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THE CRITICALLY ENDANGERED AND ENDEMIC ARARIPE MANAKIN (ANTILOPHIA BOKERMANNI): DIETARY ASSESSMENT FOR CONSERVATION PURPOSES

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ABSTRACT.—Diet studies provide information about a species' ecology, evolution, and behavior. The Araripe Manakin (Antilophia bokermanni) is a critically endangered, endemic, and sexually dichromatic species from northeastern Brazil. Little is known about its natural history, and as an endangered bird, information about diet may be crucial for conservation plans. We analyzed the diet of Araripe Manakins and tested if food items and foraging behavior differed for males and females. We caught and banded birds, and analyzed fecal samples. Using focal observations, we collected foraging behavioral data, including vegetation strata used, foraging bout duration and gathering method. Based on data gathered from 40 females and 54 males, we found that the Araripe Manakins' diet contains both plant and animal items including 10 different types of fruits and three orders of invertebrates. Clidemia biserrata was the most important plant item consumed, representing 80% of the diet. There was a substantial overlap of 68% of food items in the diets between sexes, which did not differ statistically. However, male and female diets were unique in some aspects: females consumed more items having a more diverse diet when compared to males. Males, however, consumed more Coleoptera, and these were the second most important item in their diets. Since male and female foraging behavior does not differ, this result suggests that males choose to consume more beetles perhaps to maintain plumage color, since beetles are rich in carotenoids. Results also provide important data about which plants can be used in the management or recovery of Araripe Manakins' habitats. Received 26 August 2016. Accepted 4 February 2017.

Key words: Antilophia bokermanni, Brazil, conservation, diet, foraging, frugivory, Pipridae.

Diet is one of the strongest selection pressures influencing a bird's life, affecting both the fecundity and survival of adults (Charnov and Krebs 1974, Murphy and Haukioja 1986, Nur 1990). Regrettably, for most tropical species, even general information about foraging habits and diet are still missing (Harris et al. 2005, Alho 2008). Because habitat degradation in the Tropics is in many cases severe and ongoing, threatening the continued existence of many bird populations, data relative to diets are important for appropriate conservation, especially for endangered species (Sample and Whitmore 1993, Lopes et al. 2005).

Our study focused on the diet of the Araripe Manakin (*Antilophia bokermanni*), a critically endangered and endemic bird species of the tropical bird family Pipridae. Species in this family typically exhibit a striking dichromatism, with

males presenting colorful plumage and complex displays, and mating systems are based upon lek formation and promiscuous mating (Prum 1994). Nevertheless, one single genus in the family, Antilophia, appears to have a socially monogamous system, no lek formation, and parental investment by both sexes (Prum 1994). The genus has two species: A. galeata and A. bokermanni. The latter species, object of the current study, was described in 1998 (Coelho and Silva 1998), is critically endangered, and is the only passerine species endemic to Ceará state, Brazil (IUCN 2016). Its population size is currently estimated at only 800 individuals (Aquasis 2006, Rêgo et al. 2010, IUCN 2015, BirdLife International 2016). Similarly to the rest of the species in the family, Araripe Manakins are sexually dichromatic: females are olive-green while adult males are white, with a red helmet and black wings and tail (Coelho and Silva 1998). Despite some limited information about its conservation status and endemism, data on the species' natural history, ecology, and behavior are totally lacking, imposing serious obstacles to the development and implementation of conservation plans.

Species with strong sexual dimorphism can differ in their feeding ecology (Selander 1966, Hedrick and Temeles 1989, Shine 1989), especially if males and females have a large difference in

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body size, different coloration, and need to forage in different ways to avoid predation or to ingest different types of food given their plumage coloration requirements (Fox and Vevers 1960, Brush 1978). Recent studies with some manakins found that males and females differ in their behavior and diet and do not have the same role and significance as plant dispersers (Loiselle et al. 2007, Montaño-Centellas 2012). Consequently, information relative to the diet requirements of each sex and their particular impact and importance for the ecosystem is crucial for conservation purposes (Selander 1966, Hedrick and Temeles 1989, Shine 1989).

Habitat fragmentation is one of the main causes of species' population decline (Wilcove et al. 1998, Venter et al. 2006), and implementing recovery plans is in some cases the best solution for increasing population size (Kerr and Deguise 2004, Taylor et al. 2005). Conservation plans for endangered species usually identify which habitat conditions are essential components for the preservation and growth of populations (Casazza et al. 2016). Hence, data about which plants are critical (e.g., as food sources, for nesting and protection) for the survival of a given species are crucial to the establishment of successful conservation plans.

