

TROPHIC ECOLOGY OF THE FREE-TAILED BATS *NYCTINOMOPS*  
*FEMOROSACCUS* AND *TADARIDA BRASILIENSIS* (CHIROPTERA:  
MOLOSSIDAE) IN BIG BEND NATIONAL PARK, TEXAS

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**ABSTRACT**—We analyzed fecal pellets from 59 *Nyctinomops femorosaccus* and 54 *Tadarida brasiliensis* to assess dietary overlap in an area of sympatry. Lepidoptera, Hemiptera, and Coleoptera were the most abundant orders of insects. Niche-breadth indices were narrow overall and highest in June for both species. Indices of overlap indicated nearly complete overlap in use of resources. There does not appear to be resource partitioning of diet at the taxonomic level examined in these species during summer when sources of food are expected to be more abundant. There was a dietary shift from predominantly Lepidoptera to Hemiptera in March for *N. femorosaccus*, but not for *T. brasiliensis*. Resources other than food may impose a greater limitation on size of these populations.

**RESUMEN**—Analizamos la materia fecal de 59 individuos de *Nyctinomops femorosaccus* y 54 individuos de *Tadarida brasiliensis* para determinar el traslapo de dieta en una área de simpatría. Las órdenes de insectos más comúnmente encontradas fueron Lepidóptera, Hemíptera, y Coleóptera. La amplitud de los nichos fue pequeña en general y fue más grande en el mes de junio para ambas especies. Los índices de traslapo indicaron un compartimiento casi completo del uso de los recursos. No parece haber recursos divididos de la dieta al nivel examinado en estas especies durante los meses de verano cuando la fuente de alimentos debe ser más abundante. Hubo un cambio de la dieta predominantemente de Lepidóptera a Hemíptera en el mes de marzo para *N. femorosaccus* pero no para *T. brasiliensis*. Recursos distintos a los alimentos pueden ser más importantes limitando el tamaño de estas poblaciones.

*Nyctinomops femorosaccus* (pocketed free-tailed bat) and *Tadarida brasiliensis* (Brazilian free-tailed bat) are morphologically similar species of Molossidæ that occur sympatrically over part of their range. They are similar in overall size and morphology of wings, although *N. femorosaccus* is slightly larger than *T. brasiliensis*: mean weight is 14.5 and 12.4 g, respectively (Jones et al., 1972; Lowery, 1974; Freeman, 1981; Kumirai and Jones, 1990). The smaller but similar morphology in conjunction with greater maneuverability during flight led Freeman (1981) to propose that *T. brasiliensis* could consume certain invertebrates, such as beetles, that *N. femorosaccus* could not. Additionally, because of flight capabilities of molossids, particularly with respect to their maneuverability and speed, it is likely that few species of bats could be direct competitors for food (Freeman, 1981).

Morphologically similar bats should consume the same types of foods due to ecomorphological

constraints (Aldridge and Rautenbach, 1987). This hypothesis predicts that *N. femorosaccus* and *T. brasiliensis* will exhibit significant dietary overlap. Similarities in shape of jaw shared by these two species also indicate they should consume similar types of soft-bodied prey (such as moths). Therefore, under the ecomorphology hypothesis, these morphologically similar species will use similar foraging habitat and feeding strategies resulting in significant overlap in diet (Freeman, 1981; Grant, 1986; Aldridge and Rautenbach, 1987). Alternatively, niche theory states that these two similar species should partition resources (assuming resources are limited) as a means of avoiding competition (MacArthur, 1958; Pianka, 1973; Vogt, 1981). Therefore, when in sympatry, they may exhibit dietary or temporal partitioning, or both, as a means of reducing the effect of competition. For example, diet of sympatric species of *Myotis* showed evidence of increased specialization

versus the diet of the same species in allopatry, suggesting the species were partitioning food where they overlapped geographically (Husar, 1976). The two kinds of partitioning are not mutually exclusive; for instance, activity of predators may be influenced by activity of prey; therefore, the bats may exhibit different temporal patterns of activity because they have partitioned their prey, which happen to have different patterns of activity. The specifics of the alternative hypothesis that partitioning is occurring, however, are beyond the scope of this study.

