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FORAGING BEHAVIOR AND DIET OF THE HELMETED MANAKIN[1]

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Abstract. I studied the foraging behavior and diet of the Helmeted Manakin (*Antilophia galeata*) in the gallery forests in the cerrado (savanna) region of central Brazil. Observations of 21 color-marked birds were made from April 1988 to March 1989 on a 2.5-ha study plot in a gallery forest. They showed that Helmeted Manakins are highly frugivorous (85.7% of foraging observations were on fruits; all stomach contents analyzed had fruits while arthropods were present in only 24.5%; and 96.2% of the fecal masses collected under a nest had fruits while 61.5% had arthropods); and take fruit mostly (46.5% of the observations) while in flight (sallies). Helmeted Manakins ate fruits of 17 species of 12 families of plants, as well as arthropods such as Araneae, Orthoptera, Coleoptera, Diptera, and Hymenoptera. One to six Helmeted Manakins attended 63.6% of the mixed-species flocks observed. Green birds (females and immature males) foraged at lower heights (6.5 ± 4.6 m) than adult and subadult males, which foraged at a height (8.2 ± 4.4 m) closer to where they sang (10.2 ± 3.8 m) or called (8.4 ± 4.8 m). The Helmeted Manakin showed similarities to other manakins in the diet and foraging tactics used, even though it may not be promiscuous (Marini and Cavalcanti, in prep.) and has an unique geographical distribution among dichromatic manakins.

Key words: Helmeted Manakin; Antilophia galeata; *foraging behavior; diet; frugivory; Pipridae; Brazil.*

INTRODUCTION

The 52 species of Manakins (Pipridae: Sibley and Monroe 1990) are mostly frugivorous and promiscuous with strong sexual dichromatism. The monotypic Helmeted Manakin (*Antilophia galeata*), is also highly dichromatic (see plumage description below), but may form long term pairbonds, which leads Marini and Cavalcanti (in prep.) to suggest that it may not be promiscuous. In addition to its unusual mating system for the Pipridae, the Helmeted Manakin also has an atypical geographical distribution in forests in the cerrado (savanna) ecosystem of central Brazil, between the Amazonian and Atlantic forests (Pelzeln 1871, Hellmayr 1929, Laubmann 1940, Pinto 1944, Pinto and Camargo 1948, Fry 1970, Meyer de Schauensee 1970, Sick 1985, Sibley and Monroe 1990, Willis and Oniki 1990). Here, it is one of the most abundant passerines (pers. observ.). Only two other manakins (the Band-tailed Manakin [*Pipra fasciicauda*] and the Pale-bellied Manakin [*Neopelma pallescens*]) occur at lower densities than the Helmeted Manakin in these gallery forests (pers. observ.).

The natural history of the Helmeted Manakin is poorly known. It inhabits mostly dry and flooded gallery forests in the cerrado region (Meyer de Schauensee 1970; Sick 1985, pers. observ.), habitats structurally similar to the habitats of other manakins. Nests and eggs were described by Ihering (1900, 1902), and Marini (1992) observed its breeding biology. The only dietary description is by Schubart et al. (1965), who found fruit in stomach samples. Because of its possibly unusual mating system, atypical range and poorly known natural history, I studied aspects of this species' foraging behavior and diet, and compare them with other manakins.

STUDY AREA AND METHODS

This study was conducted in the cerrado region of Brazil, in the gallery forest of the Córrego Capetinga (a creek) of the Ecological Station of the University of Brasília, Brasília, Distrito Federal (15°58′S; 47°56′W). The 2,300-ha station is located within the Água Limpa Farm and is subject to man-made and natural fires at irregular intervals. One large-scale fire burned most of the station in September 1987, including the understory of the gallery forest studied. Whether the fire affected the plant community is unknown.

The gallery forest of the Córrego Capetinga has emergent trees up to 20–30 m high, with contin-

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TABLE 1. Percentage of use of the foraging tactics by males (adults and subadults) and greens (immature males and females). Sample size (n) represents the number of foraging observations.