The plateau where our study population occurs is a disturbed area impacted by human occupation and inappropriate resource exploitation by the local community. In addition, the multiple fresh water springs on the slopes of the plateau constitute the most important water source for nearby cities. Thus, the loss of the forest vegetation will result in a large and very negative impact on surrounding cities (Mont'Alverne et al. 1996, Lins 2009). Maintenance of the forest is strongly dependent upon seed dispersal of local plants and trees. Manakins are represented by many frugivorous species that are important seed dispersers (Snow 1971, Foster 1977, Marini 1992, Blake and Loiselle 2002, Silva and Melo 2011, Montaño-Centellas 2012, Morales-Betancourt et al. 2012), often having a substantial role in maintaining forests (Marini 1992, Loiselle and Blake 1999, Silva and Melo 2011). The Araripe Manakin is the only representative of the Pipridae family on the Araripe plateau, and despite its critically endangered status, it remains one of the most abundant species in many areas along the plateau (MGG, pers. obs.).

For the above described reasons, information about the diet of Araripe Manakins is important not only for the species' conservation but can also be relevant to human populations in the cities that obtain their water supplies from the plateau. In the present study, we describe the diet of the critically endangered Araripe Manakin and assess whether males and females have different dietary habits. Given the strong sexual dimorphism of the species, we expected to find divergences in male and female foraging habits and diets.

METHODS

We conducted this study in four areas along the slopes of the Araripe plateau, Ceará state, Brazil (7° 16' 59.50'' S, 39° 26' 26.20'' W, 695–897 m). The diet data were collected over the course of 2 years, from April 2013 to April 2015. We caught the birds using five mist nets ($12 \text{ m} \times 3 \text{ m}$) for 6 hrs each day, during 620 days totaling 18,600 nethours.

Once we caught individuals, we kept them for 5 min in a cloth bag lined with a paper towel to collect the feces deposited in the bag, which were stored in 70% ethanol and analyzed subsequently with a stereomicroscope (WF10X, Bel Photonics, Piracicaba, Brazil). Despite some level of sample degradation, fecal data analysis was the chosen method because of its less invasive nature, given the conservation status of the species, while still providing relatively good information about diet, especially fruit consumption (Remsen et al. 1993). A previous study that used forced regurgitation with the sister species (Helmeted Manakin [Antilophia galeata]) yielded more complete diet data but presented a high mortality rate (Gaiotti 2011).

Body measurements were taken to determine the degree of sexual size dimorphism, as this can be relevant to foraging behavior. Individuals were measured with a hand-held dynamometer (mm) and weighed with a spring balance (100-g precision, Pesola AG, Schindellegi, Switzerland). Body measurements included tarsus length, tail length (from uropygial gland to the tip of the longest feather), wing length (from the shoulder to the tip of the longest feather), and bill length (from the nostril to the tip of the bill). As young males

have the same olive-green plumage as females, we collected $\sim\!\!60~\mu L$ of blood from all individuals using brachial venipuncture for molecular determination of sex. Samples were kept in ethanol until analyses were performed. We used PCR analyses to determine the sex of each individual using the sexing primer 2550/2718.

Food items in the fecal samples were identified to the lowest taxonomic level possible. Seeds that could not be identified were classified as morphotypes. To determine the most important food items in the diet, we calculated the occurrence frequency (OF) and numerical frequency (NF) for each individual food item as:

$$OF = \frac{Nv}{Nind.} \times 100$$

where Nv is the number of individuals who consumed a given food item and Nind. is the total number of individuals sampled. The Nv was estimated using the presence or absence of a given food item in collected feces.

$$NF = \frac{Ni}{Nt} \times 100$$

Ni is the number of food items for a given category, and Nt is the sum of all food items for all categories. For fruits, we considered the number of seeds as the Ni, as it is difficult to estimate numbers of seeds per fruit for many species, and the same plant individual can produce fruits with varying numbers of seeds (Janzen 1969, Loiselle 1990). This is also why the Occurrence Frequency (OF; see below) was used to adjust the numbers of a given fruit consumed per individual. For invertebrates, we counted the number of body parts and considered the minimum number of individuals ingested. For example: two beetle wings and three beetle heads determined the count of three beetles. We also took into account the size similarities while grouping body parts.

