number of taxa observed in this study (13) represents between 71.0 and 89.7% of the total number of taxa expected to occur in the diet of anteaters in the study area.

By using heads for identification, a higher number of taxa was found (13) than when using mesosomes (7). The mean ($\pm$ SD) richness of heads per sample was 5.1 ± 1.6 taxa (range: 2-8 genera per sample); there were no significant differences between seasons ($F_{3, 18} = 1.71$, $P = 0.201$) or sexes ($F_{1, 16} = 0.08$, $P = 0.775$). The mean ($\pm$ SD) richness of mesosomes was 4.0 ± 1.3 genera per sample (ranging from 1 to 6). There was no difference in taxa per sample between sexes ($F_{1, 16} = 2.87$, $P = 0.110$), however, there was a marginally significant difference
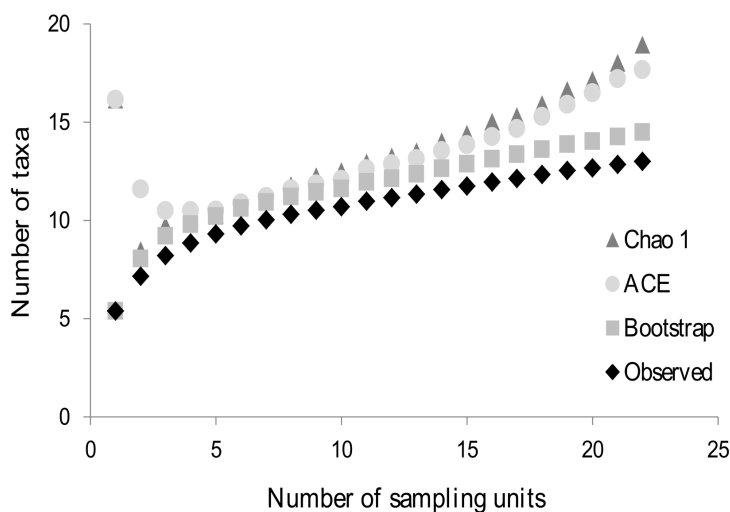
Fig. 1. Taxon accumulation curves from collected heads and mesosomes from feces (all samples pooled) of released giant anteaters in the Iberá Nature Reserve, and the three nonparametric indexes with the most stable asymptote.

between seasons ($F_{3, 18} = 2.98$, $P = 0.059$), but it was only attributed to differences between autumn and summer.

All ant diversity indicators (grouping head and mesosome data) were relatively similar in all seasons, except in autumn (**Table 2**), and between sexes (**Table 3**). Consequently, the mean number of taxa per sample did not differ significantly between seasons ($F_{3, 18} = 1.39$, $P = 0.277$) or sexes ($F_{1, 16} = 1.36$, $P = 0.261$). It is interesting to note that a single sample can contain more than a half of the total taxa found (up to 61.5%).

Taxon composition

The visual ordination of the samples did not show separation in the ingested taxa composition between seasons (NMDS: $R^2 = 0.766$, stress = 0.24; **Fig. 2a**; ANOSIM, $R = 0.047$, $P = 0.280$) or between sexes (NMDS: $R^2 = 0.826$, stress = 0.23; **Fig. 2b**; ANOSIM, $R = -0.007$, $P = 0.470$). The overlapping between seasons was mostly due to the high similarity between winter and the other three seasons (summer, spring and autumn with Sörensen indexes of 0.73, 0.91 and 0.75, respectively). The lowest similarities were observed between summer, spring and autumn (0.67 for all combinations). The highest similarity was observed in the taxa consumed by both sexes (Sörensen index equal to 1).