Tactics	Males	Greens	Total
Sally on fruit	45.5% ($n = 15$)	47.1% ($n = 24$)	46.5% ($n = 39$)
Glean on fruit	39.4% ($n = 13$)	39.2% ($n = 20$)	39.3% ($n = 33$)
Sally on arthropod	15.1% ($n = 5$)	2.0% ($n = 1$)	7.1% ($n = 6$)
Glean and screen on arthropod	0.0% ($n = 0$)	11.8% ($n = 6$)	7.1% ($n = 6$)
Total	($n = 33$)	($n = 51$)	($n = 84$)

uous canopy between 10 and 15 m high (Ratter 1980). Ratter recorded 120 plant species and found that the most common tree species include *Amaioua guianensis,* an unidentified Lauraceae, *Pouteria ramiflora, Salacia elliptica, Guatteia sellowiiana* and *Pisonia graciliflora.* Detailed descriptions of the study area and region are in Ratter (1980), Eiten (1984) and Marini (1989).

The Distrito Federal region has a well-defined dry season from May to September. Precipitation during the study period (Instituto Brasileiro de Geografia e Estatística 1989) was similar but lower than the mean precipitation from 1963 to 1981 (Comissão de Planejamento Agrícola-Distrito Federal/Fundação Zoobotânica do Distrito Federal 1984).

Birds were mist-netted from September 1986 to April 1989, on 17 net sites inside the grid, mostly from sunrise to 13:00. After capture, sex was determined by plumage (see below) and occurrence of brood patch.

Birds were collected from December 1987 to April 1989, in six other gallery forests close to the main study area between 15°45′ and 16°00′S and 47°45′ and 48°05′W. Birds were sexed by gonads and plumage, weighed and measured. Their stomachs were fixed in 70% alcohol. The stomach contents were analyzed for type and volume of food present. Food was classified as animal (arthropods) or plant (fruits, seeds and plant parts). The relative volume was visually estimated by comparing contents of different stomachs. The largest recorded stomach volume was used as the standard comparison for estimating relative volume in the other stomachs.

Observations were made primarily in the morning (06:30–13:00) on a 2.5-ha study plot marked by a grid of 34 points at 30 m intervals. Observations were from April 1988 to March 1989. Searches were made for birds at each point for 5 min, with 2–3 minutes between searching periods. I made approximately 41 visits/point during the 12-month period of study. I made 450 manakin sightings that lasted from a few seconds to 5 min. The number of sightings/month at the grid ranged from 17 to 64 ($\bar{x} = 37.5$).

I consider one sighting independent from another sighting because I sampled an individual's feeding height at the beginning of each observation period, with a mean interval of 7–8 min between two consecutive samples. Only the first foraging tactic was recorded per sighting. Also, the height of the first vocalization emitted by a bird being observed was recorded. Foraging tactics were classified according to Remsen and Robinson (1990): glean is "to pick food items from a nearby substrate, that can be reached without full extention of legs or neck"; sally is "to fly from a perch to attack a food item and then return to a perch"; and screen is to attack a food item in continuous flight. Additional observations of foraging tactics and diet and of some flocks were conducted in the 2.5-ha study plot or on another study site 5 km away in the same gallery forest. Additional observations of foraging and vocalization heights also were conducted in the 2.5-ha study plot.

The 38 individually color-marked Helmeted Manakins on the study plot during the 12-month period of study included four adult males, three subadult males, one immature male, six females and seven green individuals of unknown sex observed subsequently. I classified birds by plumage and I considered them adult males if they had black and red plumage. This included some individuals with only a few green feathers. Subadult males had green plumage mixed with black and red feathers. Green birds (females and immature males) had only a few reddish body feathers. Birds were classified as females if they had brood patches. The reproductive season (July–December) was defined by gonadal development, nesting activity, brood patch, and male behavior (Marini 1992). No male maintained the green plumage for two consecutive seasons, but none was banded when in the nest.

RESULTS

Foraging behavior. Females and immature males (green birds) used five foraging tactics: (1) sally