Studies of food habitats for the two species generally are limited in scope of sampling but do not appear to reflect evidence of partitioning of foods. For example, moths (Lepidoptera), crickets (Gryllidae), flying ants (Formicidae), stink bugs (Pentatomidae), beetles (Coleoptera), leafhoppers (Cicadellidae), and froghoppers (Cercopidae) have been recovered from fecal remains of *T. brasiliensis* from throughout its range (Bailey, 1931; Ross, 1967; Easterla and Whitaker, 1972; Freeman, 1981; Whitaker et al., 1996; McWilliams, 2005). Scattered information on diet for both species precludes comparison between sympatric populations. One study reported a preliminary analysis of foods consumed by three species of Molossidae (Debelica et al., 2006) including *N. femorosaccus* and *T. brasiliensis*. Although the focus of Debelica et al. (2006) was the larger molossid, *N. macrotis*, comparisons with *N. femorosaccus* and *T. brasiliensis* were made by incorporating some of the data from a simultaneously conducted study (Matthews, 2002). Herein, we present a more detailed account of the results of the latter study with additional sampling and analyses.

The purpose of this study was to test the hypothesis of separate use of resources between two morphologically similar species in an area of sympatric association. First, we documented and statistically evaluated dietary composition of *N. femorosaccus* and *T. brasiliensis* in sympatric association to assess dietary overlap. Second, we assessed nightly patterns of activity by frequencies of captures to determine if there were differences in temporal activity that may allow further inferences from dietary analysis.

**MATERIALS AND METHODS**—Bats were captured in mist nets at two sites that have high rates of capture of molossids (Higginbotham and Ammerman, 2002). Both sites were large, unobstructed, spring-fed water sources along intermittent creeks in the lowland

regions of Big Bend National Park, Brewster County, Texas (Tornillo Creek 13R 68°40'70"E, 32°29'95"N and Terlingua Creek 13R 63°55'12"E, 32°31'03"N). Lowland vegetational associations described by Wauer (1971) categorize both sampling sites as river floodplain-arroyo formation, with associated vegetation including mesquite (*Prosopis*), desertwillow (*Chilopsis linearis*), common reed (*Phragmites australis*), cattail (*Typha*), cottonwood (*Populus acuminata*), and acacia (*Acacia*). The springs at both sites were fairly reliable sources of aboveground water, although during the study, the surface water at Tornillo Creek disappeared from its original location and resurfaced at a location ca. 1.3 km downstream.

Sampling was conducted May–September 2000 with additional sampling in May 2001 and March 2002. During summer 2000, mist nets were set as often as possible with the majority of nights between the second and first quarter of the lunar cycle, when netting was more productive (Higginbotham and Ammerman, 2002). Three to five mist nets, depending on available water and number of assistants, were erected each sampling night. Mist nets were erected at dusk and tended until dawn unless inclement weather or lunar phase adversely affected activity of bats, in which case, nets were taken down early.

Captured bats were removed from nets, placed in numbered cloth bags and brought to a central area for processing. Time of capture was recorded for each bat and it was weighed to the nearest gram. Age was determined by ossification of the metacarpal-phalangeal joint (Anthony, 1988). Reproductive condition and sex was noted, and standard morphological measurements (length of forearm, ear, and foot) were recorded. All bats, excluding molossids, were released after processing. Cloth holding bags containing molossids subsequently were checked for fecal remains. Pellets were then removed from the bag with forceps and placed into a numbered microcentrifuge tube filled with 70% isopropyl alcohol. All bats were released <1 h from time of capture.

To obtain a reference collection of insects available to bats, a black-light trap consisting of a universal collecting system and a collecting light (BioQuip Products, Inc., Rancho Dominguez, California) was used to capture insects. The black-light trap was filled ca. 5 cm deep with a 10% solution of ethylene glycol and was placed in areas near (<5 km) netting sites periodically during May–August 2000, May–June 2001, and August–September 2002. The insect trap was operated 4–6 h after dusk. Insects collected in the black-light trap were removed, rinsed, and stored in 70% isopropyl alcohol. A representative sample of insects collected was prepared and catalogued by C. Wolfe at the University of Texas at Arlington and deposited with the National Park Service.