Most of the heads and mesosomes found belong to the genera *Camponotus* (such as *C. rufipes* and *C. punctulatus*), *Crematogaster, Pheidole* (e. g., *P. aberrans*), and *Solenopsis* (mostly *S. invicta*). Few heads of Dolichoderinae (presumably *Dorymyrmex* or *Linepithema*), *Gnamptogenys*, *Odontomachus*, *Pseudomyrmex*, *Trachymyrmex, Wasmannia* (only *W. auropunctata*) were found. Leafcutter ants, mainly from the *Acromyrmex* genus (e. g., *A. heyeri*, *A. hispidus*), and fewer still of the genus *Atta* (e. g., *A. sexdens*, *A. vollenweideri*) were recorded. Many wings and several heads with ocelli (e. g., *Camponotus*), typically from sexual caste and some sclerites from gasters and legs of ants were also found. Unexpectedly, only a few nasutti morph (Termitidae: Nasutitermitinae) termite heads were recovered. All the Nasutitermes species can be recognized by their soldiers that have a pointed snout at the front of their heads (called nasus). Some mites (Acari) and a Coleoptera head were collected, but they are not considered an item eaten by anteaters.

Abundance

In a few samples, 22 whole ants were found in perfect condition and were easily determined to species: 16 workers belonged to *S. invicta* and 6 workers to *A. hispidus*.

Heads. A total of 11 965 heads was obtained from giant anteater feces: 11 911 of ant heads (99.55%) and only 54 (0.45%) termite heads; 11 627 (97.6%) ant heads were assigned to 11 genera, while 61 (0.5%) could only be assigned

Table 2

Diversity indicators based on taxa found per season grouping heads and mesosomes.

	Summer	Autumn	Winter	Spring
Sampling units	7	2	8	5
No. of taxa observed (% of total observed)	10 (77)	6 (46)	9 (69)	10 (77)
No. mean (± SD) taxa/sample	6.0 ± 1.8a	4.5 ± 0.7a	4.9 ± 1.6a	6.2 ± 0.8a
Maximum taxa/sample	8	5	7	7
No. common taxa[1]	2	3	2	3
No. rare taxa[2]	1	3	3	2

[1] Taxa observed in all samples.
[2] Taxa observed in only one sample.
Similar lowercase letters within rows indicate no significant differences.

to the Dolichoderinae subfamily (probably *Dorymyrmex* or *Linepithema* genera). The remaining 223 heads (1.9%) could not be identified. The most common genus was *Camponotus*, present in 100% of the samples, followed by *Acromyrmex* and *Solenopsis* found in 95.5% and 90.9% of the samples, respectively. The most abundant genus was *Solenopsis* which comprised 41% of the total amount of heads, followed by *Acromyrmex* with 31.9% (**Table 4**, **Fig. 3**). The number of heads per sample did not

Table 3

Diversity indicators based on taxa found per sex, grouping heads and mesosomes.

	Female	Male
Sampling units	10	8
No. of taxa observed (% of total observed)	11 (85)	10 (77)
No. mean (± SD) taxa/sample	5.0 ± 1.6a	5.8 ± 1.0a
Maximum taxa/sample	7	7
No. common taxa[1]	2	3
No. rare taxa[2]	4	2

[1] Taxa observed in all samples.
[2] Taxa observed in only one sample.
Similar lowercase letters within rows indicate no significant differences.

differ between seasons ($F_{3, 18}$=0.65, P=0.590) or sexes ($F_{1, 16}$=0.25, P=0.624).

Mesosomes. A total of 9216 ant mesosomes were recovered from giant anteater feces, which could be assigned to 7 genera of ants. Again, *Camponotus* was the most common genus, present in 100% of the samples, followed by *Acromyrmex* (90.9%) (**Table 4**). *Solenopsis* and *Acromyrmex* were the most abundant genera: 42.2% and 34.8% of the total number of mesosomes, respectively (**Fig. 3**). No termite mesosome was recovered from feces of giant anteaters. The number of mesosomes per sample did not differ between seasons ($F_{3, 18}$=0.90, P=0.462) or sexes ($F_{1, 16}$=0.87, P=0.365).