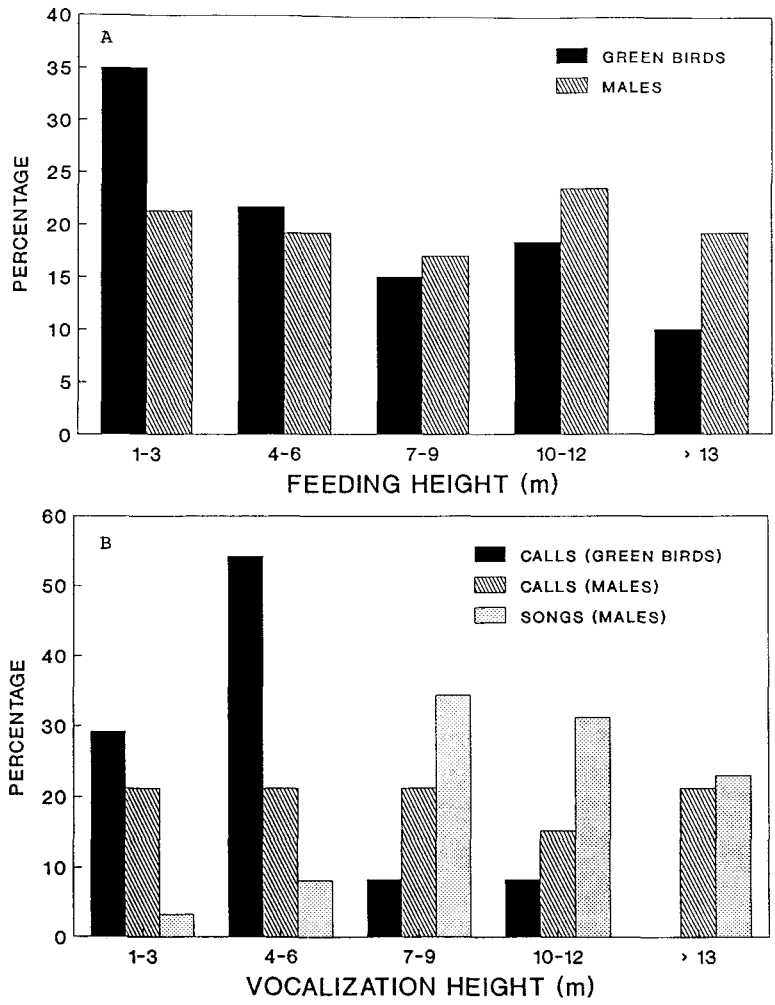

FIGURE 1. Top (A), percentage of feeding behavior by green birds (females and immature males) (solid bars) (n = 60) and by adult and subadult males (cross-hatched bars) (n = 47) by height. Bottom (B), percentage of calls by green birds (females and immature males) (solid bars) (n = 24), and calls (cross-hatched bars) (n = 33) and songs (open gray bars) (n = 61) by adult and subadult males by height.

on fruit, (2) glean on fruit, (3) sally on insect, (4) glean on insect, (5) screen on insect on a substrate. Adult and subadult males used tactics 1, 2 and 3. There were no differences in the use of foraging tactics between males (adults and subadults) and immature males and females (Table 1) (G = 0.04, df = 2, P > 0.975). Sallies on fruits were more common (46.5%) than any other tactic (Table 1). Birds ate more fruit (85.7% of 84 observations) than arthropods (14.3%).

Green birds fed at significantly (t = 2.02, P < 0.025) lower mean heights (6.5 ± 4.6 m, mean ± 1 SD; n = 60) than males fed (8.2 ± 4.4, mean ± 1 SD; n = 47) (Fig. 1A). Green birds also called ("*qua*" notes) at significantly (t = 6.6, P < 0.001) lower mean heights (4.7 ± 2.2 m, mean ± 1 SD; n = 17) than males sang (an eight note piercing whistle) (10.2 ± 3.8 m, mean ± 1 SD; n = 61) or called ("*qua*" notes) (t = 3.5, P < 0.001) (8.4 ± 4.8 m, mean ± 1 SD; n = 33) (Fig. 1B). However, because the foraging heights were not distributed normally (Fig. 1A), comparison of means may not be valid and a G-test was used. No significant difference (G = 3.75, df = 4, P > 0.1) in foraging heights between green birds and males was detected.

Mixed-species flocks. I observed the Helmeted Manakin participating in 14 out of 22 mixed-

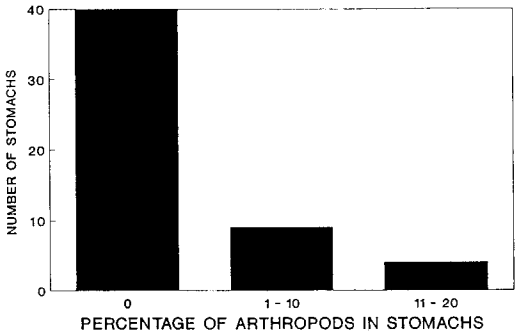

FIGURE 2. Frequency (number) of stomachs (n = 53) with various categories of percentage of arthropods in the total volume of the stomachs.

