

Diet of *Tadarida brasiliensis* (Mammalia: Chiroptera) in Northwestern Argentina

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In Argentina, the study of feeding habits of bats was practically restricted to frugivorous species, whereas data on the insectivorous bat diet was scarce and anecdotal. Thus, the aim of this study was to analyze the diet of *Tadarida brasiliensis* along the Yungas Forest, Argentina, at sites with different degrees of disturbance. Through the analysis of feces, arthropod orders were identified, volume and frequency of occurrence were estimated for each food item, and the niche breadth was estimated for the species. Finally, the diet was compared between capture sites, sexes, and seasons; finding variations among sites and seasons. The diet of *T. brasiliensis* contains arthropods belonging to nine orders and one undetermined taxon. Lepidoptera, Hymenoptera, and Coleoptera represent the highest volume proportions in the diet. The results add new and important information about the biology of *T. brasiliensis* in the southern part of its distribution.

Key words: foraging activity, insectivorous bats, Molossidae, Yungas Forests

INTRODUCTION

At present, there are more than 1,300 recognized species of bats worldwide (Fenton and Simmons, 2014), and about 75% of them feed on insects (Hutson *et al.*, 2001). Insectivorous bats are voracious predators of nocturnal insects, including many crop and forest pests, providing substantial ecosystem services (Boyles *et al.*, 2011). The food habits of these bats can be influenced by several factors, including the time of nightly emergence (Erkert, 1982; Lee and McCracken, 2001), seasonally-changing energy and nutrient demands (Kunz, 1974; Anthony and Kunz, 1977; Barclay, 1994; Kunz *et al.*, 1995; Lee and McCracken, 2002), temporal and spatial distribution of their prey (Kunz, 1988; Wolda, 1988; Whitaker *et al.*, 1996; Henry *et al.*, 2002), and prevailing climatic and meteorological conditions (Wellington, 1945; Anthony *et al.*, 1981; Lee and McCracken, 2005). Dietary studies of insectivorous bats are critical for understanding their role in the ecosystem and as regulators of insect abundance (Debelica *et al.*, 2006).

Tadarida brasiliensis is a widely distributed molossid bat; it is found from southern Chile and

Argentina, including the Islas Malvinas, to Oregon, southern Nebraska and Ohio in United States of America, and the Greater and Lesser Antilles (Simmons, 2005; Barquez *et al.*, 2015). This is an insectivorous and migratory species that usually forms large colonies with millions of individuals (Barquez *et al.*, 2015). *Tadarida brasiliensis* consumes enormous quantities of insects, including several lepidopteran species of economic importance (Lee and McCracken, 2002, 2005; Cleveland *et al.*, 2006; Riccucci and Lanza, 2014). Thus, this bat species brings positive economic and environmental benefits (Cleveland *et al.*, 2006; Boyles *et al.*, 2011; Wanger *et al.*, 2014).

Several studies have been conducted on the diet of *T. brasiliensis* giving information about different aspects, as daily and seasonal patterns (Whitaker *et al.*, 1996; Lee and McCracken, 2005), foraging activity in different types of land use (Lee and McCracken, 2002), and the pest control service provided by the species (Cleveland *et al.*, 2006; Boyles *et al.*, 2011; McCracken *et al.*, 2012). However, these studies were restricted to the northern hemisphere, the information about the diet of *T. brasiliensis* in its southern portion of distribution is scarce.

In Argentina, the study of feeding habits of bats has focused principally on frugivorous species (Iudica, 1995; Iudica and Bonaccorso, 1997; Gianini, 1999; Sánchez *et al.*, 2012a, 2012b), whereas data on the insectivorous bat diet are scarce and anecdotal (Bracamonte and Lutz, 2013; Lutz, 2013). Moreover, the evaluation of the effects of variables, such as alteration degree of habitat, sex, and season on the diet of bats is nonexistent in Argentina. In the present study, we describe the diet of *Tadarida brasiliensis* in the southern extreme of the Yungas Forests in Argentina, and evaluate differences in diet between conserved and disturbed sites, sexes, and seasons. Because of its wide foraging range on horizontal and vertical scales (Fenton and Griffin, 1997; Lee and McCracken, 2002, 2005) we expect that this species has a diverse diet. Regarding the effects of the three analyzed variables, previous studies of *T. brasiliensis* found daily and seasonal variations (Whitaker *et al.*, 1996; Lee and McCracken, 2005) and, in three major types of land use, differences in foraging activity (Lee and McCracken, 2002), but no significant differences between sexes (Kunz *et al.*, 1995; Lee and McCracken, 2002). Therefore, we expect to observe differences in diet of *T. brasiliensis* among types of sites and seasons but not between males and females.