Diet preference

As the numbers of heads and mesosomes of each taxon (ants and termites) were strongly correlated (R^2=0.915, P<0.001), taxon preference was based only on heads because they provide greater resolution. The number of heads of each taxon found in the diet of *M. tridactyla* was related to the availability analyzed on different spatial scales (large and small) in the INR (Calcaterra et al. 2010b, 2014, respectively) (**Table 4**). On a large scale, the relationship was low and non-significant (R^2=0.25, $F_{1, 16}$=2.39, P=0.166). Nevertheless, the relationship was higher and significant on a small scale (R^2=0.42, $F_{1, 20}$=6.52, P=0.031).
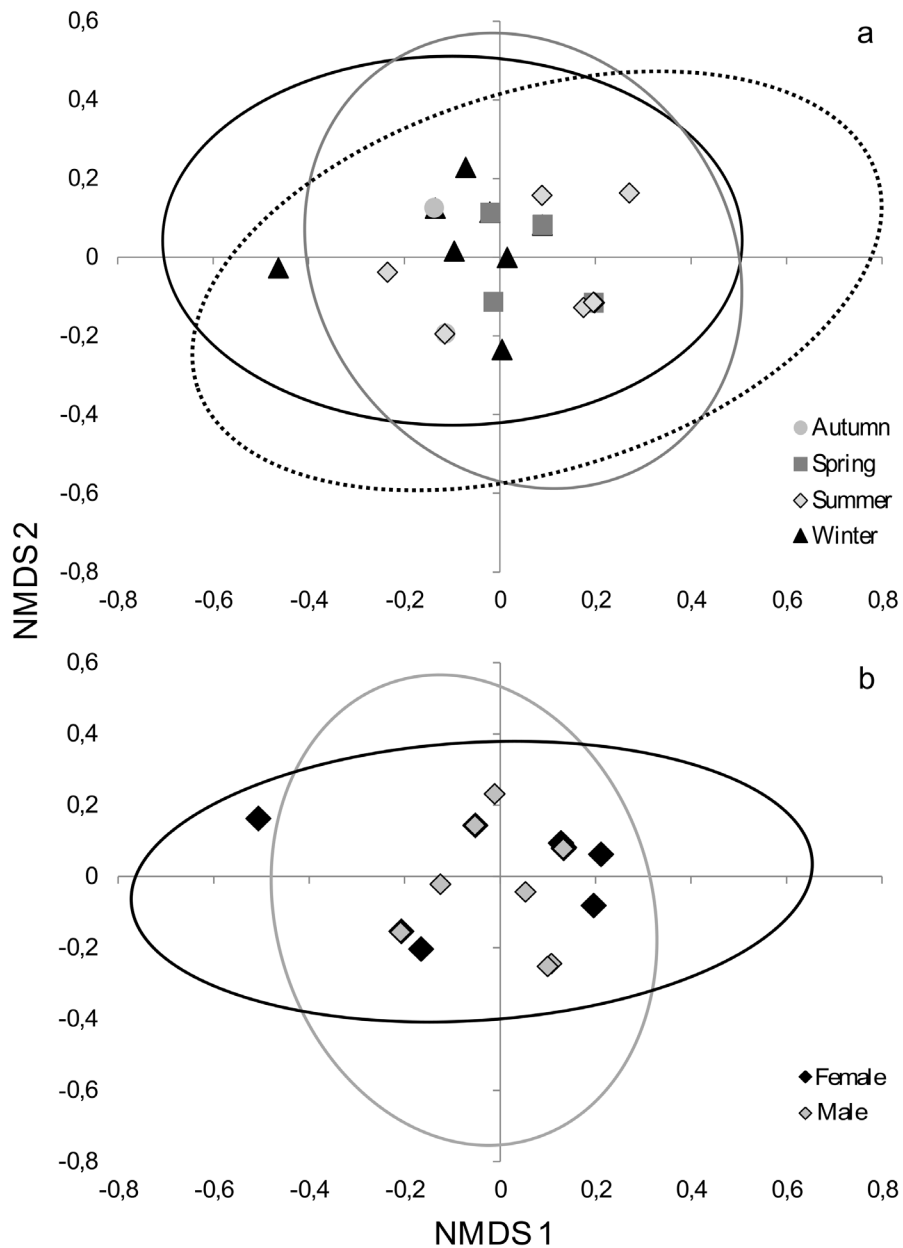
Fig. 2. Nonmetric multidimensional scaling ordination plot from presence of heads and mesosomes of taxa found in feces samples of giant anteaters in (a) different seasons ($R^2 = 0.766$, stress $= 0.24$) and (b) sexes ($R^2 = 0.826$, stress $= 0.23$). The ellipses represent 95% confidence. Note that autumn does not have a confidence ellipse because with two points the program is not capable of calculating it.

