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Folivory by a tropical tanager: species of plants used and the relationship between leaf consumption and fruit abundance

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ABSTRACT. Folivory, or eating leaves, is unusual for small passerines. Puerto Rican Spindalises (*Spindalis portoricensis*, Thraupidae), tanagers endemic to the island of Puerto Rico, are known to feed on leaves, but little is known about the possible importance of leaves in their diet. Our objectives were to determine the different species of leaves eaten, the percentage of their diet consisting of leaves, and the relationship between leaf consumption and fruit abundance. We used data from previous studies where the foraging activity of Puerto Rican Spindalises was systematically sampled, and from additional observations made throughout the island. We documented 160 records of folivory, with spindalises feeding on 44 plant species in 25 plant families, including monocots, dicots, gymnosperms, and pteridophytes. Spindalises fed on young leaves of 26 plant species, and mature leaves of 19 plant species. Spindalises were primarly frugivorous (83.9% of diet), but leaves were the second most frequent food item in their diets (8.9% of diet). We also found that leaf consumption was negatively correlated with the abundance of ripe fruit, suggesting that leaves were particularly important food items when less fruit was available. The frequency of folivory by spindalises in our study was less than reported for other folivorous passerines such as plantcutters (*Phytotoma* spp.) and saltators (*Saltator* spp.). Nonetheless, folivory may help spindalises cope with human-dominated landscapes and other environmental changes on small islands.

RESUMEN. **Folivoria en un tráupido tropical: especies de planta utilizadas y la influencia de la abundancia de frutos sobre la frecuencia del consumo de hojas**

La folivoría, entiéndase el consumo de hojas, es poco usual en pequeños Passeriformes. La Reina Mora (*Spindalis portoricensis*) es un ave endémica a la isla de Puerto Rico que se conoce por consumir hojas, pero se sabe poco al respecto. Los objetivos de este estudio lo fueron el determinar la variedad de especies de planta que consume esta ave, determinar el porcentaje de la dieta compuesto por hojas, y examinar la relación entre la frecuencia de récords de folivoría y la abundancia de frutos en el ambiente. Para esto juntamos datos observacionales provenientes de estudios sistemáticos sobre la alimentación de la Reina Mora, así como datos de observaciones informales colectados en distintos puntos de la isla. Documentamos 160 récords de folivoría en la Reina Mora que incluyeron hojas de unas 44 especies de planta pertenecientes a 25 familias que incluían monocotiledóneas, dicotiledóneas, gimnospermas, y pteridófitas. La Reina Mora es principalmente frugívora (83.9% en promedio), pero las hojas constituyeron el segundo tipo de alimento más importante en su dieta (8.9% en promedio). Hallamos que el consumo de hojas estuvo negativamente correlacionado con la abundancia de frutos en el ambiente. La proporción de la dieta de la Reina Mora compuesta por hojas es menor que las reportadas para otros Passeriformes folívoros como los cortarramas (*Phytotoma* spp.) y los Saltator (*Saltator* spp.). Sin embargo, es posible que la capacidad de la Reina Mora de consumir hojas sea uno de los factores que ayuda a esta especie a sobrevivir en paisajes antropogénicos, así como de lidiar con cambios y fluctuaciones ambientales en islas.

Key words: Caribbean, digestion, ecological plasticity, frugivory, generalist consumers, resource use, stripe-headed tanager

Only about 3% of all bird species are known to feed on leaves (Morton 1978). Folivorous birds have the advantage of having access to one of the most abundant, easily obtainable, and predictable food resources in terrestrial ecosystems. However, constraints in avian gut physiology, the poor nutritional quality of leaves, the presence of indigestible materials such as lignins and cellulose, and leaf chemical defenses are factors believed to prevent folivory by most passerines (Morton 1978, Bosque et al. 1999, López-Calleja and Bozinovic 1999, Bucher 2003, Karasov and Martínez del Río 2007).