MATERIALS AND METHODS

Study Area

The study area belongs to the subtropical Yungas Forests ecoregion (Burkart *et al.*, 1999). It is distributed from the borderline with Bolivia to the north of the province of Catamarca (22–29°S), including three neighboring provinces, Jujuy, Salta, and Tucumán (Brown *et al.*, 2001). The surveyed area corresponds to the montane forest district, which is extended approximately between 700 and 1500 m (Burkart *et al.*, 1999; Brown *et al.*, 2001). The observed vegetation is typical of the district, which is dominated by tall trees, such as *Cedrela lilloi* (Meliaceae), *Enterolobium contortisiliquum* (Fabaceae), and *Cinnamomum porphyrium* (Lauraceae); smaller trees, less than 20 m, as *Allophylus edulis* (Sapindaceae), *Celtis boliviensis* (Celtidaceae), among others, are also recorded. Bushes as *Urera baccifera* (Urticaceae), *Piper tucumanum* (Piperaceae), and *Solanum* spp. (Solanaceae), as well as small and tall herbs (Cabrera, 1976) are present; the epiphytes are abundant, and lichens, ferns, bromeliads, and mosses are dominant (Brown *et al.*, 2001). The climate is warm and humid; the annual precipitation varies between 900 and 1000 mm, and rainfall is concentrated mainly in summer and lasts for about 5–6 months (Burkart *et al.*, 1999).

Sampling

The individuals were collected in eight different localities (Fig. 1), four conserved sites of the Yungas Forests and four places with different types of disturbance. The sites were selected from pairs at different latitudes (see Appendix). The

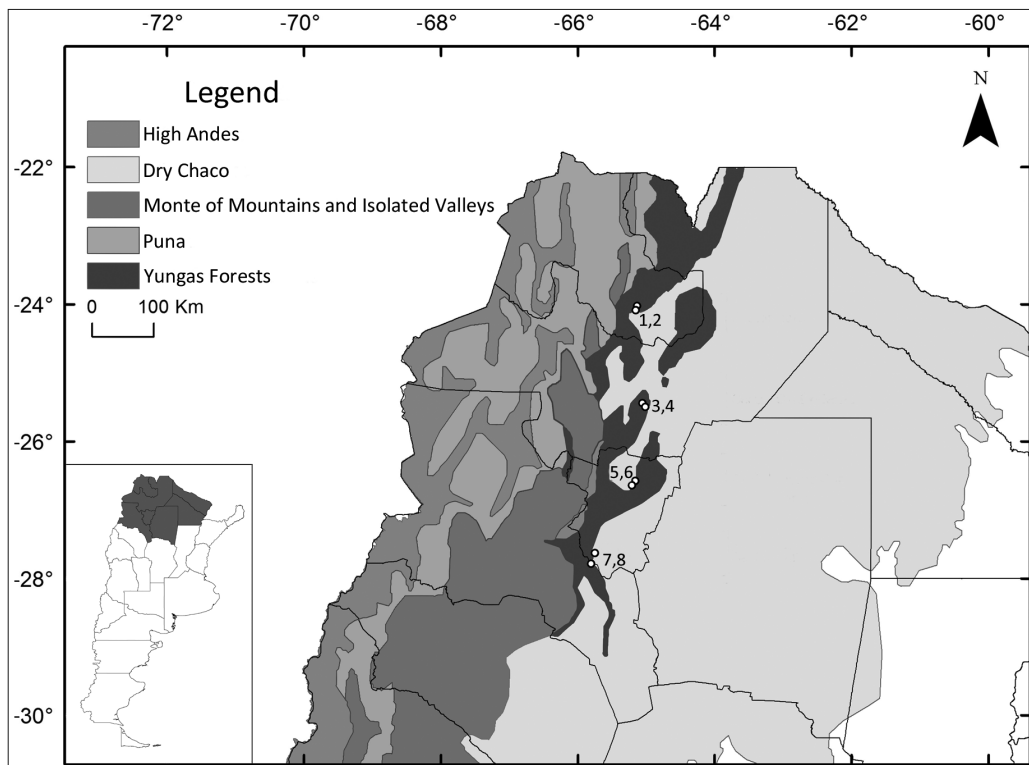


FIG. 1. Collection localities in the Yungas Forests ecoregion, Northwestern Argentina