Table 4

Number (percent of samples) of heads and mesosomes of ants and termites recovered from 22 samples of 5 grams of feces of released anteaters in Iberá Nature Reserve. Ant availability was obtained from the literature at two spatial scales: large scale (~14 000 ha in Calcaterra et al. 2010b) and small scale (~500 ha in Calcaterra et. al. 2014).

| Taxa	Consumed		Availables	
	Head	Mesosome	Large scale	Small scale
Solenopsis	4909 (91)	3891 (86)	138 (55)	1286 (94)
Acromyrmex	3811 (96)	3204 (91)	4 (15)	0
Camponotus	2031 (100)	1570 (100)	35 (40)	166 (78)
Pheidole	666 (59)	381 (50)	132 (75)	355 (78)
Atta	87 (18)	142 (36)	2 (10)	8 (11)
Crematogaster	71 (14)	27 (36)	2 (10)	125 (78)
Dolichoderinae	61 (41)	0	5 (10)	77 (56)
Wasmannia	47 (14)	1 (5)	-	404 (28)
Trachymyrmex	2 (5)	0	6 (5)	5 (17)
Gnamptogenys	1 (5)	0	1(5)	-
Odontomachus	1 (5)	0	-	0
Pseudomyrmex	1 (5)	0	-	0
Isoptera	54 (55)	0	-	-
Unidentified	223 (46)	0	-	-
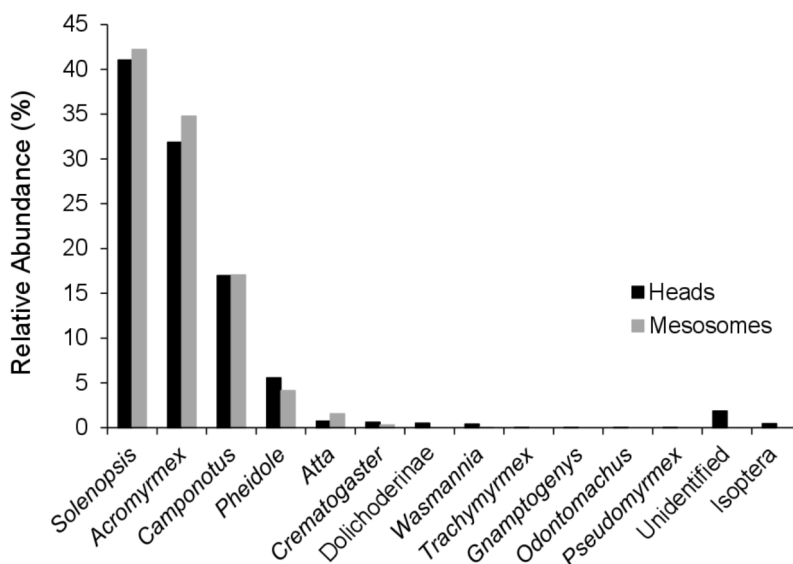
Fig. 3. Relative abundance of identified heads (black bars) and mesosomes (grey bars) of ants and termites from feces of giant anteaters.

