

Fruit Consumption by Birds and Bats on Two Species of Columnar Cacti in a Semi-Arid Andean Enclave of Venezuela

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ABSTRACT.—The columnar cacti *Stenocereus griseus* and *Subpilocereus repandus* in the semi-arid enclave of Lagunillas produce a large biomass of fleshy fruits consumed by both birds and bats. In this paper we quantify the consumption of fruits of both cacti by birds and bats. For two weeks during the fructification periods of *S. griseus* and *C. repandus* ripe fruits were offered to birds during the day and to bats at night. Bats consumed larger amount of *C. repandus* pulp than birds, while the consumption of *S. griseus* was the same for both groups. Birds consumed more *S. griseus* than *C. repandus* fruits, whereas bats consumed the fruits of both cacti species in equal amounts. We believe that the different results are due to the morphological characteristics of these fruits; *C. repandus* has fruits with cryptic coloring that makes their detection difficult for flying frugivores with color vision, while *S. griseus* has red fruits, which makes them conspicuous to avian frugivores. An ancillary preference study supports this notion, as birds were more likely to consume red-colored morphs of *S. griseus* compared to white-colored morphs. On the other hand, bats do not distinguish colors and consume both cacti species in equal amounts. This suggests that *S. griseus*, at least, presents an intermediate bird-bat dispersion syndrome, which, in principle, would guarantee greater fitness in comparison to *C. repandus*.

KEYWORDS.—Andes, birds, bats, columnar cacti, frugivory, Venezuela, arid zones.

INTRODUCTION

Studies on frugivory have been carried out in a variety of environments, most of these being humid forests. However, the arid and semi-arid ecosystems of the world have received little attention (Jordano 1992). Semi-arid ecosystems in the Neotropics have a great variety of columnar cacti that produce a large biomass of fleshy fruits (Gibson and Nobel 1986, Sosa 1991). These fruits constitute an important source of food for a large variety of animals, principally birds and bats (Gonzalez-Espinoza and Quintana-Ascensio 1986, Rodriguez, 1988, Wendelken and Martin 1988, Olin *et al.* 1989, Leon and Dominguez 1991, Santos 1995, Silvius 1995, Valiente-Banuet *et al.* 1995, Sosa and Soriano 1996, Soriano *et al.* 1999, Godínez-Álvarez *et al.* 2002).

The syndromes characteristic of fruits

adapted for dispersion by birds and mammals have been described on numerous occasions (van der Pijl 1972, Heithaus 1982, Janson 1983, Howe 1986, Silvius 1995, Soriano *et al.* 1991, 1999). However, little is known about the possibility that these two groups of animals consume and disperse the seeds of the same type of fruit. There are very few cases in which both birds and bat frugivory has been noted for the same plant species (August 1981, Estrada *et al.* 1984, Charles-Dominique 1986, Fleming 1988, Debussche and Isenmann 1989, Godínez-Álvarez *et al.* 2002).

In the semi-arid enclave of Lagunillas, Merida State, Venezuela, *Stenocereus griseus* and *Cereus repandus* (= *Subpilocereus repandus*) are the two most abundant species of columnar cacti. Their fruits are principally consumed by the glossophaginae bats *Glossophaga longirostris* and *Leptonycteris curasoae* (Soriano *et al.* 1991, Sosa and Soriano 1996) and a great number of frugivo-

rous birds (Soriano *et al.* 1999), such as: *Melanerpes rubricapillus* (Picidae), *Mimus gilvus* (Mimidae), *Thraupis episcopus* (Thraupidae), and *Tachyphonus rufus* (Thraupidae). These plants have asynchronous periods of fructification, causing possible reduction of competition among dispersers while simultaneously guaranteeing the presence of a food resource throughout the year (Sosa and Soriano 1996).

The fruits of these cacti present a set of morphological characteristics, which can be interpreted as adaptations that favor ornithocory and/or chiropterocory. Thus, the fruit of *S. griseus* is an intense red color when ripe (both the pulp and the pericarp). In this phenophase it loses its areolas. This species also has a white morph with the same red fruit shape and size. However, this morph has white pulp and a green pericarp. On the other hand, *C. repandus* produces fruits without thorns that, upon ripening, keep the green color of the pericarp while retaining a white colored pulp (Soriano *et al.* 1991, Sosa and Soriano 1996, Soriano *et al.* 1999).

