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Source: The Wilson Journal of Ornithology, 129(1):191-195.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/1559-4491-129.1.191
URL: http://www.bioone.org/doi/full/10.1676/1559-4491-129.1.191

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The Wilson Journal of Ornithology 129(1):191–195, 2017

Diet of the Crested Guan (*Penelope purpurascens*) in Panama: Leaf-eating by a Tropical Frugivore

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ABSTRACT.—We studied the diet of Crested Guans (*Penelope purpurascens*; Galliformes: Cracidae) in lowland tropical forest on Barro Colorado Island, Panama. From June-August 2015 we collected observations of foraging adults using five-minute focal follows of randomly chosen individuals. A total of 141 food items were recorded over 565 minutes of observations. Although Crested Guans are believed to be primarily frugivorous, we found that they consumed a high proportion of leaves (61.7% of items) and insects (24.8%), with fruits comprising a minority of items (13.5%). Guans preferred to eat young leaves, which are more tender and contain higher levels of nitrogen than mature leaves; however, young leaves also contain higher levels of tannins and other secondary defensive compounds, raising new questions about the mechanisms by which arboreal birds digest leaves. Recent studies have found similarly high levels of leaf consumption in other species of guans and chachalacas, suggesting that folivory may be more widespread in the family Cracidae than previously realized.
Received 9 June 2016. Accepted 26 July 2016.

Keywords: cracid, El Niño, folivory, foraging ecology, Neotropics, *Penelope*.

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INTRODUCTION

The Crested Guan (*Penelope purpurascens*) is a large arboreal galliform bird that inhabits lowland and lower montane forests from Mexico south through Central America, Colombia, northern Venezuela, and southwestern Ecuador (Vaurie 1968, Eley 1982, Gilbert and Schulenberg 2013). Despite its large geographic range, many populations of the Crested Guan have decreased significantly or been extirpated entirely. The IUCN Red List designates the Crested Guan as a species of Least Concern (BirdLife International 2016), but in 2010 Partners in Flight identified it as a species of High Concern due to its declining population of fewer than 50,000 individuals (Gilbert and Schulenberg 2013). In Mexico, where 50% of the population is believed to have been lost over the last century, the Crested Guan is listed as Threatened. It is primarily threatened by hunting throughout its range, but deforestation and logging activity also pose additional concerns (Gilbert and Schulenberg 2013).

Most of what is known about the Crested Guan comes from anecdotal reports from the 1940s and 1950s (reviewed in Gilbert and Schulenberg 2013). It is thought to be primarily frugivorous and recent reports have focused on its potential role as a seed disperser of tropical forest trees (Howe and Miriti 2004). Crested Guans have been observed to consume a wide variety of fruits, including figs (*Ficus* spp.), *Schefflera morototoni* (Wetmore 1965), *Bumelia peninsularis*, *Guatteria* spp. and *Chiona mexicana* (Leopold 1959), and *Spondias mombin* (Sutton and Pettingill 1942, Gilbert and Schulenberg 2013). In Costa Rica and Panama, guans are reported to be major consumers of nutmeg (*Virola surinamensis*; Caziani and Protomastro 1994, Howe and Miriti 2004). One early report mentioned that guans might consume acorns, green leaves, and insects (Wagner 1953 in Delacour and Amadon 1973); however, no systematic surveys of the Crested Guan's diet have been conducted, so the extent to which they rely on other sources of food is not known. Our objective in this study was to provide direct observational data on the diet of the Crested Guan in a lowland tropical forest in Panama.

OBSERVATIONS

On 5–7 days per week from June to August of 2015, SAP observed Crested Guans on Barro Colorado Island (BCI; 09° 12′ N 79° 49′ W), central Panama, a 1,560-ha reserve operated as a field research site by the Smithsonian Tropical Research Institute. BCI consists of lowland tropical forest habitat; the mean annual temperature is 26°C and it receives approximately 2,600 mm of rainfall annually with a marked four-month dry season from January to April (Karr 1982). Due to a severe El Niño drought this past year, the summer was unusually dry: June 2015 was the third driest June since records began in 1925 (STRI 2015). The biota, climate, geology of BCI are described extensively by Leigh (1999).

Crested Guans are common on Barro Colorado Island and are unusually easy to observe due to the absence of hunters. Foraging guans were observed from the ground, usually with the aid of binoculars, using the focal follow method (Altmann 1974). Guans were observed foraging alone and in groups of up to five individuals. The behavior of a randomly chosen focal individual was recorded at thirty-second intervals over the course of a set sampling period, typically five minutes, for a total of ten observations per period. If the focal individual moved out of sight during this period, recording ceased until it was relocated; or, in the event that it could not be found and additional birds were present, another focal individual was randomly selected and a new sampling period began. If the focal individual consumed food at any point during the five-minute focal follow, the item consumed (fruit, insects, mature leaves, or young leaves) was identified. All observations were made in the morning and mid-afternoon (between 0803 and 1350 CST). A total of 565 minutes of observations were accumulated over the six-week period.