species flocks that had from three to eleven species (x = 5.0). The flocks were observed in January (n = 4), February (n = 2), March (n = 5), May (n = 5), June (n = 1), July (n = 1), September (n = 2), November (n = 1) and December (n = 1) and had from one to six ($\bar{x}$ = 2.7) Helmeted Manakins. Both adults, subadult males and green birds attended the flocks. Of the additional 36 species observed in the 22 flocks, the most common were: White-lined Tanager (*Tachyphonus rufus*) in seven flocks, Black-goggled Tanager (*Trichothraupis melanops*) in six flocks, Russet-mantled Foliage-gleaner (*Philydor dimidiatus*), Green-winged Saltator (*Saltator similis*), White-bellied Warbler (*Basileuterus hypoleucus*), and Pale-breasted Thrush (*Turdus leucomelas*) each in five flocks, and Variable Antshrike (*Thamnophilus caerulescens*), Buff-breasted Wren (*Thryothorus leucotis*), and Flavescent Warbler (*Basileuterus flaveolus*) each in four flocks. I could not identify all the species present in five of the 22 flocks.

Diet based on stomach contents. The stomachs of 53 individuals (23 adult males, 6 subadult males, 7 immature males, 11 females and 6 unsexed green birds) revealed a non-significant (χ^2 = 1.65, df = 1, P = 0.20) trend toward higher occurrence of arthropods in the stomachs of the green birds (females, immature males and indeterminates) than in males in the total annual value (Table 2). There were also no significant difference (χ^2 = 0.93, df = 1, P = 0.34) in the occurrence of arthropods between the reproductive and non-reproductive seasons. Roughly 25% of the stomachs of all individuals had arthropods, but they always comprised less than 20% of the food volume (Fig. 2). I did not identify the seeds and fruits of the stomach contents, but there were approximately 20–30 kinds of fruits and seeds. Among the arthropods in stomach samples were five specimens of Araneae, four of the suborder Orthognatha (one Lycosidae and probably one Salticidae), at least two species of Diptera (one specimen with 3 mm body length, and 50 specimens with 2 mm body length) and at least two species of Hymenoptera (three specimens of Formicidae and two of Vespidae).

Diet based on foraging observations. Plants in which I observed fruits being eaten most frequently include: *Miconia cuspidata* (n = 16), *Piper tectonifolium* (n = 13), a Solanaceae vine (n = 12), *Amaioua guianensis* (n = 10), *Miconia hirtella* (n = 5), *Cecropia* (possibly *pachystachia*) (n = 4). I also saw them feeding twice on *Miconia pseudonervosa,* and once on *Ouratea castaneifolia, Phytholacca dodecandra, Smilax siringoides, Guateria sellowiana, Guarea macrophylla, Guapira* sp., two shrubby species of Rubiaceae and a tree in the family Lauraceae. Small and round fruits, such as the melastomes, were swallowed whole. *Piper* was consumed through several consecutive bites when the bird was perched. The *Amaioua* fruits were manipulated with the beak and swallowed piecemeal, apparently due to relatively large size (approximately 10 × 20 mm).

Diet based on fecal masses under a nest. Of 26 fecal masses collected under a nest found on 9

TABLE 2. Percentage of stomachs with arthropods of adult and subadult males, females and others (immature males and indeterminates) in the reproductive and non-reproductive seasons. Sample size (n) represents the number of stomachs.

Season	Males	Females	Others	All
Non-reproductive	14.3% (n = 14)	16.7% (n = 6)	25.0% (n = 4)	16.7% (n = 24)
Reproductive	20.0% (n = 15)	40.0% (n = 5)	44.4% (n = 9)	31.0% (n = 29)
Annual	17.2% (n = 29)	27.3% (n = 11)	38.5% (n = 13)	24.5% (n = 53)

TABLE 3. Food types, foraging tactics and flock behavior of manakin species.

