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DIET OF BRAZILIAN FREE-TAILED BATS (CHIROPTERA: MOLOSSIDAE: *TADARIDA BRASILIENSIS*): A REVIEW

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ABSTRACT—The insectivorous Brazilian free-tailed bat (*Tadarida brasiliensis*) inhabits North, Central, and South America. Since the 1920s the diet of these bats has interested scientists. The aim of this review is to catalog the published studies that explore the diet of *T. brasiliensis* and speculate how modern methods of analysis may be useful. The 19 studies reviewed reveal moths (Lepidoptera) and beetles (Coleoptera) as the two most common food items. Eighteen other orders of insect are commonly identified.

RESUMEN—El murciélago de cola libre (*Tadarida brasiliensis*) habita el Norte, Centro y Sur de América. Desde la década de 1920, la dieta insectívora de estos murciélagos ha interesado a los científicos. El objetivo de esta revisión es catalogar los estudios publicados que exploran la dieta de *Tadarida brasiliensis* y examinar cómo los métodos modernos de análisis pueden ser útiles. Los 19 estudios revisados revelan que las polillas (Lepidoptera) y los escarabajos (Coleoptera) son los dos alimentos más comunes. Otros dieciocho órdenes de insectos son comúnmente identificados.

The small, insectivorous, Brazilian free-tailed bat (*Tadarida brasiliensis*) has engendered curiosity from scientists worldwide. Inhabiting North, Central, and South America, *T. brasiliensis* is one of the most widely distributed mammals in the western hemisphere (Wilkins, 1989; McCracken et al., 2008). With northern limits extending into Oregon, *T. brasiliensis* ranges southward to Argentina and is the most abundant bat species in the southwestern United States (Wilkins, 1989; Tuttle, 2005). During the summer months, females form enormous maternal roosts where they rear their pups (Tuttle, 2005; Ammerman et al., 2012). Near nightfall, the bats emerge from their roost and ascend to altitudes of nearly 3,000 m (McCracken et al., 2008). Scientists have speculated that high-altitude migration of various insects, including moths, could be the attracting feature for the high-altitude flight of *Tadarida* (McCracken et al., 2008; Krauel et al., 2017).

The sheer number of individuals and their potential impact on insect populations is a popular subject of interest, although most studies that document their diet do so only as a secondary focus. The aim of this review is to catalog the published studies that explore the diet of *T. brasiliensis* and speculate on how modern methods of analysis may be useful.

Current diet analyses show that *T. brasiliensis* feeds on a diversity of insects that includes beetles, true bugs, flies, and grasshoppers, but moths appear to be, by far, the most common and abundant food (Whitaker and Odegard, 2019). In all but one of the 19 studies reviewed, moths (Lepidoptera) are a significant item in the diet of these bats (Table 1), and since the 1920s scientists have concluded that moths make up the majority of the diet of *T. brasiliensis* (Storer, 1926). Additionally, in 13 of the 19 studies, Lepidoptera were the most abundant item in the

TABLE 1—Most common food items found in the diet of *Tadarida brasiliensis* and the corresponding studies detailing the year of collection, location of collection, season/time of collection, and the method used to analyze the diet. — = data not available.

Authors	Year of publication	Year of collection	Location	Season/time	Method of study	Most common food item
Alurralde and Díaz	2018	2012–2015	Yungas Forest, Argentina	Year round	Visual identification	Lepidoptera
Damián	2009	2005–2006	La Boca Cave and El Salitre Cave, Mexico	April–September	Visual identification	Lepidoptera
Damián	2009	2004–2005	San Francisco Cave, Mexico	November–May	Visual identification	Lepidoptera
Hernández	2005	2004–2005	La Boca Cave, Mexico	May–October	Visual identification	Lepidoptera
Hernández-Vila	2018	2016–2017	Cuernavaca, Mexico	March, April, August, September, November, December	Visual identification	Coleoptera
Krauel et al.	2017	2010–2012	Frio Cave, USA	August–November	DNA analysis	Lepidoptera
Kunz et al.	1995	1988	Eckert James River Cave, USA	May–July	Visual identification	Lepidoptera
Lee and McCracken	2005	1995	Bracken Cave and Eckert James River Cave, USA	June–August	Visual identification	Lepidoptera
Lee and McCracken	2005	1996–1997	Frio Cave, USA	May–August	Visual identification	Lepidoptera
Lee and McCracken	2002	1996–1997	Frio Cave, USA	May–August	Visual identification	Lepidoptera
Long et al.	1998	1995	Sacramento Valley, USA	April–September	Visual identification	—
Matthews et al.	2010	2000–2002	Big Bend National Park, USA	March, June, July	Visual identification	Lepidoptera
McCracken et al.	2012	2006	Seco Creek, USA	April–September	DNA analysis	—
McWilliams	2005	1998	Carlsbad Cavern National Park, USA	April–September	Visual identification	Lepidoptera
Olmedo et al.	2021	2019	Estancia and Paititi Nature Reserve, Argentina	March–December	Visual identification	Diptera
Ross	1961	1959	Madera Canyon, USA	—	Visual identification	Lepidoptera
Ramirez and Pardo	2010	2006	Regional Rancheria Natural Park, Colombia	March–December	Visual identification	Coleoptera
Storer	1926	1919	Mitchel Lake, USA	—	Visual identification	Lepidoptera
Whitaker and Odegard	2009	1991, 2012, 2013	Congress Avenue Bridge, USA	October, February, September	Visual identification	Lepidoptera
Whitaker and Rodriguez-Duran	1999	1992–1993	Guajataca Canyon, Puerto Rico	May–April	Visual identification	Diptera
Whitaker et al.	1996	1991	Eckert James River Cave, USA	Morning	Visual identification	Lepidoptera
Whitaker et al.	1996	1991	Eckert James River Cave, USA	Evening	Visual identification	Coleoptera