Such phenotypical characteristics seem to indicate that the production of red colored ripe fruits in *S. griseus* is a strategy utilized by this species for attracting birds as possible dispersers. By contrast, the ripe fruits having a green pericarp and white pulp (e.g., *C. repandus* and the white morph of *S. griseus*) are cryptic, or less attractive to this group of vertebrates (Soriano *et al.* 1999). In the case of bats the color of the fruits should have no effect upon their selection behavior as this is based on olfaction (Debussche and Isenmann 1989).

The objective of this study is to quantify the proportion of fruits of *S. griseus* and *C. repandus* cacti that is removed by birds and bats and determine the approximate degree to which these cacti are associated with each of these two groups of animals. An ancillary objective is to determine color preferences of avian frugivores for the two morphs of *S. griseus*.

MATERIALS AND METHODS

Field work was carried out in the locality of Caparú in the arid enclave of Lagunillas,

3 km SE of the town of San Juan de Lagunillas (8°29'N, 71°20'W), Merida State, Venezuela, at an altitude of 820 m. The area is characterized by scarce rainfall during the greater part of the year, a yearly average temperature of 25.5°C, and thorny shrub vegetation dominated largely by cacti (Sarmiento *et al.* 1971).

Consumption experiments were carried out during the months of June and August, which are the peak fruiting months for *C. repandus* and *S. griseus*, respectively (Sosa and Soriano 1996). We selected seven plants from each species, attaching one or two fruits to each one with a wire base during six days and six nights in the case of *S. griseus* and 13 days and 13 nights for *C. repandus*. When the weight loss of a given fruit exceeded 50% of its initial weight, it was replaced with a new one. In addition, three control fruits, covered with plastic mesh having 5 x 5-mm holes, allowed the evaluation of daily weight losses from evaporation and consumption by arthropods. The fruits were weighed between 0600 and 0630 and between 1830 and 1900 hours, which allowed the differences in consumption during the day (birds) and during the night (bats) to be determined. In the case of *S. griseus*, a total of 62 fruits and 18 controls was offered during the day while 62 fruits and 18 controls were offered during the night. For *C. repandus*, 111 fruits and 39 controls were offered during daytime and 111 fruits and 39 controls were offered at night. All the weight values were quantified using an Ohaus field scale, Model SCOUT, with an accuracy of 0.1 g.

In view of the fact that the fruits offered during these periods were not necessarily consumed at the end of the day or night, subtracting total evaporation and consumption by arthropods from their weight could result in underestimating the amount actually consumed by the frugivores. For this reason, the control value was divided by two. This was an attempt to compensate for the small losses due to evaporation of the fruit consumed at both the beginning of the day and the night and the greater losses for those consumed at the end of both the day and of the night. Also, the results obtained on rainy days and nights were omit-

ted from the final calculations, since this factor affected weights and, undoubtedly, the activity of the animals.

For each set of data for daytime hours and night hours, a consumption index (CI) for birds and bats, respectively, was calculated using the following quotient:

$$CI = \frac{Pi - \left(\frac{Pc}{2}\right) - Pf}{Pi}$$

Where Pi = weight of the fruit offered, Pc = average weight lost by the control fruits, and Pf = weight of the fruit consumed. The proposed consumption index varied between 0 and 1, these values indicating no consumption by the animals or complete depletion of the pulp offered, respectively. The differences between consumption by birds and by bats for each species of cactus were evaluated. In addition, consumption of the fruits of *S. griseus* and *C. repandus* for each taxonomic group was determined as well. Both of these analyses were evaluated for statistical significance using a *t* Student test.