Netting effort was calculated in net-hours, which is the total number of hours each net was open per netting night. Overall frequencies of capture of bats at both sites were calculated as number of captures divided by total net-hours for each netting night. To assess temporal patterns of activity, total number of each species captured per 1-h interval after sunset was calculated and divided by total net-hours for each interval summed over all netting nights. Individuals in

March were not included with data from May, June, July, and September. Because March is near the time of migration and foraging activity is reduced due to shorter days, we believed these captures do not reflect the same patterns seen during warmer months and to combine them would be inappropriate.

Fecal samples were examined using methods of Debelica et al. (2006). Fragments of insects were identified to order (and occasionally to family) by comparisons with voucher specimens and with the aid of several guides to insects (Comstock, 1940; Borror and DeLong, 1964; Whitaker, 1988). Relative volume of each order of insect was visually estimated to the nearest 1%. Percent frequency of occurrence also was calculated for comparisons to other studies. This technique is used often in fecal studies of bats and has been shown to be a reliable estimate of dietary composition (Kunz and Whitaker, 1983).

Breadth of trophic niche was estimated from fecal samples for each species, with a separate index calculated for pooled fecal samples for June, July, and September 2000 and March 2002, using Levins' Index (Krebs, 1989). The index ranges from 0 to  $n$ , where  $n$  corresponds to number of categories of prey. To standardize breadth of trophic niche on a scale of 0 to 1, Levins' measure of standardized breadth of niche was calculated (Krebs, 1989).

Overlap in trophic niche between *N. femorosaccus* and *T. brasiliensis* was estimated using a modification of MacArthur and Levins' measure of overlap proposed by Pianka (1973). The measure of overlap ranges from 0 (no overlap in resources between species) to 1.0 (complete overlap of resources). For interspecific overlap, a separate index was calculated for each random sampling of interspecies pairs in June, July, and September 2000 and March 2002, with maximum number of pairs equal to size of the smallest sample of the two species. The measure also was calculated monthly on averaged data for each species. For intraspecific overlap, a separate index was calculated for each random sampling of intraspecific pairs in June, July, and September 2000 and March 2002.

Multivariate analysis of variance (MANOVA) was applied to assess significant differences in composition of the insect fauna in diets between species within each month. We defined an experimental unit as all fecal pellets collected from a single individual. We used Lepidoptera, Hemiptera, and Coleoptera as three variables and grouped remaining orders and unidentified Insecta as a fourth category, because they were represented by few remains of insects in most samples. Uneven size of samples between species and months may reduce power of the MANOVA; therefore, we used a Type IV sums of squares for all tests. Further, to assess robustness of the MANOVA in light of unequal samples, we employed a weighted  $\chi^2$  analysis to the data. Data were weighted by number of samples divided by number of pellets for all species and months to alleviate potential bias in analysis. Contingency table analysis with Bonferonni-corrected post hoc tests resulted in identical results compared to the MANOVA. We report only results of the MANOVA for this study.

**RESULTS**—Temporal variation, based on rates of capture after sunset, in drinking activity between species was apparent to some extent (Fig. 1). *Tadarida brasiliensis* was captured more often immediately following sunset than *N. femorosaccus*. For *T. brasiliensis*, there was modest variation in activity throughout the night until 7–8 h after sunset when activity increased. Peak activity for *Nyctinomops femorosaccus* occurred 5–6 h after sunset.

Fecal samples were collected from 59 *N. femorosaccus* and 40 *T. brasiliensis* during sampling in June, July, and September 2000 and March 2002. In addition, fecal samples from 14 *T. brasiliensis* were collected during May 2000; however, no *N. femorosaccus* was captured in May 2000. Number of pellets collected per individual was 2–21 (mean  $5 \pm 3$ ). Prey items were Lepidoptera (moths), Hemiptera (true bugs), Coleoptera (beetles), Hymenoptera (ants, wasps, bees), Diptera (flies), Orthoptera (grasshoppers and crickets), and Insecta (all other insects). For comparison with previous studies, we also treated Homoptera (hoppers), which is now in the order Hemiptera (Triplehorn and Johnson, 2004), as a separate order. In many cases, identification of insects was to family; however, because this was not always possible, dietary comparisons were made only across orders.