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Primarily frugivorous birds that occasionally feed on leaves include species in disparate families such as Neotropical tanagers (Thraupidae), African mousebirds (Coliidae), saltators (Cardinalidae), finches (Fringillidae), bowerbirds (Ptilonorhynchidae), and wattlebirds (Callaeidae) (Morton 1978, Pérez-Rivera 1994, Guix and Ruiz 1998, Carlo et al. 2004, Rodríguez-Ferraro 2007). However, folivory by small passerines remains a poorly documented and poorly understood phenomenon.

Our objective was to document folivory by Puerto Rican Spindalises (*Spindalis portoricensis*), frugivorous tanagers endemic to Puerto Rico. Puerto Rican Spindalises (hereafter, spindalises) are members of the family Thraupidae (true tanagers) and are dichromatic with a length of about 17 cm and a mass of 26 to 31 g (Oberle 2010). They are a common species found in forests, agricultural lands, and urban areas (Acevedo and Restrepo 2008). Specific objectives were to document the different species of leaves eaten by spindalises, determine the proportion of the diet consisting by leaves, and examine the possible relationship between frequency of folivory and fruit abundance.

METHODS

To examine the diversity of leaves used by spindalises, we compiled a list from observations made from 1991 to 2010 by R. A. Pérez and T. A. Carlo in several municipalities in Puerto Rico, including Humacao, Barranquitas, Juana Díaz, Caguas, and San Juan. To this list, we added records from two systematic field studies conducted in 1997, 1998, and 2004 in the municipalities of Ciales and Utuado (Carlo 1999), and Cayey (Carlo and Aukema 2005). Our list included the plant species used (identified to the lowest taxonomic level possible), plant family, number of folivory records, age of ingested leaves (i.e., young or mature), location, and habitat type where the observation was made (Supplementary Table S1). Young leaves were distinguished from mature ones by differences in coloration, size, and position along branches.

To estimate the percentage of the diet of spindalises consisting of leaves, we used data collected during two previous studies (Carlo 1999, Carlo and Aukema 2005). Carlo (1999) studied avian foraging behavior at four sites in montane secondary forests ranging in size from 4 to 10 ha, with 20 or more independent foraging observations of spindalises made at each site, including Aurora (Cialies municipality), Cialitos (Cialies municipality), Caguana (Utuado municipality), and Frontón (Ciales municipality). In addition, Carlo and Aukema (2005) studied avian foraging behavior at the Carite State Forest (Cayey municipality). The Aurora site was a 4-ha montane forest plot sampled in June and July 1997 by conducting observations for 5 h per day on 10 different days for a total of 50 h of observation (Carlo 1999). The sites at Cialitos, Frontón, and Caguana ranged in size from 4 to 10 ha and observations were made at these sites from February to September 2008, with total observation times of 1200 h per site (see Carlo et al. 2003 for further details).

The Carite site was sampled by observing spindalises along four 50-m transects separated by a distance of at least 1 km. Each transect was sampled for 2 h a day on 8 d for a total of 64 observation hours (Carlo and Aukema 2005). During these observations, all food items ingested by spindalises were recorded and classified as fruit, arthropods, flowers, or leaves. To calculate the frequency of food types in the diet, we considered only the presence and absence of food types during observations, and did not consider quantities ingested. The total number of foraging observations used to calculate the frequency of different food types in the diet of spindalises was 441, including 20 at Aurora, 266 at Cialitos, 65 at Caguana, 47 at Frontón, and 43 at Carite.