diet of *Tadarida*. In 1919, fecal samples from the “First Artificial Roost” at Mitchell Lake in Texas, USA, were sent to the United States Bureau of Biological Survey, where experts determined the samples consisted mainly of Lepidoptera parts (Storer, 1926). Since then, scientists have found remarkably similar results from roosts in North, Central, and South America.

From 1995 to 2019, various studies have detailed the abundance and frequency of Lepidoptera in *Tadarida* diets. Three studies examined the diet of the bats from

Eckert James River Cave, Texas. Whitaker et al. (1996) compared morning and evening feeding bouts and found Lepidoptera to make up 96% of foraged prey during the morning bouts. Lee and McCracken (2005) found Lepidoptera to be the most abundant component in the diet items during the summers of 1995, 1996, and 1997. Similarly, Kunz et al. (1995) showed both pregnant and lactating females during the summer months (May–July) foraged on Lepidoptera more than any other insect. In Big Bend National Park in Texas, Matthews et al.

(2010) found that in June, July, and March of 2000–2002, Lepidoptera constituted the greatest percent volume of prey in fecal samples. Bracken Cave in Texas houses more than 20 million of these bats (Bat Conservation International, <https://www.batcon.org/see-bats-live/visit-bracken-cave-preserve/>), and Lee and McCracken (2005) found Lepidoptera to make up the greatest percent frequency and percent volume of the diet of bats from this location. Lee and McCracken (2002), Krauel et al. (2017), and Lee and McCracken (2005) all reported similar results from examination of bat feces from Frio Cave, Texas. Whitaker and Odegard (2019) compared the diet of bats from underneath the Congress Avenue Bridge, Texas, during 1991, 2012, and 2013 and found moths to be the dominant insect. McWilliams (2005) reports that Lepidopteran occurred in 92.6% of fecal pellets collected from Carlsbad Caverns National Park, New Mexico. Olmedo et al. (2021) found Lepidoptera in 91% of the fecal samples examined from Estancia and Paititi Nature Reserve, Argentina. Both Damián (2009) and Hernández (2005) found Lepidoptera to make up the greatest proportion of digested items in La Boca Cave, Mexico. Lastly, according to Alurralde and Díaz (2018), Lepidoptera constitute the greatest volume and frequency of the diet of *T. brasiliensis* year-round in the Yungas Forest, Argentina.

Four additional studies have stated less-explicit results regarding the abundance and frequency of Lepidoptera found in the diets. McCracken et al. (2012) conducted a study to specifically determine the species of Lepidoptera eaten in Seco Creek, Texas and found 27 different species. Long et al. (1998) found that moths made up a significant proportion of the diet of the Mexican free tails in the Sacramento Valley, California. Whitaker and Rodriguez-Duran (1999) report moths being the third most abundant food item in the diet of bats from Tunel Negro, Puerto Rico. Finally, Ross (1961) found moths to be the most abundant insect in the stomachs of *Tadarida* from Madera Canyon, Arizona.

Beetles (Coleoptera) are the second most common food found in *Tadarida* diets. Ramirez and Pardo (2010) report that *T. brasiliensis* in Regional Rancheria Natural Park, Colombia, exclusively feed on insects belonging to Coleoptera. Similarly, Hernández-Vila (2018) report that *T. brasiliensis* in Cuernavaca, Mexico, mainly feed on Coleoptera. Lee and McCracken (2005) found Coleoptera to have the second-greatest frequency in the diet of bats from Bracken Cave, Eckert James River Cave, and Frio Cave in 1995–1997. Damián (2009) report Coleoptera as the second-greatest volume and frequency in the diet of bats in La Boca Cave, El Salitre Cave, and San Francisco Cave in Mexico. Whitaker et al. (1996) found that lactating females in Eckert James River Cave fed primarily on Coleoptera during their evening foraging bouts, making up 63% by volume of their evening diets. Kunz et al. (1995) deduce that Coleopterans constituted

26.4% (frequency) of the diet in females from Eckert James River Cave. Olmedo et al. (2021) found Coleoptera in 36% of the fecal samples from Estancia and Paititi Nature Reserve. Whitaker and Odegard (2019) showed Coleoptera to be the second most common prey item for bats roosting under the Congress Avenue Bridge in 1991. Matthews et al. (2010) identified Coleoptera as the third most abundant item during June, July, and September of 2000 and March of 2002 in Big Bend National Park. Lee and McCracken (2002) concluded that Coleoptera had the second-greatest percent volume of diet items from Frio Cave. Krauel et al. (2017) found Coleoptera to be the third most frequent food item in the diets of bats in Frio Cave. McCracken et al. (2012) found three different species of Coleoptera in the diet of bats from Seco Creek, Texas. Lastly, Whitaker and Rodriguez-Duran (1999), Long et al. (1998), and Storer (1926) found remnants of Coleoptera in their examinations, but other insects were notably more abundant.