separation distance between each pair of sites ranged from three to 18 km. In total, 10 surveys of three nights each, between September 2012 and October 2015, were conducted. The sites were selected according to the vegetation structure. In conserved sites, the vegetation was the typical for the montane forest district, where all vegetation strata were recorded. In disturbed sites, the structure of the vegetation was altered and some of the typical strata were missing, usually the bushes and small trees. Additionally, the proportion of native forest in the landscape, as a measure of forest loss, was calculated with ArcGIS 10.1 (ESRI, 2011; Rodríguez-San Pedro and Simonetti, 2015). Forest cover ranged from 98 to 100% in conserved sites and from 79 to 88% in disturbed sites. The source of data used in the GIS analysis was the Instituto Geográfico Nacional of Argentina. The bats were captured using six 12 m mist nets set after sunset, inside the forest and over streams or rivers, and kept open for periods of six hours. External measurements, age, sex, and reproductive condition were recorded from all captured individuals following Díaz *et al.* (1998). Each bat was placed in a separate, clean, cotton cloth bag for at least three hours, and then the feces deposited in the bags were collected (see Lee and McCracken, 2005).

Dietary Analysis

From each bat, up to 10 of the largest and most intact fecal pellets were examined; according to Whitaker *et al.* (1996) five pellets are sufficient to give a reliable estimate of the diet of one individual. Each pellet was soaked and softened in a Petri dish with 70% ethyl alcohol and examined under a dissecting microscope (Lee and McCracken, 2005). Arthropod remains were sorted and identified to the lowest possible taxonomic level (usually family) following Whitaker (1988), Shiel *et al.* (1997), and Whitaker *et al.* (2009). In addition, some samples were confirmed with the help of entomologists. Volume and frequency of occurrence of each food item were estimated. The volume of a prey item for each individual was averaged over all samples collected for that individual bat to provide an index of the proportional contribution of arthropod taxa to the diet of sampled bats (Whitaker, 1988; Lee and McCracken, 2005). The frequency of occurrence is the number of bats in which a particular prey item was identified and provides a standardized measure of the commonness of each prey item in the diet of the bat (McAney *et al.*, 1991). The Levins' measure of niche breadth, $B = 1/\sum p_i^2$, and its standardized version $B_a = B-1/B-n$, were also estimated to assess dietary heterogeneity (Krebs, 1999; Lee and McCracken, 2005), where p_i is the proportion of individuals consuming a particular prey item i and n is the number of possible resource states. B is maximal when the species does not discriminate among resources and has the broadest possible niche. Levins' B is minimal when all the individuals occur in only one resource, showing maximum specialization. The range of B is from 1 to n , whereas B_a is expressed on a scale from 0 to 1 (Krebs, 1999).

Statistical Analysis

The differences in the diet of *T. brasiliensis* among sites, sexes, and seasons were separately evaluated using a Non-metric multidimensional scaling analysis (NMDS — Clarke, 1993). This approach produces an ordination based on a dissimilarity matrix and attempts to represent the pairwise dissimilarity between objects in a low-dimensional space. The algorithm

generates stress values and when these are equal to or below 0.1 are considered fair, while values equal to or below 0.05 indicate good fit. To test significant differences in species diet composition, we performed for each variable a Nonparametric Multivariate Analysis of Variance (NPMANOVA — Anderson, 2001). We determined the average volume of consumed prey as the response variable, and the capture site (disturbed/conserved), sex of bats (male/female), and season (wet/dry) as explanatory variables. For each run we used the Bray-Curtis similarity index for 10,000 permutations. The Similarity Percentage Procedure (SIMPER — Clarke, 1993) analysis was used to determine which arthropod taxa contribute most to the differences among the variables. All the analyses were conducted using the free software PAST 3.11 (Hammer *et al.*, 2001).

