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DIET AND FEEDING BEHAVIOR OF THE HORNED GUAN (*OREOPHASIS DERBIANUS*) IN MEXICO

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ABSTRACT.—The Horned Guan (*Oreophasis derbianus*) is endemic to humid montane forests of southern Mexico and Guatemala. This species is considered endangered because of their small populations, the loss and fragmentation of habitat, illegal trade, and overexploitation by subsistence hunters. We update information about the species' diet and foraging behavior by integrating the results generated during two and a half decades of research on the Horned Guan's ecology at the El Triunfo Biosphere Reserve, in Chiapas, Mexico, with additional published information compiled from other areas. Based on nearly 450 hrs of direct observations of free-ranging guans and 530 discrete feeding events, we found that during the breeding season Horned Guans feed primarily on fruits from six species of plants and leaves from one species. Horned Guans were not observed eating animal matter, corroborating its specialized frugivore-folivore habits. Our study increases the known plant taxa found in the Horned Guan's diet in El Triunfo from 40 to 63 (Supplemental Material), and globally to 101 species (Supplemental Material). For 48 taxa in El Triunfo, only fruits were consumed, while for eleven taxa consumption was restricted to leaves, and to flowers for one species; for four taxa both fruits and leaves were consumed. We found significant differences between males and females in the location of foraging on trees and diet composition. Young birds are fed fruits of *Citharexylum mocinnii* and leaves of *Solanum appendiculatum* by their mothers, both of which are rare in the diet of adult males. The conservation of the Horned Guan requires the long-term protection of suitable habitat that maintains the plant species important in their diet. *Received 21 March 2016. Accepted 18 January 2017.*

Key words: conservation of Neotropical montane forest birds, El Triunfo Biosphere Reserve, foraging behavior, frugivory, Horned Guan, Mexican cloud forest, *Oreophasis derbianus*.

The Horned Guan (*Oreophasis derbianus*) is endemic to the humid montane forest of southern Mexico and Guatemala (Andrle 1967, Howell and Webb 1995, del Hoyo and Motis 2004). At the global level, the species is currently considered endangered (Brooks 2006, BirdLife International 2015), because of small population sizes and threats from hunting, deforestation, and illegal trade (CONAP 2001, Eisermann and Avendaño 2006, SEMARNAT 2010, BirdLife International 2015, del Hoyo and Kirwan 2015). Although there are many published descriptions of its biology and ecology in the wild and in captivity (Álvarez del Toro 1976; González-García 1984, 1986, 1988, 1991, 1994, 1995, 1997a, b, c, 2001, 2005a, b, 2007, 2009; González-García and Bubb 1989; Gómez de Silva G. et al. 1999; Méndez 2000, 2010; González-García et al. 2001, 2006a, b; Secaira and Cornejo 2003; Montes 2005; Pozo V. et al. 2005; Rivas Romero and Cóbar Carranza 2005, 2007; Rivas-Romero et al. 2005; Secaira 2005; Abundis 2006; Eisermann et al. 2007; Secaira and Cornejo 2007; Tovar et al. 2007, 2009; Cornejo 2009; Dierenfeld et al. 2009; Ramos and González-García 2009), important aspects of its ecology are still unknown (e.g., home range and seasonal and patterns of movements).

Taxonomically, this species is placed in a monotypic genus, *Oreophasis*, and individuals have a 'horn' (naked coral-red bony structure growing on top of the head). It is one of the few bird species that feeds predominantly on fruits and leaves, as well as nectar and flowers (Klasing 1998, Muñoz and Kattan 2007, Rivas Romero 2008, Méndez 2010).