With these values, we used a modified version of the Kawakami and Vazzoler (1980) Dietary Importance Index (DIi):

$$DIi = (OFi \times \overline{AF}i) / \sum (OFi \times \overline{AF}i) \times 100$$

OFi is the Occurrence Frequency for a given food item, and $\overline{AF}i$ is the average of the numerical frequency for the food item.

We calculated the diversity of food items for male and female diets using the Shannon Diversity Index (H; Shannon 1948) and the amount of food item overlap between sexes using the Bray-Curtis Dissimilarity Index (Bray and Curtis 1957). We compared male and female overall diet composition using one-way analysis of similarity (ANO-SIM). We also tested whether DIi consumption of each food item by males and females differed with a Student t-test when the data had a normal distribution and a Mann-Whitney U-test for nonparametric data. All statistical analyses were performed with the statistics package PAST 3.0 (Hammer et al. 2001) with the α-level set at <0.05. All values are presented as mean \pm standard deviation, unless noted otherwise.

In addition, we also collect foraging behavior data by using focal observations of color-banded individuals during 90 min in the morning (0900-1030 hrs Brazil Time [BRT]; n = 10 females and 7 males) and 60 min in the afternoon (1500-1600 hrs; n = 11 females and 9 males) for 1 week. We recorded the vegetation strata where individuals foraged, the foraging behavior employed (gathering methods), the duration of feeding bouts and whether males and females were together. The strata were classified according to height as: canopy (>7 m), understory (2-7 m) and ground (0-2 m). We followed Remsen and Robinson's (1990) classification scheme for foraging behavior for four categories: hang, hang up, hang down, hang upside-down. We added an extra category named fly-catch based on our previous observations of foraging behavior by Araripe Manakins.

RESULTS

We caught 183 Araripe Manakins from which we obtained 94 individual fecal samples. Of these, 30 female samples and 42 male samples contained identifiable food materials of both plant and animal origin. We found 10 different types of fruits and beetles, spiders and ants (Table 1). We identified fruits from three plant genera/species: *Byrsonima sericea* (Malpighiaceae), *Clidemia biserrata* (Melastomataceae), and *Cecropia* sp. (Urticaceae), while the other seven were classified as morphotypes.

Clidemia biserrata was the most consumed item with an occurrence frequency (OF) of 22.34%

Food item	Females		Males		Pooled	
	OF (%)	NF (%)	OF (%)	NF (%)	OF (%)	NF (%)
Morphotype I	10.53	10.3	10.81	3.94	10.64	7.53
Cecropia sp.	3.51	0.47	8.11	1.38	5.32	0.89
Morphotype III	12.28	2.38	13.51	1.58	12.76	2.04
Clidemia biserrata	21.05	51.35	24.32	84.81	22.34	65.96
Byrsonima sericea	1.75	0.16	5.40	0.39	3.19	0.26
Morphotype VI	14.03	30.43	8.11	3.94	11.70	18.79
Morphotype VII	7.02	0.80	5.40	0.39	6.38	0.62
Morphotype VIII	10.53	2.38	0.00	0.00	6.38	1.33
Morphotype IX	3.51	0.32	0.00	0.00	2.13	0.18
Morphotype X	3.51	0.32	5.40	0.39	4.25	0.35
Ants	1.75	0.32	8.11	0.59	4.25	0.44
Spiders	3.51	0.32	10.81	0.80	6.38	0.53
Beetles	5.26	0.50	24.32	1.80	12.76	1.06

TABLE 1. Occurrence frequency (OF) and numerical frequency (NF) for food items consumed by female (n = 40) and male (n = 54) Araripe Manakins and pooled species consumption (n = 94).

(Table 1). It also was the most important food item representing 80.92% of the Araripe Manakins' diet, followed by fruit Morphotype VI (DIi = 11.82%) and Morphotype I (DIi = 4.32%) (Table 2). The most consumed animal items were beetles (OF = 12.76%), followed by spiders (OF = 6.38%; Table 1).

Males and females presented differences in their diets: females ingested two extra fruit species not ingested by males: Morphotypes VIII and IX (Table 1). Females also had a more diverse diet (H = 1.89, e[^] = 0.27, D = 0.36) when compared to males (H = 0.72, e[^] = 0.18, D = 0.72). However, the overall diet of males and females had a

TABLE 2. Dietary Importance Index (DIi) of each food item consumed by female (n = 40) and male (n = 54) and pooled Araripe Manakins (n = 94).

