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DIET OF THE MEXICAN MARBLED TOAD (*BUFO MARMOREUS*) IN CONSERVED AND DISTURBED TROPICAL DRY FOREST

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ABSTRACT—We collected data on diet of the marbled toad (*Bufo marmoreus*) on conserved and disturbed areas of tropical dry forest on the coast of Jalisco, Mexico, during 2000 and 2001. Although the diet of *B. marmoreus* consisted of 19 prey taxa, the moderately low dietary diversity measure ($H' = 1.51$) reflected the dominance in the diet of only 3 groups of prey: ants, beetles, and termites. Toads in the conserved area consumed greater proportions of ants (36.7% by volume), whereas toads in disturbed forest consumed greater proportions of beetles (53.1% by volume). Diet diversity was significantly lower in the disturbed area. However, abundance, size, and weight of toads was similar in both areas, suggesting that prey availability was not affected by disturbance.

RESUMEN—Registramos información sobre la dieta del sapo marmóreo (*Bufo marmoreus*) en áreas conservadas y perturbadas del bosque tropical seco en la costa de Jalisco, México, durante el 2000 y 2001. Aunque la dieta de *B. marmoreus* consistió de 19 taxa de presas, el moderadamente bajo valor de diversidad ($H' = 1.51$) reflejó la dominancia en la dieta de solamente 3 grupos de presas: hormigas, escarabajos y termitas. Los sapos en el área conservada consumieron mayor proporción de hormigas (36.7% en volumen), mientras que en el área perturbada consumieron mayor proporción de escarabajos (53.1% en volumen). La diversidad de la dieta fue significativamente menor en el área perturbada. Sin embargo, la abundancia, tamaño y peso de los sapos fue similar en ambas áreas, sugiriendo que la disponibilidad de las presas no fue afectada por la perturbación.

Amphibians occupy many diverse habitats across the globe; however, they are sensitive to a number of natural and anthropogenic factors. Amphibian declines have numerous potential and complex causes, including habitat modification (e.g., Delis et al., 1996; Anderson et al., 1999; Lynn and Lindle, 2002). Toads of the genus *Bufo* have been regarded either as indiscriminate predators feeding on a wide variety of arthropods (Zug and Zug, 1979) or as highly selective feeders relying mainly on ants and coleopterans (Flowers and Graves, 1995; Hirai and Matusi, 2002). Because forest disturbance has been reported to affect the structure of arthropod communities (e.g., Greenberg and Thomas, 1995; Heliölä et al., 2001), knowledge of food habits might be important for understanding the influence of habitat disturbance on anuran populations.

The Neotropical marbled toad *Bufo marmoreus* is endemic to Mexico, where it inhabits the tropical dry forest in coastal areas of the states of Colima, Guerrero, Oaxaca, Jalisco, and Veracruz (Smith and Smith, 1976). The tropical dry forest is considered one of the most threatened

tropical habitats (Primack, 1998), and in Mexico, it has been reduced to about 70% of its original area (Dirzo and Trejo, 2001). Because there are limited data available on the biology of the marbled toad (Ramírez-Bautista, 1994), we report on the food habits of this species. We specifically evaluate diet differences in toads inhabiting conserved and disturbed areas of tropical dry forest on the coast of Jalisco.

Our study was conducted in the coastal region of the state of Jalisco, Mexico. Vegetation type in the area is tropical dry forest. Toads were collected in an area of conserved forest in the Estación de Biología Chamela, a reserve approximately 3 km from the coast, and in an area of modified forest adjacent to the reserve. Mean annual temperature is 24.9°C, with an average annual rainfall of 748 mm, 80% of which falls from July through October after a 7 to 8 mo dry season (November to June) (Bullock, 1986; Lott et al., 1987). During the dry season, most of the trees lost their leaves. The conserved forest featured lush undergrowth during the rainy season and the canopy was about 15 m. The disturbed area consisted of a matrix of cattle pastures with almost no canopy, patches of secondary forest with moderate undergrowth and sparse to moderate canopy, and patches of primary forest. In the study area, *B. marmoreus* is active mainly during the rainy season. Therefore, field activities were conducted during this season (August to October) of 2000 and 2001. Three small watersheds within the reserve constituted the conserved area, and 3 small watersheds outside the reserve constituted the disturbed area. Nearest collecting sites between conserved and disturbed areas were ca. 15 km apart. Elapsed time of collecting between conserved and disturbed areas was no longer than 72 h, and the search was conducted at each area after sunset (between 2000 and 0400 h) in thirty 100-m × 10-m transects randomly established. Search effort was the same for both areas (120 person hours).