The larger number of foraging records from Cialitos allowed us to examine the proportion of folivory records relative to fruit availability. Fruit abundance in Cialitos was measured once a month from February to September 1998 using a sample of 190 tagged fruiting plants belonging to 29 species that included fleshy-fruited epiphytes, hemiparasites (mistletoes), shrubs, and trees (Carlo et al. 2003, 2004). The density of fruiting plant species was obtained by surveying 24 independent circular vegetation plots (11-m-radius) evenly spaced throughout the 10-ha plot. Tagged plants were visited monthly and the number of ripe fruits estimated using the midpoint of abundance categories that increased in quasi-logarithmic fashion (i.e., 1–10, 11–50, 51–100, . . . , 5000–10,000, and >10,000). We used the average fruit scores for each species as our estimate of fruit abundance at Cialitos. To obtain an estimate of ripe fruit per hectare

Fig. 1. Top left, a female Puerto Rican Spindalis feeding on mature leaves of day jazmine (*Cestrum diurnum*, Solanaceae) in an urban area of San Juan, Puerto Rico. Beak marks are visible on the leaves of the day jazmine. Bottom left, a female Puerto Rican Spindalis feeding on young shoots of a winged yam (*Dioscorea alata*, Dioscoraceae) in Carite State Forest in Cayey, Puerto Rico. Right, beak marks left on a mature leaf of mistletoe (*Phoradendron hexastichum*, Viscaceae) by a male Puerto Rican Spindalis in Carite State Forest (Photo credit: T. A. Carlo).

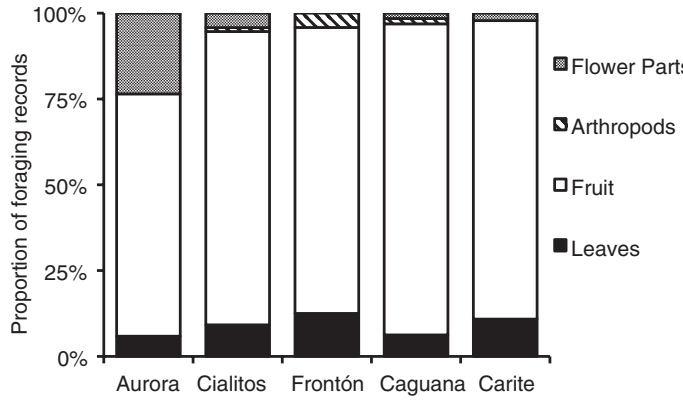

Fig. 2. Major food items in the diet of Puerto Rican Spindalises at five sites located in montane secondary forest in Puerto Rico. Folivory was recorded at all sites and leaves were the second most frequent food type in their diet.

for each fruiting plant species per month, we multiplied each of the ripe fruit mean estimates for each species by the corresponding plant species density. Resulting numbers were then added across species to obtain the total fruits per hectare for each month.

RESULTS

We documented 160 records of folivory, with spindalises feeding on 44 plant species in 25 plant families, including monocots, dicots, gymnosperms, and pteridophytes (Supplemental Table S1). Folivory was observed frequently in species such as the day jasmine (*Cestrum diurnum*), the white pear or "Chayote" (*Sechium edule*), mistletoes (*Phoradendron* spp.), ingas (*Inga* spp.), and winged yams (*Dioscorea alata*; Fig. 1, Supplemental Table S1). Spindalises consumed young leaves of 20 plant species and mature leaves of 16 species; for some species, spindalises consumed both young and mature leaves and,