Other orders of insects found in the diet of these bats include the following: Diptera (17 studies), Hemiptera (15 studies), Hymenoptera (11 studies), Neuroptera (10 studies), Homoptera (9 studies), Trichoptera (9 studies), Orthoptera (7 studies), Ephemeroptera (6 studies), Aranea (5 studies), Odonata (4 studies), Isoptera (3 studies), Plecoptera (3 studies), Psocoptera (2 studies), Ixodidae (1 study), Megaloptera (1 study), Mecoptera (1 study), Blattaria (1 study), and Actinotrichia (1 study). Two of the studies, McCracken et al. (2012) and Krauel et al. (2017), have identified the genus and species of items found in the diet; however, the other 17 studies only reported the order and sometimes family.

Bats are the second-largest order of mammals, distributed worldwide, and perhaps the most maligned and least understood of any other mammal (Tuttle, 2005). One of the more positive attributes of bats is their perceived role in their environment as pest foragers. Of the identified food items, pests include insects in the families Culicidae (order Diptera), Pentatomidae, and Lygaeidae (order Hemiptera), Crambidae, Erebidae, Noctuidae, and Pyralidae (order Lepidoptera), and Gryllidae (order Orthoptera). Surprisingly, only four studies reviewed here found mosquitoes to be part of the *Tadarida* diet; Whitaker and Odegard (2019) found mosquitos to make 0.1% of volume and 1% frequency of fecal contents from bats under the Congress Avenue Bridge. Whitaker and Rodriguez-Duran (1999) also found less than 1% frequency of mosquitoes in their diet analysis of *T. brasiliensis antillarum* in Puerto Rico. Olmedo et al. (2021) found mosquitos to make up ~12% of the relative frequency of prey in the digestive tract of bats in Estancia and Paititi Nature Reserve. The results of these three studies were based on visual identification of fecal pellets. As discussed by Rabinowitz and Tuttle (1982), the differential digestibility of prey types greatly biases the conclusions of manual fecal analysis. Storer (1926) concludes that there

is no doubt that bats eat mosquitos, but because of how digestible the body parts are, it is possible they went undetected in all the other 15 studies reviewed. In addition, sampling biases may lead to misconceptions about the diet of these animals. Differences in the season or time of night in which samples are collected might influence prey availability. For example, Parajulee et al. (2004) determined that moth abundance is positively correlated with temperature and negatively correlated with wind velocity; two conditions that frequently fluctuate. Furthermore, the understanding of the impact these bats have on pest control might be underestimated. If bats consistently forage on insects carrying eggs, the magnitude of their impact on their prey could be greater than now thought. Perhaps with a more modern approach to analyzing the diet of these animals, we can determine the beneficial impact they might have on humans, the ecosystem services they deliver, and how conservation efforts need to be structured.

In the reviewed articles, 15 of the 19 studies relied on morphological evidence of prey in dissected fecal samples and two relied on examination of stomach contents. A serious limitation of this method is that visual inspection and microdissection of samples strongly bias the results toward insects with hard shells such as beetles or large scales such as moths. This technique is much less likely to reveal remains of soft-bodied or fragile species such as mayflies and mosquitoes (Rabinowitz and Tuttle, 1982). Modern molecular techniques such as DNA barcoding have been shown to drastically improve the validity and certainty of diet studies in fish (Ward et al., 2005), amphibians and reptiles (Vences et al., 2012), and mammals (Borisenko et al., 2008). This approach has been used to assess the diet of other bat species and has yielded surprising results. For example, Jones et al. (2020) used DNA barcoding to examine the diet of frog-eating bats (*Trachops cirrhosus*) and discovered previously unknown frog species and hummingbirds as part of their diet. These results inspired follow-up behavioral studies that showed that bats readily attacked a hummingbird mount. Additionally, Zeale et al. (2011) used DNA barcoding to identify over 6,000 species of arthropod prey from fecal pellets of three species of insectivorous bats. Two of the studies reviewed in this article, Krauel et al. (2017) and McCracken et al. (2012), used DNA extracted from fecal pellets to identify items in the diet of *Tadarida*. In fact, the study by Krauel et al. (2017) is the fourth of the reviewed articles to find evidence of mosquitos. Using modern molecular approaches to study diets can be leveraged to gain a more accurate assessment of what these bats are eating, leading to fascinating new questions.

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