Stomach contents were extracted by stomach flushing (Legler and Sullivan, 1979) within 15 min after capture. After this procedure, toads were measured (snout-vent length: SVL), weighed, and released at the capture site. Food items were preserved in 70% ethanol and were classified as follows: lepidopterans were classified either as plume moths (Alucitidae) or ''other Lepidoptera,'' opiliones were classified either as Laniatores (suborder) or ''other opilones,'' and all other prey were classified to order, except for ants, which were classified to family (Formicidae). Prey were counted and measured volumetrically by using the fluid displacement method of Milstead (1957). Calculations were made of the relative abundance by numbers (%N), relative abundance by volume (%V), and the relative number of stomachs the food item occurred in (%F) for each taxon. From these data, we calculated the index of relative importance: IRI = (%N + %V) (%F) (Pinkas et al., 1971). Values of IRI (range = 0 to 20,000) indicate the relative importance of food items. Unidentified materials (digested items that could not be identified) and material considered to be ingested accidentally (parts of plants, sand, and stones) were not considered in the analyses.

To test for the variation in diet between toads of conserved and disturbed areas, we compared frequency of occurrence and volume of main prey items (>15% by volume) by Mann-Whitney *U*-tests. Dietary diversity and overlap were estimated using the index of relative importance. We calculated the Shannon-Wiener Index (H′) to estimate diet diversity (see Krebs, 1999). The diversity index increases with an increase in the number of dietary items, so low values represent dietary specialists and high values represent dietary generalists. Differences between dietary H′ values of toads of conserved and disturbed areas were compared using Hutcheson's *t*-test (see Magurran, 1988). As a descriptive measure of dietary concordance among toads of conserved and disturbed areas, we used Schoener's (1970) percent overlap index. This estimate makes no assumption about overall food availability in the habitat. An alpha level of 0.05 was used in all statistical tests. Means are reported ±1 *SE*.

We examined the stomach contents of 36 *B. marmoreus* individuals. Of the 36 individuals, 18 were collected in the conserved area (SVL = 55.3 ± 3.8 mm, range = 27 to 83 mm; weight = 17.8 ± 3.2 g, range = 2 to 45 g) and 18 in the disturbed area (SVL = 49.3 ± 3.0 mm, range = 29 to 83 mm; weight = 11.7 ± 2.6 g, range = 1.8 to 45 g). There was no significant difference in size between toads of conserved and disturbed areas. Therefore, possible differences in the diet of toads between areas due to body size were not analyzed.

Stomach contents for the entire sample of toads consisted of 19 types of terrestrial arthropods (Table 1). However, a few groups composed the greatest portion of the diet. Ants

TABLE 1—Stomach contents of *Bufo marmoreus* in conserved and disturbed tropical dry forest. The top line in each entry is presented as follows: percent in numbers / percent in volume (mm^3) / percent of frequency of occurrence. The number in the second line of each entry corresponds to the index of relative importance (IRI).

Food item	Conserved forest (n = 18)	Disturbed forest (n = 18)	Pooled (n = 36)
Acari	1.94 / 0.94 / 22.22 64.12	—	0.58 / 0.21 / 11.11 8.85
Araneae	0.24 / 0.13 / 5.55 2.09	2.92 / 1.53 / 22.22 99.10	2.12 / 1.22 / 13.88 46.47
Opiliones	—	0.10 / 0.00 / 5.55 0.60	0.07 / 0.00 / 2.77 0.21
Opiliones (Laniatores)	0.24 / 0.47 / 5.55 4.0	0.31 / 1.25 / 11.11 17.43	0.29 / 1.08 / 8.33 11.50
Coleoptera	2.42 / 5.46 / 50.0 394.74	23.11 / 53.14 / 77.77 5931.71	16.89 / 42.71 / 75.0 4470.98
Collembolla	0.72 / 0.02 / 16.66 4.05	—	0.219 / 0.01 / 5.55 0.610
Diptera	0.48 / 0.02 / 11.11 5.68	0.10 / .03 / 5.55 0.77	0.21 / 0.03 / 8.32 1.12
Hemiptera	0.24 / 0.04 / 5.55 1.37	—	0.80 / 2.931 / 8.33 0.35
Homoptera	0.24 / 0.12 / 5.55 2.05	1.35 / 0.08 / 1.11 8.03	1.02 / 0.09 / 8.33 5.84
Hymenoptera (Formicidae)	27.67 / 36.66 / 83.33 5361	18.30 / 28.88 / 72.2 3408.5	21.14 / 30.79 / 88.8 4616.2
Isoptera	64.56 / 30.04 / 38.89 3677.6	52.40 / 11.04 / 22.22 1409.9	56.10 / 15.36 / 36.11 2580.9
Lepidoptera	0.48 / 16.25 / 11.11 185.9	—	0.07 / 3.11 / 2.77 8.8
Lepidoptera (Alucitidae)	0.24 / 1.20 / 5.55 8.0	—	0.07 / 0.27 / 2.77 0.9
Neuroptera	0.24 / 7.73 / 5.55 44.3	0.20 / 0.24 / 5.55 5.0	0.21 / 1.93 / 8.33 17.9
Orthoptera	0.24 / 0.96 / 5.55 6.6	0.10 / 0.00 / 5.55 0.6	0.14 / 0.22 / 5.55 2.0

(Formicidae) were the most frequently consumed, followed by termites (Isoptera) and beetles (Coleoptera). Volumetrically and numerically, ants dominated, followed by termites and beetles. Ants presented the highest IRI values, followed by beetles and termites (Table 1). The rest of the items presented IRI values well below the former groups of prey (range = 0.20 to 46) (Table 1). Ants, beetles, and termites constituted 88.9% by volume and 91.2% by number of the diet. Dietary diversity measure (H′) for the entire sample was 1.51.