RESULTS

We analyzed a total of 334 samples from 40 individuals of *T. brasiliensis* and recorded arthropod fragments from nine orders, four suborders, seven families, and one undetermined taxon (Table 1). We also identified some fragments of the genus *Camponotus* (Hymenoptera, Formicidae), but in a very small volume. The percentage volume of arthropod orders was highest for Lepidoptera, Hymenoptera, and Coleoptera, representing together the 79% of the diet (Fig. 2A); if we add Homoptera, Hemiptera, and Diptera to the above cited orders, the percentage reaches 98% of the diet. Trichoptera, Araneae, and

TABLE 1. Orders, suborders and/or families of arthropods found in the diet of *T. brasiliensis* from Northwestern Argentina. Average percent volume (Vol) and frequency of occurrence (Freq) of each item are indicated, as well as the Levins' measure of niche breadth and its standardized version

Order	Suborder/Family	Vol (%)	Freq (%)
Araneae	Undetermined	0.82	30
Coleoptera	Carabidae	3.39	10
	Chrysomelidae	1.78	15
	Scarabeidae	12.08	35
	Undetermined	0.24	5
	Total Coleoptera	17.49	75
Diptera	Brachycera	0.55	15
	Nematocera	2.15	47.5
	Culicidae	0.66	10
	Total Diptera	3.36	70
Hemiptera	Undetermined	6.04	80
Homoptera	Cicadomorpha	0.73	15
	Fulgoromorpha	6.95	62.5
	Delphacidae	1.87	37.5
	Total Homoptera	9.55	67.5
Hymenoptera	Formicidae	24.61	52.5
Lepidoptera	Undetermined	36.71	95
Neuroptera	Crisopidae	0.35	15
Trichoptera	Undetermined	0.87	15
Undetermined	Undetermined	0.20	10
Levins' index B		4.17	
Std Levins' index B_a		0.40	

Neuroptera, all together, only represented 2% of the diet of *T. brasiliensis* (Fig. 2A).

Lepidoptera, Hymenoptera, and Coleoptera have the highest frequencies of occurrence, registered in 75–95% of the analyzed individuals (Fig. 2B). By contrast, Trichoptera and Neuroptera were the most uncommon consumed orders, observed only in 15% of analyzed bats. *Tadarida brasiliensis* showed a high value of niche breadth ($B = 4.17$, $B_a = 0.40$), indicating that it consumes a great diversity of prey.

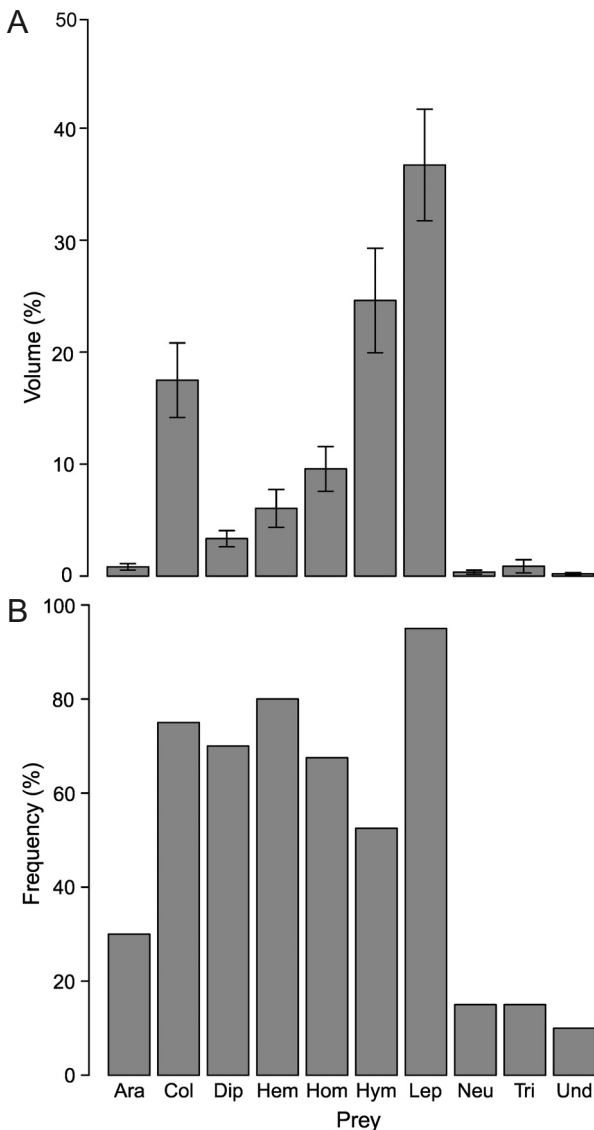


FIG. 2. Percent volume (A) and frequency of occurrence (B) of each prey order identified in the diet of *T. brasiliensis* sampled from eight sites of Yungas Forests, Argentina. For the percent volume, Standard Error for each prey order is showed. Abbreviations for arthropod orders: Ara, Araneae; Col, Coleoptera; Dip, Diptera; Hem, Hemiptera; Hom, Homoptera; Hym, Hymenoptera; Lep, Lepidoptera; Neu, Neuroptera; Tri, Trichoptera; and Und, Undetermined