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An ecologically relevant characteristic is that many of the seeds consumed pass through the digestive tract unharmed, defecated in viable condition with different species-specific rates of germination (González-García 2009, Ramos and González-García 2009). Horned Guans are considered to play an important role as seed dispersers, affecting the composition and structure of cloud forests (Silva and Strahl 1991, Sedaghatkish 1996, Muñoz and Kattan 2007). Because of their large size, movements and specialized diet, information on plant-animal interactions, such as seed dispersion and effects on forest dynamics are relevant for understanding the structure and function of the endangered montane forest ecosystems they inhabit (Howe et al. 1985, Strahl and Grajal 1991, Jordano 2007). In their assessment of available information on cracid diets, Muñoz and Kattan (2007) concluded that "few rigorous quantitative studies on cracid diets are available" and few studies had "evaluated seasonal and habitat variations in resource availability and cracid responses to such variation." This missing information is essential for understanding aspects of the Horned Guan's ecology, behavior, population dynamics, and habitat requirements needed to develop conservation management recommendations. Consequently, there is a need for an updated assessment of the Horned Guan's diet and ecology and its relationship to seasonal fruit availability (Muñoz and Kattan 2007). We synthesize published information on the Horned Guan's diet and foraging ecology, seasonal fruit production and reproductive phenology from Mexico and Guatemala (González-García 1984, 1991, 1994, 2005a, 2007, 2009; Solórzano 1995; Méndez 2000, 2010; Solórzano et al. 2000; Dierenfeld et al. 2009; Ramos and González-García 2009; Quiñónez Guzmán 2011; Rivas-Romero and Soto-Shoender 2015), and analyze unpublished foraging observations from the El Triunfo Biosphere Reserve collected 1982–2006 and 2011–2014 to provide a reassessment of the diet and foraging behavior of the Horned Guan in Mexico.

METHODS

The El Triunfo Biosphere Reserve is located in the central portion of the Sierra Madre de Chiapas (15° 09′ 10″ and 15° 57′ 02″ N, 92° 34′ 04″ and 93° 12′ 42″ W). The El Triunfo Biosphere Reserve (450 to 2,750 m) has a total area of 119,117 ha, including one of the most extensive (~50,000 ha) contiguous areas of mesophilous forest in Mexico (Challenger 1998, INE 1999). Annual precipitation ranges from 2,000 and 4,500 mm and annual average temperature between 14–30 °C, with a relative dry season between November and April and a rainy season from May to October (INE 1999).

El Triunfo reserve harbors 10 vegetation types; the dominant ones being the mesophilous mountain ('cloud') forest, tropical humid ('rain') forest, and pine-oak forest. Tropical deciduous forests are found along the bottom of ravines and of sheltered hillsides at lower altitudes (INE 1999). The reserve is divided into five core zones. Our research was conducted in the 11,594 ha Zone I, El Triunfo (INE 1999). In El Triunfo, the Horned Guan is restricted to mesophilous mountain forest. Zone I Cloud forest (altitude range 1,700–2,400 m) is characterized by the *Quercus-Matudaea-Hedyosmun-Dendropanax* community (Ramírez and Williams Linera 1990; Long and Heath 1991; Pérez-Farrera et al. 2004; González-García 2005a, b), although it can use other forest types at lower altitudes seasonally. A detailed description of the plant species composition and structure of the Horned Guan's preferred habitat in El Triunfo Biosphere Reserve was conducted by FG-G (unpubl. data), and a similar study is known for Volcán San Pedro, Sololá, Guatemala (Pardo Villegas 2007).

We observed foraging behavior and diet of Horned Guans mostly during the reproductive season from February to May of 1982–1984, 1987–1992, January–June and August–December 1993. No field work was conducted during July and August 1993. Our searches covered 861.8 km on trails within a 2.6 ± 0.65 km (mean ± SD, $n =$ 6 trails) radius of the main visitors' camp. Guans were usually found by the sounds they made during courtship or foraging (e.g., wing flapping, defecating) and by visiting trees known to be used regularly for foraging. Our systematic search of the study area assured that we were able to detect shifts in diet when guans began feeding on new species of trees, and the systematic quantification of our observations allowed us to objectively compare the diet of males and females as well as adults and young. Our data will be slightly biased towards the most commonly used species, and thus should be interpreted as a first approximation to

quantifying the relative frequency of plant species in the diet of Horned Guans. Guans were more easily detected from early October to May when courting males perform deep, slow and soft 7-note "mooing" courtship calls to attract females, and perform conspicuous short flights from tree to tree (González-García 1995, Gómez de Silva G. et al. 1999). Beak-clacking, the only one of 13 described calls that is similar among males and females, is also heard during this period. We observed foraging, diet, and courtship behavior with 10 × 40 binoculars or a 18–36 × 50 mm telescope from distances of 10 to 50 m. Length of events were measured with digital watches or chronometers from direct observations in the field.