There was some diet variation in toads of conserved and disturbed areas. Although 5 prey items (Acari, Collembolla, Hemiptera, Lepidoptera, Alucitidae) were absent in the diet of toads from the disturbed area, 3 groups (Formicidae, Coleoptera, Isopoda) composed the highest proportion of the diet in both areas (Table 1). Whereas ants were the most important item in the conserved area (36.7% by volume), beetles were the dominant item in the disturbed area (53.1% by volume). Using frequency of occurrence values, we detected no significant difference in the importance of ants, termites, and beetles in the diet of toads from disturbed and conserved areas. However, there was a significant difference in volume of beetles (Mann-Whitney U-test: $U = 17.0$, $P = 0.001$) between conserved and disturbed areas. Because we did not quantify potential availability of food resources, we cannot speculate whether this difference was a result of selective foraging, or might simply reflect the relative availability of various prey groups. The diversity index was significantly different for conserved (H′ = 1.54) and disturbed (H′ =

0.97) areas ($t = 35.07$, $df = 34$, $P < 0.05$). Dietary overlap between both types of areas was 48.2%.

Although the diet of *B. marmoreus* consisted of 19 prey taxa, the moderately low dietary diversity measure ($H' = 1.51$) reflects the dominance in the diet of only 3 groups of food items. In general, toads of the genus *Bufo* have been regarded as indiscriminate predators because they consume a wide variety of arthropods, as well as unpalatable prey (Zug and Zug, 1979). However, several studies have indicated that bufonids are selective feeders. According to the review by Clarke (1974) on diet information of *Bufo*, ants and beetles were the most frequent food items in 26 of 29 cases. Studies that are more recent have reported similar results, with bufonids feeding mainly on ants or beetles (e.g., Toft, 1981; Sweet, 1992; Flowers and Graves, 1995; Hirai and Matusi, 2002; Isacch and Berg, 2002), including, in some cases, also termites (e.g., Strüssmann et al., 1984). Our results with *B. marmoreus* agree with these previous studies, because ants and beetles were among the 3 most important food groups taken by this species. In general, ants and various beetle groups (e.g., carabids and harpalids) are unpalatable to many predators because they contain formic acids and quinones, respectively. Clarke (1974) suggested that food habits that exploited prey unpalatable for other predators accounted for the worldwide success of *Bufo*, by reducing food-related competition with other insectivorous predators. The same explanation might account for the wide distribution of *B. marmoreus* in Mexico. The striking similarity in food profiles of bufonids, dominated by ants and beetles, reported by authors in a variety of environments strongly suggests that they are selective feeders. The importance of termites in the diet of *B. marmoreus* suggests that this species is also an opportunistic feeder, because termites have been reported to be active and available throughout the year in tropical habitats with a marked seasonality (Teixeira-Filho et al., 2003).

The conclusion by Toft (1980, 1981) that toads are active foragers was supported by our data. According to Toft (1981) and Donnelly (1991), there might be a correlation between an active foraging strategy and the occurrence of prey that is difficult to digest in the diet (e.g., chitinous or noxious prey). This is characteristic of the ants and beetles that contributed significantly to the diet composition of *B. marmoreus* in our study. Termites, considered a relatively sedentary prey, with clumped distribution, are also an important prey in the diet of active foragers (Teixeira-Filho et al., 2003).

Although diet diversity was lower in the disturbed area, abundance, size, and weight of toads were similar in conserved and disturbed areas, suggesting that prey availability was not significantly limited by disturbance. According to the optimal foraging theory (reviewed by Begon et al., 1986), a wider feeding niche would be expected if prey were less abundant and available. Therefore, the narrower feeding niche of *B. marmoreus* in the disturbed area further suggests that prey availability was not negatively affected by disturbance. Whereas habitat modification is detrimental to many species of anurans, it might benefit others. Several species of *Bufo* have been reported to respond positively to habitat modification (e.g., Duellman, 1999; Mazerolle, 2003). Forest disturbance frequently results in an increase in temperature and decrease in relative humidity, imposing physiological constrains on amphibians. A number of structural and physiological features (reviewed by Duellman and Trueb, 1994) allow toads (*Bufo*) to be remarkably tolerant of dry conditions. Therefore, the tolerance to drier conditions might be the critical feature that enables *B. marmoreus* to survive the negative effects of disturbance, and to be active and forage efficiently under the environmental conditions of the modified forest.

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