Variations in percentage volume of prey orders were observed between conserved and disturbed sites, males and females, and wet and dry seasons. These patterns were also registered in the NMDS, which showed a stress value of 0.07, indicating a good fit of the algorithm. The observed variations by sites were significantly different according to the NPMANOVA ($F = 4.85$, $d.f. = 1$, $P = 0.006$), and the SIMPER analysis showed that Lepidoptera and Hymenoptera were the insect orders most contributing to the dissimilarities (Fig. 3A). Lepidoptera was mostly consumed in disturbed sites, whereas Hymenoptera was mainly consumed in conserved ones. The observed variations between sexes were not significantly different according to the NPMANOVA ($F = 0.57$, $d.f. = 1$, $P = 0.525$). Finally, the observed variations by seasons were significantly different according to the NPMANOVA ($F = 4.06$, $d.f. = 1$, $P = 0.015$). As well as in the sites comparison, the SIMPER analysis showed that Lepidoptera and Hymenoptera were the insect orders most contributing to the dissimilarities (Fig. 3C). We observed higher proportions of moths in the wet season and higher proportions of ants in the dry season.

DISCUSSION

This study is the first to report the diet of *T. brasiliensis* in Argentina, adding important information in the southward part of the distribution of the species. Our analyses show a diverse diet including nine orders and seven families of arthropods. Until now, data from only the northern distribution of *T. brasiliensis* were known, and those results from multiple studies show a comparable diversity (12 insect orders) with our research (Whitaker *et al.*, 1996; Whitaker and Rodríguez-Durán, 1999; Hernández Cienfuegos, 2005; Lee and McCracken, 2005). The heterogeneity observed in the diet of *T. brasiliensis* was also reflected in the value of Levins' measure of niche breadth ($B = 4.17$). Similar values were found by other authors ($B = 4.40$ – 4.90 — Lee and McCracken, 2005), confirming that this insectivorous bat has a diverse diet.

Our data indicate that Lepidoptera are the most common prey of *T. brasiliensis*, consistent with other similar studies (Ross, 1961, 1967; Whitaker *et al.*, 1996; Lee and McCracken, 2005). Also, based on the cranial and dental morphology of the species (Freeman, 1981a, 1981b), soft-bodied insects would be common in the diet of this species. *Tadarida brasiliensis* has thinner jaws, more but smaller teeth, and less developed cranial crests than