Species	Food type[a]	Foraging tactic[b]	Flock behavior[c]	Author[d]
Pipra aureola	F			1
Pipra fasciicauda	F, I		P	2
Pipra filicauda	F			3
Pipra mentalis	F, I	P, F (S)	P	4, 5, 6, 7, 8, 9
Pipra erythrocephala	F, I	P	P	1, 3, 10
Pipra rubrocapilla	F, A			11
Pipra chloromeros	F, I		P	2
Pipra pipra	F, I	P, F (S)	P	1, 9, 10, 12
Pipra coronata	F, I	F (S)	P	2, 3, 9
Pipra serena	F, I	P	P	10, 13
Pipra villasboasi	F, I			1
Pipra nattereri	I			1
Pipra isidorei	F			3
Antilophia galeata	F, A	F (S, C), P	P	1, 14
Chiroxiphia linearis	F, I	D		9, 15, 16, 17, 18
Chiroxiphia lanceolata	F	F (S, H)		7, 9
Chiroxiphia pareola	F	F (S)		3
Chiroxiphia caudata	F, I	F (H), P		19, 20
Masius chrysopterus	F, I	F	P	3, 21
Ilicura militaris	F			19, 22
Corapipo gutturalis	F, I	F (H), P	P	10, 23
Corapipo leucorrhoa	F, A	F (S)	P	7, 9, 24, 25
Manacus candei	F	F (S)		9
Manacus aurantiacus	F, I	F (S)		9
Manacus vitellinus	F	F, P, J		6, 7
Manacus manacus	F, I	F (S), P	P	1, 3, 10, 11, 12, 26
Machaeropterus regulus	F, I	F (S)		3, 12
Machaeropterus deliciosus	I, F		P	3, 27
Xenopipo atronitens	F, I		P	1, 3
Chloropipo flavicapilla			P	3
Heterocercus flavivertex			P	3
Heterocercus linteatus	F, I			1
Neopelma chrysocephalum	F, I	P, F (S)	P	3, 10
Neopelma pallescens	I			1
Tyranneutes stolzmanni	I, F		P	1, 2, 28, 29, 30
Tyranneutes virescens	I, F	P	P	10
Piprites griseiceps	F, I	F (S)	P	9
Piprites chloris	I		P	3, 30

[a] Food types are as follows: F = fruits, I = insects, A = arthropods. The order of the food types represents the order of citation by the author or the frequency of citations.

[b] Foraging tactics are as follows: F = in flight (S = sally; H = hover; C = screen), P = perched, J = jumping, D = depends on kind of fruit. The order of the foraging tactics represents the order of citation by the author or the frequency of citations.

[c] P = participate in mixed-species flocks.

[d] Authors are as follows: 1. Schubart et al. 1965; 2. S. K. Robinson pers. comm.; 3. Hilty and Brown 1986; 4. Skutch 1949; 5. Gradwohl and Greenberg 1980; 6. Worthington 1982; 7. Moermond and Denslow 1985; 8. Levey 1988; 9. Stiles and Skutch 1989; 10. Willis 1977; 11. Novaes 1973; 12. Cymerys 1991; 13. Prum 1985; 14. This study; 15. Wagner 1945; 16. Foster 1977; 17. Foster 1978; 18. Wheelwright et al. 1984; 19. Davis 1946; 20. Foster 1987; 21. Prum and Johnson 1987; 22. Sick 1985; 23. Prum 1986; 24. Skutch 1967; 25. Ridgely and Gwynne 1989; 26. Snow 1962; 27. Willis 1966; 28. Pinto 1953; 29. Wiley 1980; 30. Munn 1985.

October 1988, 25 had fruit seeds, 15 also had remains of arthropods and one had only arthropods. By far, the two most common fruits were *Miconia hirtella* with 450 seeds present in 12 fecal masses and *Cecropia pachystachia* with 760 seeds in 11 fecal masses. Four to 35 seeds of five other species were present in five or fewer fecal masses, including two species of Solanaceae, and three unidentified species. Among arthropods, there were 42 specimens of Orthoptera in four fecal masses, six specimens of Araneae in four, two Coleoptera in two, one Diptera and one Formicidae, and at least nine unidentified insects. Some clean seeds (apparently regurgitated) also found under this nest were Lauraceae (n = 90), Annonaceae (n = 31), Myrtaceae (n = 17), Solanaceae (n = 9), and *Virola* sp. (n = 2).

DISCUSSION

The Helmeted Manakin is highly frugivorous: all stomach samples had fruits (Fig. 2), while arthropods were present in only 24.5% (Table 2)

TABLE 4. List of families (n = 12) and species (n = 17) of plants consumed by the Helmeted Manakin.