Of 141 items consumed, the majority were leaves ($n = 87$, 61.7%; Table 1). Insects ($n = 35$, 24.8%) and fruit ($n = 19$, 13.5%) were consumed less frequently (Table 1). Of the leaves consumed, 82.8% were young and 17.2% were mature. Five plants were identified, including *Adelia triloba* (Euphorbiaceae), *Capparis frondosa* (Capparaceae), *Faramea occidentalis* (Rubiaceae), *Hybanthus prunifolius* (Violaceae), and *Ouratea lucens* (Ochnaceae). Of the 106 leaf and fruit foraging observations, 46.22% were of *Capparis frondosa*, followed by *Hybanthus prunifolius* (21.70%) and *Adelia triloba* (17.92%). Of 121 foraging bouts recorded, nearly all occurred in trees ($n = 112$,

TABLE 1 Food items consumed by Crested Guans, Barro Colorado Island, Panama. July–August 2015.

Item	Local name	Scientific name	Part eaten	No. observations	Percent observations
Fruit	Espino amarillo	*Adelia triloba*	Fruit	19	13.47%
Insects	Not identified	Not identified	Not identified	35	24.82%
Leaves	Caper	*Capparis frondosa*	Young leaves	46	32.62%
	Caper	*Capparis frondosa*	Mature leaves	3	2.13%
	False coffee	*Faramea occidentalis*	Young leaves	1	0.71%
	False coffee	*Faramea occidentalis*	Mature leaves	6	4.26%
	Flor aguacero	*Hybanthus prunifolius*	Young leaves	25	17.73%
	Wild pigeon plum	*Ouratea lucens*	Mature leaves	6	4.25%
TOTAL				141	100%

92.6%); guans foraged on the ground eight times (6.6%) and once in lianas (0.8%). Despite the amount of time spent foraging for leaves, the Crested Guans appeared ill-equipped for the activity. It often took several attempts pecking at a leaf, during which small, beak-shaped bites were torn off, before the full leaf was obtained. This process was time-consuming and clumsy, requiring up to 2 min.

DISCUSSION

Our findings suggest that Crested Guans may eat more leaves and less fruit than previously thought. Folivory is relatively rare in birds, possibly because leaves provide insufficient energy for the high metabolic demands of flight (Dudley and Vermeij 1992) and because several defense mechanisms deter leaf predation, including toughness, fiber content, and tannins (Coley 1983). Crested Guans appear capable of consuming exceptionally well-defended leaves. For example, guans were observed to eat mature leaves of *Ouratea lucens* on six occasions, which is surprising since leaves of *O. lucens* toughen rapidly after expansion and this expansion occurs relatively early in the leaf's development (Kursar and Coley 1991).

We found that Crested Guans, like most leaf predators on BCI (Coley 1983), eat young leaves more often than mature leaves. Young leaves are less tough than adult leaves and contain higher amounts of nitrogen, which can be a limiting resource (Coley 1983). Two of the plants identified in this study, *Faramea occidentalis* and *O. lucens*, are known to have especially high nitrogen content. Of 34 species surveyed on BCI, young *O. lucens* leaves contained the highest levels of nitrogen (Coley 1983). Similarly, young *F. occidentalis* leaves are significantly less tough and contain more nitrogen than mature leaves—2.17% of leaf dry mass and 1.61% of leaf dry mass, respectively (Coley 1983). The nitrogen content of *Capparis frondosa* and *Hybanthus prunifolius* have yet not been assessed, but it is possible that they are similarly high. The nitrogen levels of *Capparis linearis*, a dominant tree species closely related to *C. frondosa*, are higher than average (per unit dry leaf 5.5 g/m^2 *C. linearis* versus 4.3 g/m^2 average; Coley 1983). However, young leaves also contain high levels of tannins, complex chemical compounds that lower leaf palatability and can be toxic to leaf predators (Giner-Chavez 1996). Further research is needed to identify the physiological effects of tannins and other secondary defensive compounds on Crested Guans, as well as potential behavioral or physiological mechanisms that allow digestion of leaves.

Although Crested Guans were not previously known to rely heavily on leaves, folivory has been reported in several closely related species, including the Chaco Chachalaca (*Ortalis canicollis*; Caziani and Protomastro 1994), the Cauca Guan (*Penelope perspicax*; Muñoz et al. 2007), and the Rusty-margined Guan (*Penelope superciliaris*; Zaca et al. 2006). Both the Cauca and Rusty-margined Guans appear to rely on leaves to a greater extent during the dry season, when fruit is less abundant, although the chachalaca consumes leaves year-round. The present study on Crested Guans was conducted during the rainy season, when fruit should have been available. It is possible that the El Niño-induced

drought of 2015 could have lowered fruit abundance, although this is unlikely since fruit scarcity typically does not occur until the year *after* an El Niño event, and then only when it is followed by an unusually wet dry season (Wright et al. 1999). Therefore, our results support the small number of studies cited above suggesting that folivory may be more widespread among guans and chachalacas (Cracidae) than previously realized, certainly during times of fruit scarcity and possibly year-round.