Data on foraging behavior come from 449.5 hrs of observation (885.5 hrs of search time conducted during Feb to May of 1987–1992 and during Jan–Jun and Aug–Dec 1993: mean 8.79 ± 2.47 hr/day) with a mean of 3.15 ± 2.92 hrs (1–590 mins) of continuous daily observation over 101 days. Mean observation per individual was 2.96 ± 2.65 hrs. We observed 520 foraging behavior events of which we recorded 263 events by females, 208 events by males, and 49 events by individuals of unknown sex. Additional data on diet and feeding behavior were gathered during observation conducted during March 2011–January 2012, February 2012–January 2013, February 2013–April 2014 as part of long-term monitoring programs for Horned Guans. The observation method used was based mainly on *ad libitum* and all occurrences sampling during opportunistic encounters. Using that sampling method, we gathered data on frequencies and durations of behaviors for single guans, pairs (1 pair = 1 male and 1 female), or females with chicks or juveniles were recorded during different sampling periods (Altmann 1974, Martin and Bateson 1986, Lehner 1996).

Although birds were not individually marked, based on individual differences in plumage characteristics, body size, and shape of horn, as well as the locations and time of the observation, our data are based on 15–18 different males, 12–14 different females, and 10–13 different chicks or juveniles. We determined the diet by identifying field-collected specimens of the flowers, fruits and leaves of the plants on which the guans were feeding, and by identifying seeds collected from fecal samples.

We recorded: 1) Total time guans were observed on a given tree species; 2) Total time guans were observed feeding on a given tree species; and 3) Frequency of occasions guans were observed feeding on a given fruit species. These three parameters were highly correlated: total time spent in a tree species versus duration of feeding time observed on that species of tree ($r^2 = 0.90$, $P < 0.001$, df = 19) and versus frequency of occasions observed feeding in that tree species ($r^2 = 0.88$, $P < 0.001$, df = 19); time observed feeding and the number of occasions observed feeding in the same tree species ($r^2 = 0.85$, $P < 0.001$, df = 19). However, there is no relationship between the total time spent in a tree species and the percentage of time spent foraging on that tree species ($r^2 = 0.0523$, $P = 0.32$, df = 19). Given the high correlation among the three parameters we used, we were able to more easily analyze the frequency of feeding events to evaluate the diet of Horned Guans.

We compared the seasonal phenology of fruit production (Solórzano 1995, Solórzano et al. 2000) with the diet and reproductive cycle of the guans. Student's *t*-test and non-parametric tests (X^2, Mann-Whitney *U*-test) were used to evaluate the level of significance of the comparisons. Most data are presented as mean ± SD and median for the total time spent in the trees and duration of feeding visits. All tests were performed using Statistica (StatSoft Inc. 2003).

RESULTS

We observed 520 foraging events on 21 plant taxa, 83% of the observations consisted of only fruits, 17% of only leaves, and 1% of leaves and fruits of the same species and flowers. Consumed fruits were mostly ripe, but occasionally during the breeding season, unripe fruits were eaten. Leaves were only consumed at young tender stages. We tallied more than 500 mins of feeding observations at trees (see below), the mean % foraging time of the total time spent on a tree was 28.3 ± 7.3 mins.

Horned Guans fed most frequently on seven taxa (Table 1), with 50% of the feeding observations occurring evenly on two species: *Symplococarpum purpusii* and *Citharexylum mocinnii*. *Morus insignis, Dendropanax* sp., *Conostegia volcanalis*, and *Hedyosmun mexicanum* each

TABLE 1. Feeding observations of Horned Guans *Oreophasis derbianus* by age and during courtship feeding in the El Triunfo Biosphere Reserve, Chiapas, Mexico.

	Frequency of observations			
Species plants	Adult Horned Guans *N* (%)	Chicks and fledglings *N* (%)	Courtship feeding *N* (%)	Total *N* (%)
Symplococarpum purpusii	108 (25.4)		21 (67.7)	129 (25.4)
Citharexylum moccinii	90 (21.2)	33 (62.2)		123 (24.2)
Solanum appendiculatum	63 (14.8)	7 (13.2)		70 (13.8)
Morus insignis	53 (12.5)		4 (12.9)	57 (11.2)
Hedyosmun mexicanum	26 (6.1)			26 (5.1)
Conostegia volcanalis	25 (5.8)		1 (3.2)	26 (5.1)
Dendropanax sp.	22 (5.1)	11 (20.7)	2 (6.4)	35 (6.9)
Other species*	37 (8.7)	2 (3.7)	3 (9.6)	42 (8.3)
Total	424 (100)	53 (100)	31(100)	508 (100)