Monthly variation in dietary composition was observed for both *N. femorosaccus* and *T. brasiliensis* (Table 1). Lepidoptera accounted for greatest volume of prey in *N. femorosaccus* in June and July (48.3 and 64.8%, respectively), with diets in September and March consisting mostly of Hemiptera (61.7 and 56.9%, respectively; Table 1). Lepidoptera comprised the greatest volume for *T. brasiliensis* in June (58.8%), July (92.3%), and March (76.3%), with Hemiptera representing 76.3% of total volume of prey in September (Table 1). A shift in food from predominantly Lepidoptera to Hemiptera was exhibited by both species during September, with Coleoptera being the next-most-common prey in both. Homoptera and Orthoptera were exclusively in *N. femorosaccus* and Hymenoptera was a minor component in diet of both species (Table 1).

Lepidopterans could not be identified below order, with the only obvious differences being size of proboscis, legs, and wings. In both species, most hemipterans were in the family Lygaeidae

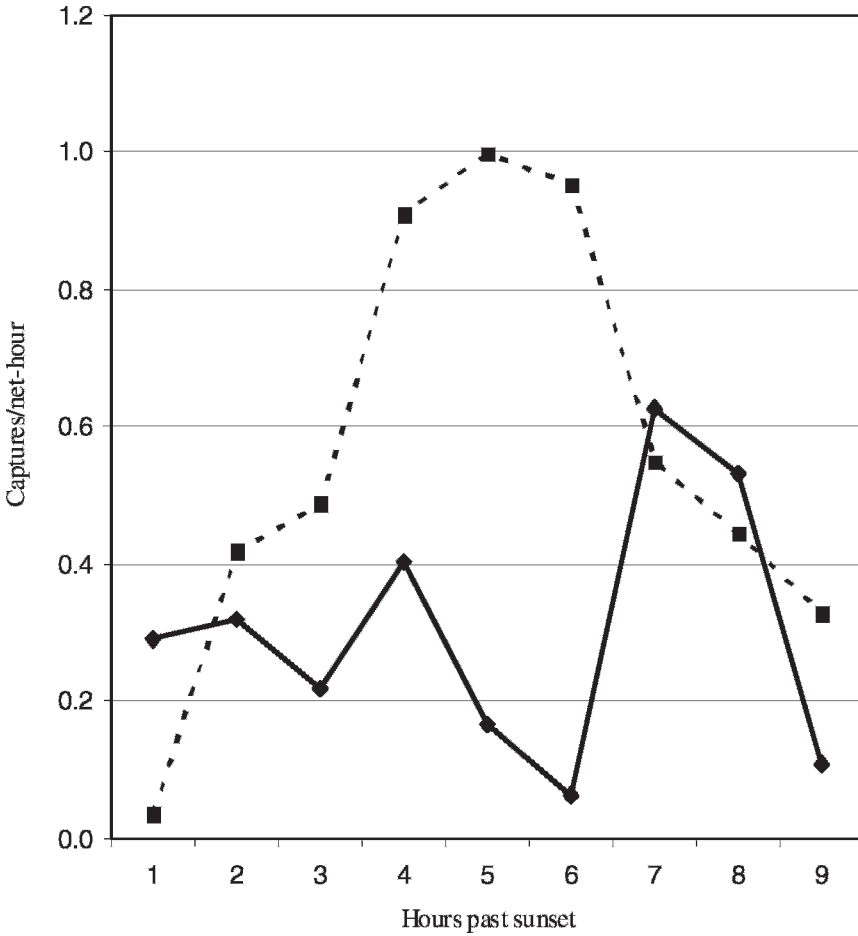


FIG. 1—Variation in rates of capture of 137 pocketed free-tailed bats (*Nyctinomops femorosaccus*; dashed line) and 116 Brazilian free-tailed bats (*Tadarida brasiliensis*; solid line) at two sites in Big Bend National Park, Brewster County, Texas, during 18 netting nights in May, June, July, and September 2000.

TABLE 1—Mean percentage volume (percentage of occurrence in parentheses) of prey in fecal samples of pocketed free-tailed bats (*Nyctinomops femorosaccus*) and Brazilian free-tailed bats (*Tadarida brasiliensis*) collected in June, July, September 2000 and March 2002 in Big Bend National Park, Brewster County, Texas.