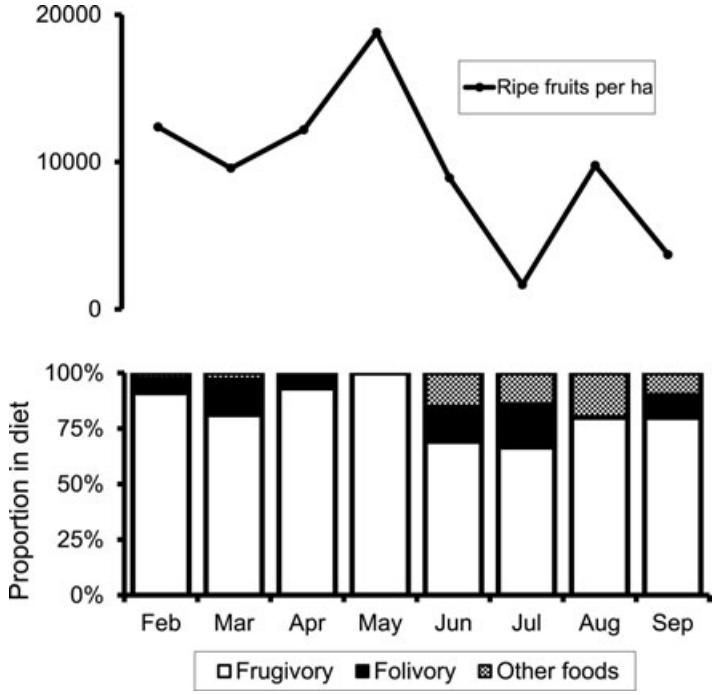

Fig. 3. The frequency of folivory records in the diet of Puerto Rican Spindalises was inversely related to the monthly abundance of ripe fruits at the Cialitos study site during an 8-mo sampling period.

for others, the age of leaves consumed was unknown. Only young leaves were consumed for 15 plant species, and only mature leaves were consumed for eight species (Supplemental Table S1).

Our estimates of leaves in the diet of spindalises ranged from 5.3% to 12.2% across the five study sites (mean = 8.9 ± 1.3% [SE]). Percentages for other food items ranged from 66.7% to 100% (mean = 83.9 ± 4.3%) for fruit, 0% to 21% for flower parts (mean = 5.3 ± 4.0%), and 0% to 4.1% for animal foods (mean = 1.3 ± 0.7%; Fig. 2). We sometimes observed spindalises feeding on leaves from plants that had ripe fruit, as well as feeding on both fruit and leaves from the same plant (e.g., *Solanum esculentum*, *Cestrum diurnum*, and *Muntingia calabura*). At Cialitos, folivory was observed during all months except May, showing consistency throughout the year despite fluctuations in fruit abundance (Fig. 3).

The frequency of folivory was higher when less fruit was available (Spearman $\rho = -0.80$, $r^2 = 0.47$, $P = 0.016$; Fig. 3). In Humacao, most observations of folivory by spindalises were made during the breeding season (December–March), which is also the driest period of the year when fruits are less abundant.

DISCUSSION

Puerto Rican Spindalises are generalist frugivores that use the fruits of numerous plant species in Puerto Rico (Wetmore 1916, Carlo 1999, Carlo et al. 2003). Our results indicate that leaves are the second most frequent food type in the diet of spindalises. However, the negative correlation between folivory records and the density of fruit resources shows that folivory by spindalises can be seasonally driven by resource fluctuations.

Folivory by spindalises is notable because they feed on leaves from a wide variety of plants species and families, and do so even when those plants have fruit (e.g., *Cestrum diurnum, Muntingia calabura,* and *Phoradendron hexastichum*). These observations suggest that leaves are not food items of last resort for spindalises, but are an important part of their diet. Folivory by females during the breeding

season also suggests that leaves could supply important nutrients needed by gravid females. For example, we observed spindalises feeding on the leaves of *Sechium edule*, and these leaves are known to be high in protein and lipid content (Rao et al. 1990).

The broad and plastic diet of spindalises may explain their success in novel anthropogenic habitats such as urban landscapes. In a comparative sense, this could be important because other species of spindalises in the Caribbean are not as locally widespread and abundant as the Puerto Rican species. For example, Hispaniolan Spindalises (*Spindalis dominicensis*) are uncommon outside montane forest sites (Keith et al. 2003). In addition, folivory may help spindalises in Puerto Rico survive after periods of fruit scarcity caused by major and regular disturbances such as hurricanes.

In conclusion, leaves from a wide variety of plant species are regular food items for Puerto Rican Spindalises, and we estimate that they compose about 9% of their diet. Additional studies are needed to determine if there are differences in the frequency of folivory among male, female, and juvenile spindalises, to determine if leaves of some plant species are preferred, and to examine the digestive physiology of spindalises. The frequency of folivory by spindalises in our study was less than reported for other folivorous passerines such as plantcutters (*Phytotoma* spp.) and saltators (*Saltator* spp.; Bosque et al. 1999). Nonetheless, folivory may help populations of spindalises cope with human-dominated landscapes and other environmental changes on small islands.