Item	Females	Males	Pooled
Morphotype I	6.45	1.92	4.32
Cecropia sp.	0.09	0.49	0.24
Morphotype III	1.74	0.96	1.42
Clidemia biserrata	64.16	94.36	80.62
Byrsonima sericea	0.01	0.09	0.05
Morphotype VI	25.34	1.44	11.82
Morphotype VII	0.33	0.09	0.23
Morphotype VIII	1.49	0	0.23
Morphotype IX	0.06	0	0.02
Morphotype X	0.06	0.09	0.09
Formicidae	0.03	0.21	0.1
Aracnidae	0.06	0.38	0.16
Coleoptera	0.14	1.93	0.8

substantial overlap of 68% of food items (Bray–Curtis Index = 0.68), and did not differ statistically (ANOSIM test, R = -0.002, P = 0.46; Fig. 1). Perusing the data allowed us to verify that males ingested animal items more frequently (Table 1) and that these items were also twice as important in their diets (Table 2). Additionally, males consumed significantly more beetles than did females (t = 2.78, P = 0.006).

During focal observations, we recorded 29 adult males and 32 females foraging and using five different gathering behaviors (see Methods). The most frequently used method was 'hang,' performed 83.09% by females and 80.49% by males, followed by 'hang down' (Fig. 2). The behaviors

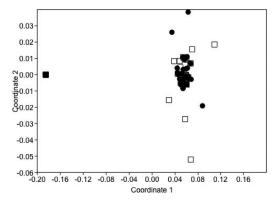


FIG. 1. Pooled Araripe Manakins' diet overlap using Bray–Curtis similarity index. Males = empty squares; females = filled circles.

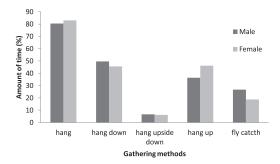


FIG. 2. Percentage of each gathering method performed by female and male Araripe Manakins during our focal observations (n = 15 females and 11 males).

'hang upside down' and 'fly catch' were performed only in the morning (Fig. 3). We did not find differences between male and female duration of foraging behavior (t = -0.7, P = 0.46), strata used (U = 4.0, P = 1.0), or gathering methods (t = -3.93E-16, P = 1.0). Both sexes spent a higher percentage of time on the ground and never visited the canopy during the afternoon (Fig. 4).

We found no difference between male (mean = 20.65 ± 0.10) and female mass (mean = 20.69 ± 0.16) (U = 4118.5, P = 0.86). Moreover, while males have longer wings (U = 3994.5, P < 0.001), tails (t = 5.13; P < 0.001), and tarsi (U = 3260.5, P < 0.001), females have longer bills (U = 4694.5, U = 0.003).

DISCUSSION

Despite some expected fecal sample degradation, we were able to document Araripe Manakins' diet and confirm the existence of some divergences between the male and female diets. Similar to several other studied manakins (Marini 1992, Loiselle and Blake 1999, Lopes et al. 2005, Gaiotti 2011, Silva and Melo 2011, Montaño-Centellas 2012), Araripe Manakins consume both fruits and arthropods, although fruits were more representative and seem to be the primary item of their diet. The number of fruit species ingested by Araripe Manakins was similar to that found for other manakin species (Foster 1977, Silva and Melo 2011, Morales-Betancourt et al. 2012).

In this study, *Clidemia bisserata* was the most consumed item for both sexes, and also had the highest Dietary Importance Index (DIi), demonstrating the relevance of this plant for this critically endangered bird. Two other manakin species, *Manacus manacus* and *Pipra erythrocephala*, also consume high levels of plants of the *Clidemia* genus (Morales-Betancourt et al. 2012). The phenology of *C. bisserata* may contribute to our findings, since it is one of the few plants in the Araripe plateau that provides fruit year-round (Linhares et al. 2010), allowing Araripe Manakins continuous easy access. Quite possibly, individuals learn the location of plants that are providing

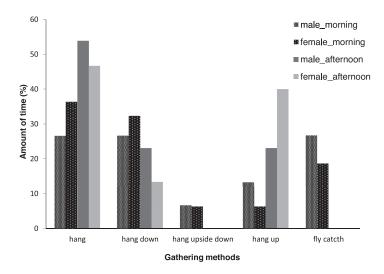


FIG. 3. Percentage of each gathering method performed by female and male Araripe Manakins during our observation sessions in the morning (0900–1030 hrs Brazil Time [BRT]; n = 10 females and 7 males) and afternoon (1500–1600 hrs; n = 11 females and 9 males).