* Other species with < 9 observations: *Trophis cuspidata, Prunus sp., Amphitecna montana, Lauraceae, Ocotea chiapensis, Urera caracasana, Cestrum aff. guatemalae, Ugni myricoides, Spathacanthus parviflorus, Nectandra rudis, Quercus sp., Prunus brachybotrya, Licaria excelsa/L. glaberrima*.

contributed 5.1% to 11.2% of the observations. Horned Guans consumed leaves of *Solanum appendiculatum* during 13.8% of the observations. The use of the seven plants species varies significantly depending of age and courtship (adults: $X^2 = 125.37$, df = 6, $P < 0.001$; chicks and fledglings: $X^2 = 121.8$, df = 6, $P < 0.001$; courtship: $X^2 = 87.5$, df = 6, $P < 0.001$) (Table 1). Seeds of *Ocotea chiapensis*, *Dendropanax* sp., *Oreopanax* sp., *Eugenia capulli*, *C. mocinnii*, *Urera caracasana*, *Smilax* sp., *S. purpusii*, leaves of *S. appendiculatum* and *P. brachybothrya*, and other unidentified plant material were found in 12 different fecal droppings (average number of seeds per excrement was 101.5 ± 85.17, range = 1–342, $n = 12$). All seeds found in fecal samples were intact, suggesting that guans digest only pulp. No traces of arthropods or vertebrates were found (one dropping contained three small (2–3 mm) undigested white larvae that seemed to have colonized the dropping). Guan feces that include leaves generally included small pebbles. No pebbles were detected in feces without leaves. Feces often contained seeds of *Dendropanax* sp. and *Smilax* sp., and some whole fruits were undigested, suggesting gentle treatment during digestion or being consumed when unripe (Tables 2–3).

Guans consumed leaves from eleven taxa (Supplemental Material), the most frequent of those were *S. appendiculatum* and of *P. brachybotrya,* which they fed on during the breeding season and later. Leaves of the latter species were eaten whole or in fragments by males, females, chicks and juveniles. During 39 mins of observation in a *P. brachybothrya* tree, one male Horned Guan ate 179 times (4.6 leaves/min). One female and her two chicks were also observed feeding on green leaves of the same tree species. In total, at El Triunfo, the diet of guans is based on 63 plant species of 32 families (Supplemental Material).

Guans revisit the same plants or group of the same plants if they are bearing abundant fruit. Feeding visits can be on consecutive days and even in different months. For example, one female with one juvenile (age 4–5 months based on the horn size) revisited the same *P. matudae* tree with abundant fruit in October, November and December 2012. During 5.48 hrs of observations, we observed this female with her juvenile feeding together on *P. matudae* tree. The female fed 13 times, the juvenile 18 times, and both produced 36

TABLE 2. Frequency and percentage of feeding events of male and female Horned Guans (*Oreophasis derbianus*) on the most important food trees in the El Triunfo Biosphere Reserve, Chiapas.

Fruits species	Females	%	Males	%
Citharexylum moccinii	72	45.6	13	7.5
Symplococarpum purpusii	24	15.2	83	48.0
Morus insignis	21	13.3	25	14.5
Dendropanax sp.	15	9.5	7	4.0
Conostegia volcanalis	12	7.6	10	5.8
Hedyosmum mexicanum	2	1.3	23	13.3
Others	12	7.6	12	6.9
Total	158	100.0	173	100.0

TABLE 3. Reproductive phenology of the Horned Guans (*Oreophasis derbianus*) in the El Triunfo Biosphere Reserve, Chiapas, Mexico, based in all our sampling periods.

	Months											
Reproductive activity	Jan	Feb	Mar	Abr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
Courtship calls	•	•	•	•	•	•				•	•	•
Courtship feeding/following	•	•	•	•	•					•	•	
Copulation	•	•	•	•								
Selection of nest sites	•	•	•	•								
Egg laying	•	•	•	•								
Incubation	•	•	•	•	•							
Hatching/chicks/fledglings	•	•	•	•	•	•	•	•				
Care of fledglings and juveniles			•	•	•	•	•	•	•	•	•	•

feces. The female defecated every 15.3 ± 11.20 mins (range = 1–44, n = 17) and the juvenile defecated every 17.7 ± 9.50 mins (range 5–34, n = 17). Feeding bouts (defined as the time of uninterrupted feeding) for the female lasted 10.3 ± 10.6 mins (range = 2–35, n = 11) and for the juvenile lasted 5.5 ± 2.6 mins (range = 1–10, n = 14). A feeding bout began every 23.4 ± 22.0 mins (range = 1–67, n = 10) for this female, and for the juvenile it began every 17.8 ± 13.9 mins (range = 1–36, n = 13). These and other observations on *C. moccinni*, *C. volcanalis*, and *M. insignis* fruiting trees (FGG, unpubl. data), suggest this cracid species remembers the location and the time of ripening of individual fruit trees (Galleti et al. 1997).