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LITERATURE CITED

ACEVEDO, M. A., AND C. RESTREPO. 2008. Land-cover and land-use change and its contribution to the large-scale organization of Puerto Rico's bird assemblages. Diversity and Distributions 14: 114–122.

BOSQUE, C., M. A. PACHECO, AND R. B. SIEGEL. 1999. Maintenance energy costs of two partially folivorous tropical passerines. Auk 116: 246–252.

BUCHER, E. H., D. TAMBURINI, A. ABRIL, AND P. TORRES. 2003. Folivory in the White-tipped Plantcutter *Phytotoma rutila*: seasonal variations in diet composition and quality. Journal of Avian Biology 34: 211–216.

CARLO, T. A. 1999. Fruit preference and seed dispersal capabilities of fruit-eating birds in north central Puerto Rico. M. S. thesis, North Carolina State University, Raleigh, NC.

———, J. A. COLLAZO, AND M. J. GROOM. 2003 Avian fruit preference across a Puerto Rican forested landscape: pattern consistency and implications for seed removal. Oecologia 134: 119–131.

———, ———, AND ———. 2004. Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. Biotropica 36: 602–614.

———, AND J. E. AUKEMA. 2005. Female directed dispersal and facilitation between a tropical mistletoe and its dioecious host. Ecology 86: 3245–3251.

GUIX, J. C., AND X. RUIZ. 1998. Intensive folivory by *Thraupis sayaca* (Emberizidae: Thraupidae) in southeastern Brazil. Ararajuba 6: 138–140.

KEITH, A. R., J. W. WILEY, S. C. LATTA, AND J. A. OTTENWALDER. 2003. The birds of Hispaniola – Haiti and the Dominican Republic. BOU Checklist No. 21, British Ornithologists' Union, Tring, UK.

KARASOV, W. H., AND C. MARTÍNEZ DEL RIO. 2007. Physiological ecology: how animals process energy, nutrients, and toxins. Princeton University Press, Princeton, NJ.

LÓPEZ-CALLEJA, M. V., AND F. BOZINOVIC. 1999. Feeding behavior and efficiency of the Rufous-tailed Plantcutter: a small avian herbivore. Condor 101: 705–710.

MORTON, E. S. 1978. Avian arboreal folivores: why not? In: The ecology of arboreal folivores (E. E. Montgomery, ed.), pp. 123–130. Smithsonian Institution Press, Washington, D.C.

OBERLE, M. 2010. Puerto Rico's birds in photographs, 3rd. ed. Editorial Humanitas, Seattle, WA.

PÉREZ-RIVERA, R. A. 1994. Feeding ecology of the Puerto Rican Bullfinch (*Loxigilla portoricensis*) in the Carite and Guánica forests. Caribbean Journal of Science 30: 242–249.

RAO, K. S., R. DOMINIC, K. SINGH, C. KALUWIN, D. E. RIVETT, AND G. P. JONES. 1990. Lipid, fatty acids, amino acids and mineral composition of five edible plant leaves. Journal of Agricultural and Food Chemistry 38: 2137–2139.

RODRÍGUEZ-FERRARO, A., M. A. GARCÍA-AMADO, C. BOSQUE. 2007. Diet, food preferences, and digestive efficiency of the Grayish Saltator, a partly folivorous passerine. Condor 109: 824–840.

WETMORE, A. 1916. Birds of Porto Rico. U. S. Department of Agriculture Bulletin No. 326, Washington, D.C.

Supporting Information

The following supporting information is available for this article online:

Table S1. Records of Puerto Rican Spindalises (*Spindalis portoricensis*) feeding on leaves. Data were compiled from Carlo (1999), Carlo et al. (2003), and Carlo and Aukema (2005), and observations made from 1991 to 2010.