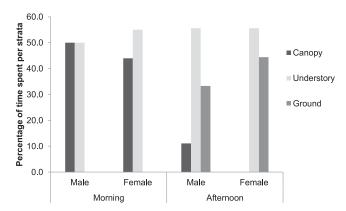


FIG. 4. Percentage of time spent by female and male Araripe Manakins in each strata during our observation sessions in the morning (0900-1030 hrs; n = 10 females and 7 males) and afternoon (1500-1600 hrs; n = 11 females and 9 males).

fruits, allowing them to return repeatedly to the same sites (Foster 1977, Wheelwright and Janson 1985).

Males and females did not differ in their foraging behavior. For all focal observations, both sexes were feeding close to each other or even on the same plant. Thus, foraging behavior does not justify the differences between male and female diets. We found that females have a more diverse diet than males. One possible explanation is that the more cryptic olive-green plumage of females provides them with a greater degree of camouflage in forested areas, thus allowing them to seek food over a broader area with less risk of predation (Pratt and Stiles 1983). Males, on the other hand, have a very bright white body coloration, with conspicuous red helmets, and may be more vulnerable to predation (Wallace 1889, Götmark 1993).

Furthermore, we found that females have a longer bill, which probably allows them to manipulate more types of fruits (e.g., larger fruits) that males may be unable to handle and ingest (Doucet 2006). Another possible explanation for the higher diversity in the female diet is their more frequent movement between territories, allowing them to forage more widely, when compared to the territorial males, which are limited to small areas. Evidence of this higher locomotion is that only females or young males (with green feathers) were recaptured in areas as far apart as 4.65 km during this study (n = 4), but no adult males were recaptured at any substantial distance from their first place of capture. This is also the case for other

manakins, wherein adult males are committed to lek sites and thus cover smaller feeding areas when compared to that of females and young males (Snow 1962, Lill 1974, Graves et al. 1983, Théry 1992).

Males consumed significantly more Coleoptera beetles when compared to females. Many studies have shown that beetles and other arthropods are rich in carotenoids (Karrer and Jucker 1948, Czeczuga 1971, Goodwin 1986, Isaksson 2009, Eeva et al. 2010). Most animals cannot produce carotenoids and rely on their diets to obtain this pigment (Thommen 1971, Brush 1981, Gray 1996), which is responsible for the red, yellow, and orange colors found in bird plumages (Fox and Vevers 1960, Brush 1978, McGraw 2004). Several studies have shown that the level of carotenoid ornamentation in birds is associated with differences in their diets (Slagsvold and Lifjeld 1985, Partali et al. 1987, Hill and Montgomerie 1994, Hill et al. 1994, Ryan et al. 1994) and that carotenoid ingestion is correlated positively to the intensity of feather coloration (Hill et al. 2002). Because the majority of red feathers result from carotenoid ingestion (Brush 1981, Owens 2006), it is very likely that adult male Araripe Manakins need to ingest food items that will result in the bright red plumage of their helmets. The consumption of beetles may be a good option when fruits rich in carotenoids are unavailable or insufficient.

The higher importance of arthropods (i.e., protein) in the male diet can also be associated to the male's overall larger size, including longer

wings, tail, and tarsi. Because arthropods have high levels of protein, the growth rate of birds on a more insectivorous diet is faster than that of frugivorous ones (Savory 1977, Johnston 1993). Since males have a less diverse diet than females, as mentioned above, they may need a more protein-rich diet. In addition, as the vast majority of plants do not have fruit year-round, males may depend upon invertebrates as a complementary item in their diet, more frequently than females.

Our results provide key information about the diet of Araripe Manakins that may be important for improving the conservations status of this endemic and critically endangered species (BirdLife International 2016). Additionally, we show that males and females differ in several aspects of their diets, indicating sex-specific requirements relative to habitat food resources. These results also contribute basic data about Araripe Manakins' feeding ecology, which can be helpful for future conservation plans applied to recover heavily degraded areas; in such cases, for example, reforestation can use plants that we now know are important to the diet of Araripe Manakins. Finally, the differences in the male and female diets raise new questions about the evident sexual dimorphism of Araripe Manakins and how male foraging behavior may be used to maintain their conspicuous coloration.

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