The mechanisms by which tropical birds digest leaves are largely unknown, except for the specialized foregut fermentation system of the Hoatzin (*Opisthocomus hoazin*; Kornegay et al. 1994). Terrestrial galliforms possess ceca, paired outpocketings of the large intestine, which aid in the digestion of plant material (Gill 1994). However, these structures are inadequately developed or entirely absent in almost all arboreal birds, potentially because of the undesirable weight of the structure in addition to the weight of partially digested plant material (Gill 1994). Future research should therefore explore the physiological mechanisms by which guans and other arboreal galliforms digest leaf material.

Basic natural history information is still lacking for most tropical forest birds (Riehl and Adelson 2008), including the Crested Guan. Further research on the diets and foraging behaviors of tropical birds will be crucial not only to the management of these little-known species, but also to understanding ecosystem-level processes such as seed dispersal and plant recruitment.

ACKNOWLEDGMENTS

We thank Enrique Marciaga, Ricardo Racines, and the other *guardabosques* (game wardens) of Barro Colorado Island for their help with this project. We are extremely grateful to Osvaldo Calderón, who identified leaf and fruit species and was crucial to the success of this study. Lolly O'Brien and Meghan J. Strong provided advice and encouragement. Funding was provided by the Princeton Environmental Institute and the Fred Fox Class of 1939 Fund of Princeton University.

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The Wilson Journal of Ornithology 129(1):195–198, 2017

Common Raven (*Corvus corax*) Kleptoparasitism at a Golden Eagle (*Aquila chyrsaetos*) Nest in Southern Nevada

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ABSTRACT.—The Common Raven (*Corvus corax*) is a ubiquitous species in the Mojave Desert of southern Nevada and California. From 5 to 24 May 2014, using remote trail cameras, we observed ravens repeatedly kleptoparasitizing food resources from the nest of a pair of Golden Eagles (*Aquila chyrsaetos*) in the Spring Mountains of southern Nevada. The ravens fed on nine (30%) of the 30 prey items delivered to the nest during the chick rearing period. Kleptoparasitic behavior by the ravens decreased as the eagle nestling matured to seven weeks of age, suggesting a narrow temporal window in which ravens can successfully engage in kleptoparasitic behavior at eagle nests. The observation of kleptoparasitism by Common Ravens at the nest suggests potential risks to young Golden Eagles from Common Ravens. *Received 11 December 2015. Accepted 6 May 2016.*

Key words: Common Raven, Golden Eagle, kleptoparasitism, Mojave Desert, Nevada.

During a study of food habits of nesting Golden Eagles (*Aquila chrysaetos*) in the Mojave Desert, we observed kleptoparasitism by Common Ravens (*Corvus corax*) at a nest containing one live eaglet (~3.5 weeks of age) and one dead eaglet (~3 weeks of age when it died prior to camera installation). Kleptoparsitism is the theft of food resources that have been procured by another individual and can be either interspecific or intraspecific in nature; this behavior has been encountered frequently across a broad range of avian species (Brockmann and Barnard 1979). Interspecific kleptoparasitic behavior by corvids against a number of species has been documented including Northern Spotted Owl (*Strix occidentalis caurina*; Hunter et al. 1993), Bearded Vulture (*Gypaetus barbatus*; Margalida and Bertran 2003, Bertran and Margalida 2004), and Osprey (*Pandion haliatus*; Yosef et al. 2012). We are aware of no previous observations by Common Raven kleptoparasitism of Golden Eagle nests during the time period when adult eagles are provisioning nestlings.

METHODS

Our study area encompassed the Mojave Desert Ecoregion of Clark County, southern Nevada, and the Desert Renewable Energy Conservation Plan (DRECP) area in San Bernardino, Riverside, Inyo, and San Diego counties of California. The landscape consists of rugged, arid mountain ranges, broad alluvial plains, and playas (Dibblee 1967). The habitat surrounding eagle nest sites investigated in this study varied widely from creosote bush shrubland (*Larrea tridentata* and *Ambrosia dumosa*) in the valleys to pinyon-juniper woodland (*Pinus* spp. and *Juniperus osteosperma*) at higher elevation sites in the Spring Mountain range. The area surrounding the nest in this study was pinyon-juniper woodland with isolated cliffs and broad, rocky washes leading to Joshua trees (*Yucca brevifolia*) and creosote bush shrublands.

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