DISCUSSION

Diet of giant anteaters reintroduced in the INR was mainly composed of ants, and very secondarily, of termites. This agrees with the diet of wild giant anteaters observed by Redford (1985) and Shaw et al. (1987) in the Brazilian states of Goias and Minas Gerais, respectively, and recently by Gallo et al. (2017) in the Chaco ecoregion in Argentina. The latter found 22 morphospecies in 14 ant genera and indicated that termites were recovered in fewer numbers than ants. In spite of the low number of taxa and individuals of termites recovered from the feces of anteaters, they appeared in the half of the samples collected in the INR.

Medri et al. (2003) observed that ants were consumed on a higher proportion than termites (81 against 19%) only in June (winter). However, winter was the season with more termites in the diet of *M. tridactyla* in the INR. It could be due to the lower availability of ants recorded in winter in the INR (Calcaterra et al. 2014) that would force the anteaters to consume more termites, as they do not decrease their abundance as ants do. This difference could also be mostly because of latitudinal variations in prey availability. In other cases, differences could be local or longitudinal. For example, Shaw et al. (1987) found in Serra da Canastra National Park in the Minas Gerais state (Brazil), a 9:1 ant:termite ratio, whereas Drummond (1992) found, in the same place, a 1:1 ratio (local variations). Meanwhile, Redford (1985) got the same relationship as Shaw et al. (1987) in the Emas National Park, in Goias state, in Brazil (longitudinal differences); whereas, Cunha et al. (2015) found slightly more termites (17%) than ants (11%) in the stomach content of a road-killed giant anteater in the Goias state (Brazil).

Regarding the natural diversity of ants and termites in Argentina, a total of 661 ant species in 71 genera, and 7 subfamilies, have been reported from all the biomes (Cuezzo 1998), whereas only around 80 termite species in 4 subfamilies have been found in 7 phytogeographical provinces: Yungas (12 spp.), Chaqueña (78 spp.), Paranaense (41 spp.), Espinal (17 spp.), Pampeana (7 spp.), Monte (7 spp.), and Subantárctica (1 spp.) (Torales

et al. 2005, 2009). These data indicate much higher ant than termite diversity, as observed in the diet of the anteaters in the Chaco ecoregion (Gallo et al. 2017). The same pattern has been reported for the INR, where more than 100 ant species and only a dozen of termite species occur (Calcaterra et al. 2010a; b, 2014; Jiménez-Peréz 2013). An alternative explanation for the discrepancy in the quantity of ants and termites recovered from feces of *M. tridactyla* in the INR and other sites could be that the cuticle of the termites is more labile (fragile) than the cuticle of the ants, and thus, it could be digested more easily by the gastric acid in the stomach of the anteaters. This supposition arose from observing that the nasuti heads found in the feces were mostly in very bad condition, sometimes only differentiated by the frontal tube. Nasutitermes have strictly chemical defense mechanisms and their soldiers have vestigial mandibles and a frontal tube which is their only weapon against predators (Scholtz et al. 2008).

Among the ants, workers of the *Solenopsis* genus were the main component (41%) of the diet of giant anteaters in the INR. The following most important ant genera were *Acromyrmex* (32%) and *Camponotus* (17%). The latter was the only genus present in all samples in the INR and it was the richest genus with five morphospecies as shown in the work of Gallo et al. (2017). These three genera comprised around 90% of the total heads counted and were also recovered from feces of *M. tridactyla* in Brazil (Medri et al. 2003). Leaf-cutting ants from the *Atta* genus (e. g., *A. sexdens*, *A. vollenweideri*) are represented in low numbers in the samples despite being present in the INR (Calcaterra et al. 2010a; b, 2014). These ants seem to be highly preferred by *M. tridactyla* in Colombia (Sandoval-Gómez et al. 2012) and denote a very important food source in the tropics, where they are more common, abundant and have larger colonies than the *Acromyrmex* species.