Prey	<i>Nyctinomops femorosaccus</i>				<i>Tadarida brasiliensis</i>			
	June (n = 6)	July (n = 34)	September (n = 12)	March (n = 7)	June (n = 9)	July (n = 8)	September (n = 10)	March (n = 13)
Lepidoptera	48 (100)	65 (100)	7 (67)	27 (100)	59 (100)	92 (100)	4 (50)	76 (100)
Hemiptera	21 (67)	22 (76)	62 (100)	57 (100)	9 (44)	3 (63)	76 (100)	17 (100)
Coleoptera	19 (67)	9 (62)	25 (75)	11 (86)	28 (56)	1 (25)	15 (90)	3 (77)
Homoptera	6 (50)	1 (21)	4 (50)	1 (14)	—	—	—	—
Diptera	—	<1 (3)	1 (8)	<1 (14)	—	—	—	2 (15)
Hymenoptera	—	<1 (9)	—	—	2 (11)	—	—	1 (8)
Orthoptera	—	<1 (9)	—	1 (14)	—	—	—	—
Unidentified Insecta	5 (50)	3 (32)	2 (25)	3 (43)	3 (44)	4 (50)	5 (60)	2 (46)

TABLE 2—Interspecific and intraspecific overlap in niche (Pianka, 1973) for pocketed free-tailed bats (*Nyctinomops femorosaccus*) and Brazilian free-tailed bats (*Tadarida brasiliensis*) in Big Bend National Park, Brewster County, Texas, during June, July, and September 2000 and March 2002.

Month	Interspecific overlap in niche		Intraspecific overlap in niche	
	Monthly average	Pair-wise average	<i>T. brasiliensis</i>	<i>N. femorosaccus</i>
June	0.959	0.563	0.602	0.389
July	0.951	0.644	0.980	0.741
September	0.951	0.778	0.895	0.598
March	0.730	0.581	0.885	0.849

(chinch bugs), while other families included Pentatomidae (stink bugs) and Miridae (leaf bugs). Coleopterans were mainly Scarabaeidae (June beetles) and Carabidae (ground beetles), while Curculionidae (snout beetles), Staphylinidae (rove beetles), and Chrysomelidae (flower beetles) also were identified. Homopterans were all Cicadellidae (leafhoppers). Orthopterans were all Gryllidae (crickets) and hymenopterans were Formicidae (ants).

Breadths of trophic niches were narrow in both species. Greatest variation in diets occurred in June, when *T. brasiliensis* and *N. femorosaccus* displayed their greatest breadth of trophic niche of 0.174 and 0.165, respectively. Breadth of trophic niche for both species were lowest in July, when Lepidoptera accounted for the highest volume across all months combined (Table 1). Overlap in trophic niche indicated substantial dietary overlap between species. The index for comparisons among monthly averages of species showed nearly complete overlap for all months, excluding March (Table 2). Trophic overlap between species generally was higher than within species, with the exception of *N. femorosaccus* in June and September, where intraspecific overlap was lower than interspecific overlap (Table 2).

Using MANOVA on monthly fecal samples from each species, we detected significant differences in diet among months ( $F = 7.084$ ,  $P < 0.001$ ). Bonferroni-adjusted post hoc analyses revealed that Lepidoptera decreased and Hemiptera increased significantly for both species in September. The hypothesis of a similar diet between species could not be rejected in the multivariate test ( $F = 1.936$ ,  $P = 0.111$ ); however, tests between subjects showed a significant difference between species for both Lepidoptera ( $P = 0.007$ ) and Hemiptera ( $P = 0.035$ ). This difference primarily was attributed to the diet in

March, which contained more lepidopterans for *T. brasiliensis* and a greater proportion of hemipterans for *N. femorosaccus*.

DISCUSSION—At our study site, coexistence of *T. brasiliensis* and *N. femorosaccus* apparently is not maintained by separation of prey at the ordinal level. Overall, no apparent pattern of dietary separation was observed between *N. femorosaccus* and *T. brasiliensis* with the exception of March, where overlap also was high (Table 2). No significant difference was detected in diet between species during summer (June and July) or autumn (September), and overlap in trophic indices was relatively high for all months.