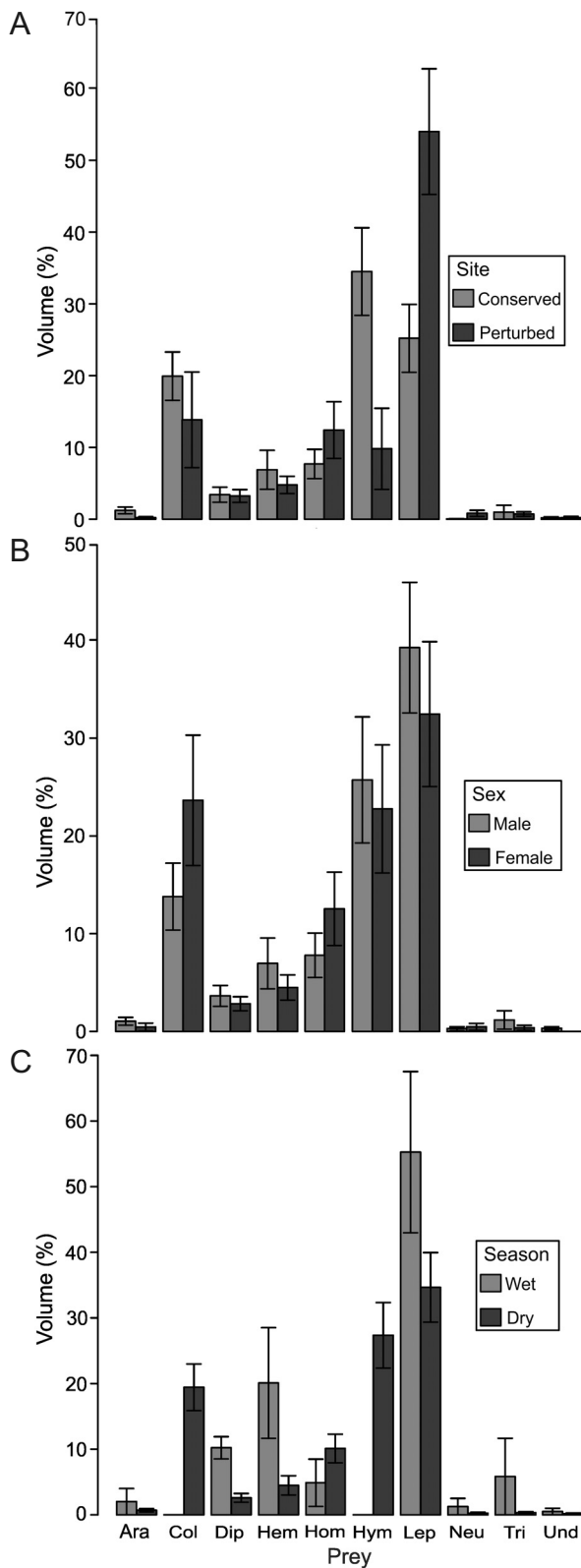


FIG. 3. Percent volume and standard error of each prey order identified in the diet of *T. brasiliensis* compared between sites (A), sexes (B), and seasons (C). Abbreviations for arthropod orders: Ara, Araneae; Col, Coleoptera; Dip, Diptera; Hem, Hemiptera; Hom, Homoptera; Hym, Hymenoptera; Lep, Lepidoptera; Neu, Neuroptera; Tri, Trichoptera; and Und, Undetermined

other molossid bats (Freeman, 1981a). The high abundance of moths consumed by this species also directly affected the value of the Levins' standardized niche breadth (B_a). The range of this index is from 0 to 1, and B_a is minimal when all the individuals occur in only one resource state (Krebs, 1999). The intermediate value reported in this study ($B_a = 0.40$), showed an elevated consumption of moths by *T. brasiliensis*, supporting the pattern suggested by Freeman (1981a).

The diverse diet of this species is influenced by several factors, including patterns of nightly foraging, flight behavior, and environmental influences (Lee and McCracken, 2005). The later was observed in this study, where significant differences were found in the diet between sites and seasons. *Tadarida brasiliensis* consumed a higher volume of moths in disturbed sites. Street lamps and other light sources, widely used over disturbed sites, produce a kind of light attractive to lepidopterans (Rydell and Racey, 1995). Thus, the disturbed sites attract high concentrations of moths, which form patches of prey at unusually high densities and often attract many species of aerial-hawking bats, including *T. brasiliensis* (Rydell, 1992; Hickey *et al.*, 1996; Lee and McCracken, 2002). On the other hand, this species consumed a higher volume of Hymenoptera from the family Formicidae in conserved sites. Ants are useful indicators of environmental disturbance, because of their fast response to changes in habitat quality, their abundance, and relatively easy sampling and identification (Brown, 2000; Kaspari and Majer, 2000; Andersen *et al.*, 2002). There is a higher diversity of these insects in native environments (Cuezco *et al.*, 2015), where species richness and composition are positively affected by tree density and structural heterogeneity of the vegetation (Silva *et al.*, 2004, 2007). Periodic but locally concentrated mating swarms of hymenopterans (Baldrige *et al.*, 1980), may account for the fact that these insects, mostly flying ants, were one of the predominant prey items in *T. brasiliensis* not only in this but also in other studies (Lee and McCracken, 2005).

We analyzed the diet of 15 females and 25 males of *T. brasiliensis*, and no significant differences were observed between sexes; similar results were found in previous studies (Kunz *et al.*, 1995; Lee and McCracken, 2002). Reproductive and lactating females of this species have high energetic demands and a broad diet (Lee and McCracken, 2002). Recent studies showed that species in the genus *Tadarida* can have gender-related variations in diet composition (Mata *et al.*, 2016). However, all the females

analyzed in this study were captured before the spring season, and pregnant and lactating females were not recorded, which is the probable reason why no differences in diet between sexes of *T. brasiliensis* were found.