The diet composition of *M. tridactyla* in the INR indicates that it consumes mostly terrestrial ant species with conspicuous nests containing from hundreds of big workers (e. g., *C. punctulatus*, *C. rufipes*, *A. heyeri*, *A. hispidus*) to several thousand small work-

ers (e. g., *S. invicta*). A colony of *S. invicta* can contain up to 250 000 workers (Tschinkel 2006). These ant species nest mostly in open habitats, such as grasslands or open savannas with grass predominance (Calcaterra et al. 2010a; b, 2014), where *M. tridactyla* searches its food (Silvestre et al. 2003; Sandoval Gómez et al. 2012; Di Blanco et al. 2015). Because of their conspicuous nests containing a large quantity of ant biomass easy to be consumed, giant anteaters can ingest a large quantity of biomass in a short time (Fernández 2003; Miranda et al. 2009). A similar selection was observed in the yellow armadillo, *Euphractus sexcinctus*, in abandoned rice fields with a high density of nests of *C. punctulatus* in the INR (Calcaterra et al. 2010a). This foraging behavior contrasts with that observed in the most forested Chaco ecoregion, where giant anteaters presumably spent more time searching than eating the ants present mostly in the leaf litter (Gallo et al. 2017). There, the most consumed ants were the army ants of the genera *Eciton* or *Labidus*, followed by above-ground ants and some few arboreal ants. This also suggests the high plasticity of giant anteaters in terms of their diet.

Redford (1985) postulated that *M. tridactyla* did not eat according to prey size or nutritional quality in captivity, but it did in the wild. They spent more time on nests with winged individuals (larger ones and present only in the warm season), which is probably related to their high nutritional value. This difference was attributed to the foraging behavior of giant anteaters that is different in captivity, where they simply have to take the prey, while in the wild they have to search and capture them. The choice of preys depends on their nutritional value, availability and response to attack. In this work, many winged individuals (sexual), a few wings, and several heads with ocelli, typically from this caste, were found. Similarly, winged termites represent a bigger source of food than worker caste to other vertebrates, like birds (Eisenmann 1961).

The size of ant workers consumed by giant anteaters in the INR was variable; they consumed both big *Camponotus* and *Acromyrmex* workers, and smaller *Solenopsis* workers. However, although colonies of *Solenopsis* species

(e. g., *S. invicta*) have many more workers than colonies of bigger carpenter and leaf-cutting ants (e. g., *C. punctulatus*, *C. rufipes*, *A. heyeri*, *A. hispidus*), the average weight of *S. invicta* workers (0.15 mg) is around sixteen times lower than the average weight of grouped workers of the biggest *Camponotus* and *Acromyrmex* species (~2.5 mg) (Calcaterra et al. 2010a). Thus, the quantity of biomass of *Acromyrmex* consumed by giant anteaters was much higher than that of *S. invicta*.

The periods of activity of *M. tridactyla* are also important as different ant species have different annual and daily foraging patterns, and this may influence their diet. Medri et al. (2003) recorded only a few ant and termite nests attacked by giant anteaters in Brazil between April and October, the coldest half of the year, when ant foraging activity is overall lower. They ate nine ant species, of which individuals of *Solenopsis* (probably conspicuous fire ant nests) were the most frequently attacked (82% of total attacked nests) and only two termite species were attacked in June (winter). In the warmer season, nests are bigger and contain a higher number of workers (sexual and brood). However, since giant anteaters mainly fed directly from the nests when breaking them (Medri et al. 2003), maybe their diet was not so much based on whether they found foraging ants than the size or age of the colony. On the other hand, there was a strong overlapping of most seasons, mainly because of the higher similarity between winter and the other seasons, including autumn although only two samples were taken in this season, whereas between 5 and 8 samples were taken in each of the other seasons. Nevertheless, reintroduced giant anteaters presented seasonal variations in habitat selection, using grasslands more frequently in winter (Di Blanco 2015). This would probably be more related to seasonal variability in ant biomass availability (Calcaterra et al. 2014) than to differences in ant composition. A more balanced design among seasons (and years) could confirm if *M. tridactyla* effectively showed seasonal variations in their diet in the INR. No difference was found between sexes in the composition of taxa (or abundance of tagma) ingested by anteaters.