Lack of partitioning in diet between these two species does not necessarily indicate absence of competition. Partitioning of food resources at finer taxonomic levels or differences in temporal or spatial foraging may contribute to coexistence of these species. In our study, temporal variations in activity were inferred from rates of capture throughout the night. Activity patterns based on these rates indicated that both species were relatively active throughout the night, with no consistent temporal partitioning. Our data demonstrate that *Tadarida* is active more often within 1 h after sunset compared to *N. femorosaccus*, while a trend of increased activity of *N. femorosaccus* appears 5–6 h after sunset, which is not exhibited by *Tadarida*. Baker and Christianson (1966) also reported that in Sonora, Mexico, most *N. femorosaccus* were captured later than other species, including *T. brasiliensis*.

Temporal variation in nightly foraging activity does not reflect differences in diet in our study. Whitaker et al. (1996) reported significant variation in diet within *T. brasiliensis*, depending on what time of the night the sample was collected. These data suggested that abundance of insects changed throughout the night and

that bats simply fed on insects that were available at the time. In our study, *T. brasiliensis* had highest activity just after sunset and again just prior to sunrise, while *N. femorosaccus* was more active in the middle of the night. The alternating activity of these species, however, does not appear to lead to any significant differences in diet. However, our analyses of activity are limited to bats being captured while drinking, which might not reflect feeding activity. Our data suggest a more seasonal dietary shift similar to recent analyses of other molossid (Andrianai-voarivelo et al., 2006).

Diet of *N. femorosaccus* was dominated by Lepidoptera during June and July 2000. These data are somewhat consistent with limited accounts of diet for this species (Ross, 1967; Easterla and Whitaker, 1972). Easterla and Whitaker (1972) reported Lepidoptera accounting for most of the volume and Hymenoptera was the next-most-abundant prey. While Lepidoptera was the main food of *N. femorosaccus* in summer during our study, it did not contribute as much in September 2000 (6.8%) or March 2002 (27.1%) and Hymenoptera contributed little to overall volume. The only other information on diet of *N. femorosaccus* was a report of Lepidoptera (100%) in one stomach and Lepidoptera (85%) and Coleoptera (15%) in another stomach from Arizona (Ross, 1967).

In our study, *T. brasiliensis* fed mainly on Lepidoptera, which accounted for the greatest volume in all months except September 2000. Dietary data available for *T. brasiliensis* are more extensive than those for *N. femorosaccus*, and shows this species to be a generalist that often consumes large amounts of Lepidoptera (Bailey, 1931; Ross, 1967; Kunz et al., 1995; Whitaker et al., 1996). Consistent with our study, McWilliams (2005) reported Lepidoptera to be the most commonly consumed prey item (92.6% of fecal pellets examined) and Coleoptera second (68%).

Our data document Hemiptera as a main food for *T. brasiliensis* and *N. femorosaccus* during part of the year. During early autumn (September) and late winter (March), abundances of hemipterans and lepidopterans likely are different from summer. Predominance of hemipterans, mainly lygaeids, during these months might not have been detected by previous dietary studies on either species because they were conducted only during early to mid-summer. A dietary study

by Debelica et al. (2006) on the larger congener, *Nyctinomops macrotis*, revealed Hemiptera (without Homoptera) to be a minor part of the diet, although that species was sampled from the same sites in September as in the present study.

Interestingly, in March, the dietary shift was accompanied by a change in overlap of niche, while in September, no change in overlap was noted (Table 2). March likely represents a time when insects are less abundant and resource partitioning could be more likely to occur. In September, the observation that *N. femorosaccus* and *T. brasiliensis* reflect the same shift in diet is evidence that the composition, but not necessarily the abundance, of available prey changed.

Our data support the hypothesis that *T. brasiliensis* and *N. femorosaccus* have similar diets due to ecomorphological constraints, which could include jaw morphology, flight characteristics, and echolocation (Freeman, 1981; Aldridge and Rautenbach, 1987). Consistent consumption of similar prey coupled with shift in diet during September, which was not accompanied by expansion in breadth of niche (more variety in diet), suggests that food was not a limiting resource for populations of bats that were sampled; with the possible exception of March, when a dietary shift and a reduction in overlap of niches between species occurred. Insectivorous bats might be less limited by availability of food (Fenton, 1982) than other resources, such as availability of maternal roost sites (Humphrey, 1975). Future studies of ecology and management of *T. brasiliensis* and *N. femorosaccus* in Big Bend National Park should focus on habitat variables of foraging and roosting sites.

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