Male and female Horned Guans had significantly different ($X^2 = 94.05$, df = 5, $P < 0.001$) diet composition, with males consuming a greater proportion of fruits (91.3% versus 79.5%) and a lower proportion of leaves (7.7% versus 19.8%) than females (Table 2). Males fed more on fruits of *S. purpusii* and *H. mexicanum* and females fed more on fruits of *C. mocinnii* and *Dendropanax* sp. and leaves of *S. appendiculatum*. The three species preferred by females (*C. mocinnii, Dendropanax* sp., *S. appendiculatum*) were the principal food species fed to chicks and might reflect the dietary needs or preferences of the chicks rather than of the adult females. Four of the seven most important plant species in the diet (*C. mocinnii*, *S. purpusii*, *M. insignis*, *C. volcanalis*) were presented by males to females during courtship feeding (Tables 1–2).

Horned Guans are mainly arboreal and tend to forage in the mid strata of the forest, sometimes on the ground, and less frequently in the canopy. Horned Guans were observed in trees with a mean height of 19.03 ± 5.3 m (range 7–40 m, n = 1,375), with the individuals located at a mean height of 14.8 ± 4.7 m (range = 3–35 m, n = 1,375). Foraging locations differed between sexes (Fig. 1). Males used trees that were significantly taller (mean = 21.5 ± 4.6 m, range = 12–40 m, n = 510) than those used by females (mean = 17.6 ± 5.3 m, range = 10–35 m, n = 768) (t-test = 11.90, df = 1,276, $P < 0.001$). Males foraged significantly higher (mean = 16.7 ± 4.3 m, range = 8–35 m, n = 510) than females (mean = 13.6 ± 4.7 m, range = 7–25 m, n = 768) (t-test = 13.58, df = 1,276, $P < 0.001$). Guans of unknown sex were

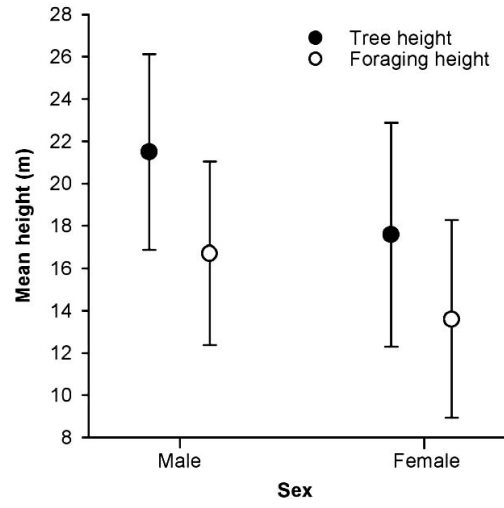

FIG. 1. Tree and foraging height of male and female of Horned Guans (*Oreophasis derbianus*) in the El Triunfo Biosphere Reserve, Chiapas, Mexico (Mean ± SD).

TABLE 4. Monthly feeding observations of the Horned Guans (*Oreophasis derbianus*) in different plants species in the El Triunfo Biosphere Reserve, Chiapas, Mexico.

	Months												
Species plants	Jan.	Feb.	Mar.	Apr.	May.	Jun.	Jul.*	Aug.*	Sept.	Oct.	Nov.	Dec.	Total
Symplococarpum purpusii		50	27	35	18								130
Citharexylum moccinii				2	119	3							124
Solanum appendiculatum			22	4	38	9			1		1		75
Morus insignis		10	46		2								58
Dendropanax sp.		4	1	6	27	1							39
Conostegia volcanalis		1	15		12								28
Hedyosmum mexicanum				15	6	5							26
Trophis cuspidata											4	5	9
Prunus sp.			3		2								5
Amphitecna montana									1		3		4
Ocotea chiapensis		4											4
Lauraceae			3										3
Nectandra rudis			2										2
Cestrum aff. Guatemalense			2										2
Spathacanthus parviflorus			2										2
Ugni myricoides				2									2
Quercus sp.			1			1							2
Licaria excels/L. glaberrima												1	1
Prunus brachybotrya					1								1
Undetermined			1		2								3
Total observations		69	125	64	227	18			2		8	7	520

* Field work not conducted during July and August. Only in 1993 was field work done from Sept to Dec.

observed using trees with a mean height of 17.4 ± 3.4 m (range 7–20 m, $n = 97$) and foraging at a mean height of 13.8 ± 2.5 m (range = 6–18 m, $n = 97$).