The spatial scale of studies is important to understand biological process, such as food resource preferences. In our case, the relationship (available/ingested ants) was higher and significant on a smaller scale that corresponds to the area where the first anteaters were released in INR (Calcaterra et al. 2014). Thus, it suggests that anteaters could be consuming their prey according to their relative abundance on this scale (~500 ha), which is similar to their usual home range (Di Blanco 2015), or even closer to the individual home range in the INR (an average of 2100 ha between males and females, Di Blanco et al. 2017) than on a large scale (~14 000 ha) that is closer to the range used for all grouped individuals of the first reintroduced population (~12 000 ha) (Di Blanco et al. 2015). We believe that the loss of relationship on a large scale could be due mostly to a poorer spatial match between the feeding sites (from where ants were incorporated to the feces) and ant collection sites (Calcaterra et al. 2010b).

This study revealed that it was possible to recover most taxa expected to be present (80%) in the diet of *M. tridactyla* in the INR. The most recognizable structures were heads and mesosomes and followed by sclerites from gasters, legs of ants and several termite heads. However, legs and sclerites of gasters could not be associated with any kind of taxa. Although it was difficult to identify ants recuperated from the feces of giant anteaters at taxonomic levels lower than genus (e. g., Gallo et al. 2017), this methodology seems at least to recover most of the ants ingested by the dwarf armadillo, *Zaedyus pichiy* (Cingulata: Dasypodidae) (Superina & Elizalde 2011). In this study, the number of workers of leaf-cutting ants (*Acromyrmex lobicornis*) recovered from feces was around 87% of the total number of ants effectively consumed in the steppe habitat in Rio Negro province, in the Argentine Patagonia. These studies illustrate that feces examination can be an appropriate method for diet estimations based mainly on heads of each taxon. Curiously, other methodologies to study anteater diets that presumably preserved heads and mesosomes better, such as stomach content of

anteaters, have been less successful to recover taxa; such is the case of a road-killed giant anteater in central Brazil, in which 71% of the stomach content could not be identified, or even differentiated between ants and termites (Cunha et al. 2015).

In summary, reintroduced giant anteaters mainly consumed terrestrial ants, as in most of the previous studies. This species, despite their specialized diet and the geographic origin of reintroduced individuals, showed high plasticity in terms of prey consumption, eaten in proportion to their abundance in nature. Thus, the higher biomass was mostly composed of the most commonly distributed and numerically abundant species (e. g., *C. punctulatus*, *C. rufipes, A. heyeri, S. invicta*) that occur mostly in open habitats, such as grasslands and open savannas of the INR. Our results also supported previous assumptions that preys consumed do not reflect habitat selection patterns found for this reintroduced population. Therefore, food resource distribution would be a poor predictor of habitat selection for giant anteaters in this study site, where open habitats are more available than forested areas. A possible explanation could be that high prey availability allows anteaters to limit foraging search time and the time spent in open habitats decreasing the risk of predation and thermal damage. Giant anteaters generally benefit from habitat heterogeneity, where they can use vegetation cover for protection and open habitats for foraging (Cardoso Da Silva & Bates 2002; Prada & Marinho-Filho 2004; Desbiez & Medri 2010; Vynne et al. 2011; Quiroga et al. 2017).

Maintenance of this habitat mosaic of open and closed habitats seems to be essential for the maintaining of self-suitable populations of giant anteaters restored in the INR. The conserving of a greater surface of these habitats, some of which are currently being threatened by the advance of the agriculture frontier, as the savannas, is also crucial for increasing the size of their populations, which will guarantee the future survival of this species within and outside of this protected area.

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