Regarding the diet of *T. brasiliensis* between seasons, we observed a higher volume of moths consumed in the wet season. Many species of lepidopterans from Northwestern Argentina show higher abundances on the wet season, due to higher abundance of food (Murúa and Virla, 2004). Meanwhile, in the dry season, a higher consumption of ants was observed. In Northwestern Argentina, many ant species conduct their nuptial flights during the dry season (Kusnezov, 1962). Moreover, *T. brasiliensis* consumed ants of the genus *Camponotus*, and several of its species conduct nuptial flights at night (Kusnezov, 1962).

Coleopterans, lepidopterans, homopterans, and hemipterans are among the major pests in farms (Oliveira, 2005). We observed these orders in high abundances in the diet of *T. brasiliensis*. Thus, the obtained results would be consistent with the role of this species as natural pest controller. However, the proportion of crop pest remains in the bats diet is unclear due to the difficulty of identifying highly masticated insect fragments in the feces to species. DNA metabarcoding analyses (see Mata *et al.*, 2016), to document predation by *T. brasiliensis*, are necessary in order to confirm the role of *T. brasiliensis* as pest controller in Argentina.

A charismatic case that emphasizes the key ecosystem service provided by *T. brasiliensis* was registered in Escaba, Northwestern Argentina, Tucumán Province. A huge maternity colony of 12 million individuals of *T. brasiliensis* was discovered in 1992 (Gamboa Alurralde *et al.*, 2017), but after a great population reduction in 2003, due to a relocation and confinement of the colony (see Regidor *et al.*, 2003), the local farmers observed higher abundances not only of insects in general, but vector insects in particular (Salomón *et al.*, 2006; Quintana, 2010). This change in the local environment of Escaba probably is an effect of the great diminution in the pest control services provided by millions of individual of *T. brasiliensis* that inhabited the dam.

This study provides baseline research in Argentina and adds important information about the diet of *T. brasiliensis*. Considering the key role as natural pest controller, more dietary studies of insectivorous bats are critical for understanding their function in the ecosystem and their role as regulators of insect abundance.

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APPENDIX

Collection localities. The localities from the Yungas Forests are listed from north to south and according to their numbers in Fig. 1. For each locality the specific site, department and province in parentheses, and coordinates and altitude in meters above sea level are provided. The number of captured bats is also added, as well as data about sex, type of site (conserved or disturbed), and season of capture (dry or wet)

1 — Las Capillas, 15 km al N de Las Capillas (Dr. Manuel Belgrano, Jujuy). 24°02'37"S, 65°07'55"W, 1061 m: 6 ♂♂, conserved site, dry season; 2 — Finca Las Capillas, 3 km al E del cruce entre río Las Capillas y ruta provincial n° 20 (Dr. Manuel Belgrano, Jujuy). 24°05'35.77"S, 65°09'07.86"W, 1141 m: 3 ♀♀ and 5 ♂♂, disturbed site, 6 in dry season and one in wet season; 3 — Metán, 6 km al O, sobre río Las Conchas (Metán, Salta). 25°28'09"S, 65°02'11.58"W, 986 m: 7 ♀♀ and 9 ♂♂, conserved site, 15 in the dry season and one in dry season; 4 — Metán, 3.5 km al W (Metán, Salta). 25°29'34.76"S, 65°00'29.95"W, 1019 m. No individual of

T. brasiliensis was captured in this disturbed site; 5 — Reserva Provincial Aguas Chiquitas, sobre río Aguas Chiquitas (Burrucacú, Tucumán). 26°36'32.40"S, 65°10'36.60"W, 605 m: 2 ♂♂, conserved site, wet season; 6 — El Cadillal, camping La Curva (Burrucacú, Tucumán). 26°37'52.08"S, 65°11'10.87"W, 555 m: 2 ♀♀ and 2 ♂♂, disturbed site, dry season; 7 — Villa de Batirua (La Cocha, Tucumán). 27°38'11.61"S, 65°44'40.29"W, 515 m: 3 ♀♀ and 1 ♂♂, disturbed site, dry season; 8 — Villa de Escaba, 22 km al SE, sobre ruta provincial n° 9 (Paclín, Catamarca). 27°47'48.48"S, 65°46'56.70"W, 538 m. No individual of *T. brasiliensis* was captured in this conserved site