The reproductive phenology of the Horned Guan can be divided into eight behavioral categories each spanning 3–9 months (Table 3) and is clearly correlated with two ecological processes: rainfall and fruit production. Incubation and fledging occur from January to May which includes the driest months of the year (Jan to Mar) and the beginning of the rainy season (Apr and May). Although Horned Guans have been observed feeding on different species of fruits and leaves at El Triunfo during all 12 months of the year (Table 4, Supplemental Material), and at least 6 species of fruits are available for the guan to eat during the whole year (Solórzano et al. 2000), the most abundant species of fruits in their diet are produced during a restricted 3–7 month period from January to August that coincides with the reproductive season (e.g., *C. mocinnii*: Jan–Jun, *S. purpusii*: Nov–Apr, *M. insignis*: Feb–Mar, and *C. volcanalis*: Mar–Aug; Solórzano 1995, Solórzano et al. 2000).

During the reproductive period, guans fed on 5–12 species of fruits (Table 4). *M. insignis* was important early in the season (Feb and Mar) and *C. moccini, Dendropanax* sp., and *S. appendiculatum* at the end of the season when these species were consumed by females and fledglings (Table 1). Data on the average monthly abundance of 10 fruit species consumed by guans, including the four most important fruit species consumed during the breeding season, shows peak fruit availability occurring form February to April (Fig. 2; Solórzano 1995, Solórzano et al. 2000).

DISCUSSION

Our observations of foraging wild Horned Guans document 24 new plant species/taxa not previously observed in their diet in El Triunfo. Additionally, Horned Guans have been reported eating flowers of *Arpophylum medium* (Orchidaecae), *Chiranthodendron pentadactylon* (Malvaceae), and *Clematis* sp. (Ranunculaceae; González-García 2005a, b; Abundis Santamaría 2006; Rivas Romero 2008), drinking nectar from the flowers of *C. pentadactylon* (Méndez 2000,

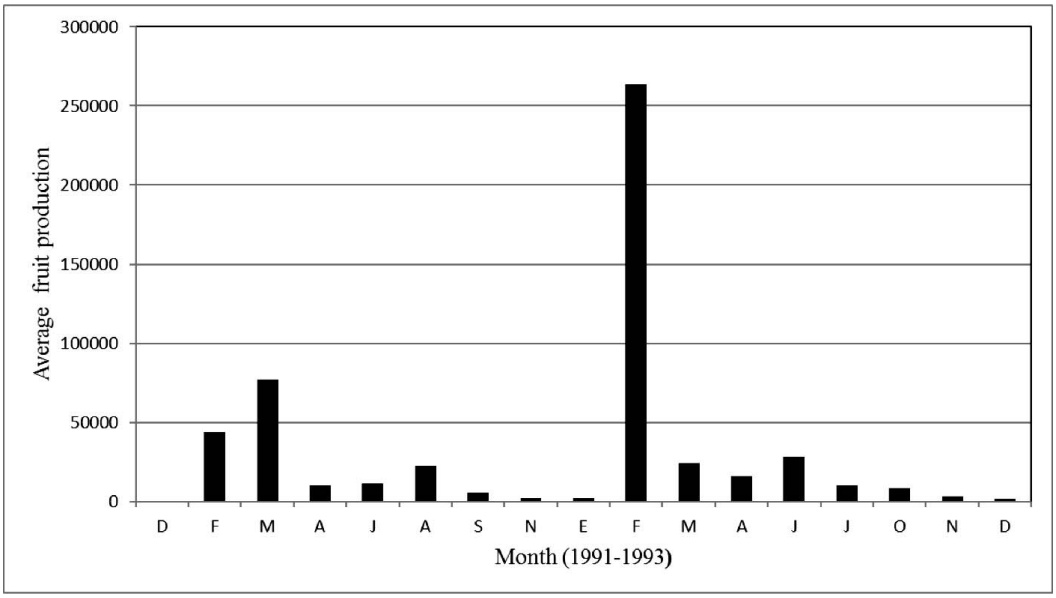

FIG. 2. Average monthly abundance of fruits of species common in the diet of the Horned Guan in El Triunfo Biosphere Reserve (pooled data from the following species: *Citharexylum mocinnii, Conostegia volcanalis, Morus insignis, Ocotea chiapensis, Trophis cuspidata, Licaria excelsa/Licaria glaberrima, Nectandra rudis, Cinnamomun zapatae, Symplococarpon purpusii*). Data adapted from Solórzano (1995).