Families	Species
Annonaceae	*Guateria sellowiana*
Lauraceae	indet. tree sp.
Melastomataceae	*Miconia cuspidata, M. hirtella, M. pseudonervosa*
Meliaceae	*Guarea macrophylla*
Moraceae	*Cecropia pachystachia*
Nyctaginaceae	*Guapira* sp.
Ochnaceae	*Ouratea castaneifolia*
Phytolaccaceae	*Phytolacca dodecandra*
Piperaceae	*Piper tectonifolium*
Rubiaceae	*Amaioua guianensis*, two indet. shruby spp.
Smilacaceae	*Smilax siringoides*
Solanaceae	indet. shruby sp. and indet. vine sp.

in which the arthropods never represented more than 20% of the total stomach volume (Fig. 2); 85.7% of the foraging observations were on fruits (Table 1); and 96.2% of the fecal masses collected under a nest had fruits while 61.5% had arthropods. There were only slight differences in foraging tactics (Table 1) and diet (Tables 1, 2) among the sex and age classes analyzed. The Helmeted Manakin's foraging tactics and the kind of food taken are similar to other manakins (Table 3). All manakin genera are known to eat fruits and insects (Table 3).

Green birds foraged more in the understory and males foraged more in the canopy (Fig. 1A). This difference may relate to males singing and calling significantly higher in the forest than green birds (Fig. 1B). Alternatively, males and green birds may be partitioning the fruits available in the forest. Differences in foraging height between males and females have been shown by several authors (see Holmes [1986] and references). However, I can not conclude that foraging height in the Helmeted Manakin differs between the sexes because green birds included both females and immature males. For the same reason, I can not correlate the foraging height of the green birds with nesting height.

The Helmeted Manakin undoubtedly eats fruits of more species of plants than the 17 species of 12 families that I could identify (Table 4). This broad use of plant species seems to be common in the Pipridae. Wheelwright et al. (1984) recorded 37 plant species of 22 families in the diet of the Long-tailed Manakin (*Chiroxiphia linearis*); Foster (1978), however, observed this species feeding on only three species of plants for five months during one year. Snow (1962) listed 105 species of plants in the diet of the White-bearded Manakin (*Manacus manacus*) with Melastomataceae and Rubiaceae, respectively, as the most common families eaten. The White-ruffed Manakin (*Corapipo leucorrhoa*) fed on several fruits, especially on Melastomataceae shrubs and trees (Skutch 1967). The Golden-winged Manakin (*Masius chrysopterus*) was observed feeding on 10 species of four families of plants (Prum and Johnson 1987).

Arthropods eaten by manakins primarily are flying insects and spiders. They include Orthoptera, Coleoptera, Diptera, Hymenoptera and Araneae by the Helmeted Manakin, Coleoptera, Diptera and Odonata by the White-bearded Manakin (Snow 1962), Araneae by the White-ruffed Manakin (Skutch 1967), and Orthoptera and Coleoptera by the Gray-headed Manakin (*Piprites griseiceps*) (Stiles and Skutch 1989). Other studies did not specify which group of insect was eaten (see Table 3). P.T.Z. Antas (pers. comm.) observed the Helmeted Manakin eating alate termites in the border of a gallery forest and Willis (1984) recorded one male following army ants to sally from twigs and leaves for small arthropods in Mato Grosso, Brazil. The high number of orthopterans in four fecal samples and of Diptera in one stomach content under the nest of the Helmeted Manakin, may be unusual among manakins.

The participation of the Helmeted Manakin in mixed-species flocks, as well as its behavior of feeding on termites in the border of a gallery forest (P.T.Z. Antas, pers. comm.), and following army ants (Willis 1984), suggests that its insect foraging may be opportunistic because of the small importance of insects on its diet. Several other manakin species have also been observed attending mixed-species flocks as non-permanent members (Table 3). Manakins join mixed-species flocks temporarily, presumably to forage for insects.

In conclusion, the Helmeted Manakin is similar to other manakins in relation to foraging tactics used and diet, even though it has an atypical range for a dichromatic manakin. Also, the proposed non-promiscuity of the Helmeted Manakin (Marini and Cavalcanti, in prep.), associated with its highly frugivorous behavior, supports Beehler's (1983) argument that frugiv-

ory "cannot, by itself, explain why some birds are polygamous and others monogamous."

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