2010; Cóbar Carranza 2006; Rivas Romero 2008; FG-G, pers. obs.), and feeding on fruits of *Oreopanax echinops*, *Dendropanax arboreus* (Araliaceae), and *Phoebe salvini* (Lauraceae; Méndez 2000, 2010; Rivas Romero 2008). Additional plants recorded in their diet are shown in Supplemental Material, which excludes an unconfirmed report of Horned Guans eating leaves of watercress (*Nasturtium officinale*: Brassicaceae) by villagers from Chiquihuite (Volcán Tacaná), in Unión Juárez, Chiapas). The known plant taxa consumed by Horned Guans is 101 range-wide (Méndez 2000, 2010: appendix II; Montes 2005; Cóbar Carranza 2006; Pardo Villegas 2007; Supplemental Material) and 63 at El Triunfo (del Hoyo and Motis 2004; González-García 2005a, b; Supplemental Material). We confirm the diet of Horned Guans is almost exclusively based on fruits, leaves, flowers and nectar, and that they consume different plant parts according to the species (Supplemental Material).

During the breeding season, Horned Guans concentrate their diet on seven species that are relatively common in El Triunfo (Long and Heath 1991, Williams Linera 1991, Gómez Velasco et al. 2004). However, the frequencies of the preferred species in Horned Guans' diet are not related to their abundance in the El Triunfo cloud forest, as other fruiting trees were more abundant in the forest than those of *S. purpusii, C. mocinnii,* and *M. insignis* which were preferred by the guans (González-García 2005a). Lauraceous plants were not as important in the diet of Horned Guans as we expected because Lauraceous fruits, rich in lipids and nutrients, have been shown to constitute an important component of the diet of many large frugivorous species in humid montane forests of the Neotropics, including the El Triunfo forest (Moermond and Denslow 1985, Wheelwright 1991, González-García 1994, Solórzano 1995, Solórzano et al. 2000, Muñoz and Kattan 2007, Bertsch and Barreto 2008).

The pattern of concentrating their diet on only a few species of fruits has been reported in other guan species such as *Penelope superciliaris* (Mikich 2002, Zaca et al. 2006), *P. obscura* (Merler et al. 2001), *P. marail* (Thery et al. 1994, Muñoz et al. 2007), *Chamaepetes goudotii* (Londoño et al. 2007), and curassows such as *Crax daubentoni* (Bertsch and Barreto 2008). Other cracids have also been reported to depend on a few plant species such as *Mitu mitu* in Peru

(four species of Moraceae: *Brosinum* sp., *Clarisia racemosa*, *Ficus* sp., and *Pseudolmenia* sp.; Torres 1989), *M. salvini* in Colombia (*Guarea guidonia*; Santamaría and Franco 2000), and *Ortalis canicollis* in Argentina (*Schinus poygamus* and *Rivina humilis*; Caziani and Protomastro 1994). Horned Guans frequently (20%) feed on leaves, showing habits similar to *Mitu mitu* which feeds on leaves with a frequency of 68% (Torres 1989), and *Ortalis canicolis* and *Penelope perspicax*, which feed on leaves with a frequency of 39% and 27%, respectively (Caziani and Protomastro 1994, Muñoz 2004, Muñoz et al. 2007).

Most seeds and some fruits observed in feces were intact suggesting that Horned Guans might have a weak gizzard, allowing seeds to pass intact through their digestive tract, and thus could play an important role as dispersers in this mountain tropical ecosystem (del Hoyo and Motis 2004). However, some large seeds such as *P. brachybothrya* fruits, found in feces, were sometimes found completely destroyed. Horned Guans have been observed eating small pebbles, and these are more frequent in fecal samples whose content include leaf remains, suggesting the need to grind plant material in the gizzard as in other bird species (del Hoyo and Motis 2004, Bertsch and Barreto 2008). The effectiveness of the Horned Guan as a seed disperser remains to be evaluated, because individuals may remain for many hours during consecutive days in the same fruiting trees, and most seeds are defecated below the parent tree (González-García 2005a, 2012). A similar feeding behavior is reported for *Pipile jacutinga* in Brazil (Galleti et al. 1997).

Horned Guans are mainly arboreal and tend to forage in the mid strata of the forest. In pairs and during breeding season, males foraged higher than females, either in a fruiting trees or any other trees. In Colombia, *P. perspicax* and *Chamaepetes goudotii* fed in the upper strata at an average height of 9.89 m and 8.6 m, respectively, and their foraging height varied over the course of the year (Ríos et al. 2006, Londoño et al. 2007). Seasonal variation in foraging height in Horned Guans remains to be evaluated.

The seasonal selection by Horned Guans of different species of fruits and different plant parts was probably dependent as much on variation of the seasonal nutritional requirements as much as on the seasonal availability of the fruits or plant parts. Both fruits and leaves consumed by guans contained about 70% water, and plant crude fiber content was similar (17% versus 13% of dry matter (DM)), in fruits and leaves, respectively (Dierenfeld et al. 2009). However, crude protein in fruits (9% DM) was considerably lower than in leaves (23% DM), suggesting that leaves may be a supplementary source of protein or nutrients (Sun and Moermond 1997, Sun et al. 1997, Muñoz et al. 2007), and may compensate for the lack of animal protein in the diet. In captivity, Horned Guans will rarely accept invertebrates, and hand-reared chicks show little interest in mealworms or crickets (Cornejo 2009). Healthy diets for captive adults contain between 5–10% crude protein (Tovar et al. 2009), which is well within the range of 9% and 23% of protein in fruits and leaves, respectively (Dierenfeld et al. 2009). The crude fat in Lauraceous fruits (*Ocotea* and *Nectandra* spp.) consumed pre- and early in the breeding season, could be seasonally important as it was considerably higher (~36–38%) than that in other foods eaten during those same periods. Ca:P ratios were adequate in both fruits and leaves, although leaves probably provided an essential source of both nutrients during breeding (and particularly) egg-laying periods when calcium needs are elevated (Dierenfeld et al. 2009).

This study and previous ones establish that Horned Guans have a highly frugivorous-folivorous diet (Merler et al. 2001, Mikich 2002, Zaca et al. 2006) that is more specialized than that of other guans and curassows (Torres 1989, Erard et al. 1991, Santamaría and Franco 2000, Jiménez et al. 2001, del Hoyo and Motis 2004, Londoño et al. 2007, Bertsch and Barreto 2008). Green leaves are a low-quality food compared to nutritious fruits (Muñoz and Kattan 2007) and are difficult to digest because of high content of structurally complex carbohydrates, and a variety of toxic and secondary compounds (Howe and Westley 1988, Bertsch and Barreto 2008). This probably accounts for leaves being a low-intake item for birds. However, leaves could be important as a source of essential nutrients (e.g., nitrogen; Morton 1978, Jiménez et al. 2001).

The dissimilarity documented in the diets of male and female guans, involved not only the type and proportion of fruit and leaf species selected, but also the size of trees and the overall heights where they foraged. During different seasons, the

sexes use different regions of the landscape that support different plant species; female guans with chicks use ravines more often than males, who select ridges and tall trees more often than females, presumably to broadcast their courtship calls greater distances (González-García 2005a). Unlike males, females have greater calcium needs during egg-laying and must search for and consume specific plant species to feed their chicks. Behavioral and physiological contrasts between the two sexes can thus be a cause of sexual dietary differences, which ultimately could have important habitat management implications to assure adequate survival of each sex.

The future does not bode well for Horned Guans which live at low densities, have a restricted geographic range, specialized habitat preferences, and a diet based on a small suite of cloud forest plant species. This species will likely be greatly affected by climate-change which is expected to reduce the cloud forest habitats of Mexico and increase variation and uncertainty in fruit production (Peterson et al. 2001, Rojas-Soto et al. 2012, Peterson and Navarro-Sigüenza 2016). Conservation-oriented research for effective management of the species (Santana C. and Jardel P. 1994) will be needed if the Horned Guan and its associated plant species are going to survive in the montane cloud forests of Mexico and Guatemala.

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