Since the availability of ripe *S. griseus* fruits having a white morph was low during the period under study, the difference in field bird consumption of the two cactus morphs could not be compared. Consequently, it was decided that preference tests be carried out under laboratory conditions using *Melanerpes rubricapillus* (4 individuals), *Mimus gilvus* (4 individuals), *Thraupis episcopus* (4 individuals), and *Tachyphonus rufus* (2 individuals), which

had previously been recorded as the principal birds consuming the fruits of this plant in the locality under study (Soriano *et al.* 1999). In the laboratory, the birds were put in separate, observable cages measuring 40 × 40 × 40 cm. A ripe *S. griseus* fruit with a red morph was placed in one cage corner while a white morph was placed in the corner opposite. Using a species of cactus with fruit color dimorphism allowed us to ascribe differences in fruit preferences based solely upon color variation rather than some other characteristic(s) (e.g. nutritional value) that might covary with color. During each consumption event, the color visited was noted and the position of the fruits was inverted. These tests were repeated 10 times per individual for each bird species examined.

During the experiments birds were never deprived of their maintenance diets and were fed before and/or after the experiments. Disturbance was kept to a minimum because the cages were placed such that they could be observed without exciting the animals. Because birds are less active in both the afternoon and on rainy days, all the tests were carried out between 0730 and 1200 hours on days when it did not rain.

RESULTS

The index for consumption of *C. repandus* fruits by bats (CI = 0.79; Table 1) was significantly greater than that for birds (CI = 0.48; $t = 2.06$; $p < 0.01$; $df = 24$). On the other hand, for the species *S. griseus*, consumption by birds (CI = 0.80) and by bats (CI =

TABLE 1. Consumption index IC, average weight of the fruit offered Pi , average weight lost by the control fruits, and average weight of the fruit consumed $Pf \pm S.E$ (N) for birds and bats on the fruits of *Stenocereus griseus* and *Cereus repandus*

		<i>S. griseus</i>			
	CI	Pi	Pf	Pc	
Bats	0.90 ± 0.03 (N = 62)	45.70 ± 5.32 (N = 62)	41.92 ± 7.10 (N = 62)	2.60 ± 0.72 (N = 22)	
Birds	0.80 ± 0.05 (N = 62)	54.51 ± 10.71 (N = 62)	40.57 ± 9.71 (N = 62)	6.20 ± 2.13 (N = 25)	
		<i>C. repandus</i>			
	CI	Pi	Pf	Pc	
Bats	0.79 ± 0.05 (N = 111)	22.21 ± 9.90 (N = 111)	17.12 ± 10.21 (N = 111)	3.04 ± 1.87 (N = 4)	
Birds	0.48 ± 0.06 (N = 92)	23.14 ± 10.92 (N = 110)	10.84 ± 8.30 (N = 110)	6.07 ± 3.04 (N = 44)	

0.90) showed no difference ($t = 2.20$; $p = 0.13$; $df = 11$). The birds, in turn, had a greater impact on *S. griseus* than on the *C. repandus* fruits ($t = 2.07$; $p < 0.01$; $df = 22$), while the bats consumed similar quantities of pulp from both species of cacti ($t = 2.11$; $p = 0.17$; $df = 17$).

The color preference experiments showed that in 40 tests, *M. gilvus* and *M. rubricapillus* always visited and consumed the red-colored fruit; in 40 tests, *T. episcopus* preferred the red morph 38 times and the white morph only twice, while *T. rufus*, in 20 tests, visited the white morph 18 times and the red morph twice.

DISCUSSION

Frugivore preference may be explained by fruit characteristics: *C. repandus* is characterized by dehiscent and thornless fruits with cryptic coloring that makes their detection difficult for frugivores with color vision, such as birds, whereas *S. griseus* has dehiscent fruits that are red in color, making them conspicuous to this type of flying frugivores. In fact, in the locality under study, we found that the community of birds associated with *S. griseus* is richer (17 species) than those associated with *C. repandus* (10 species; Soriano *et al.* 1999). Bats, which do not distinguish colors, consume both species of cacti in equal amounts. This suggests that *S. griseus*, at least, presents an intermediate bird-bat dispersion syndrome as a strategy that allows this species to increase its fitness. Plants dispersed by two or more taxa of animals show greater fitness than those dispersed by only one taxon (Fleming *et al.* 1993). This is evident in the zone under study, due to the greater population density of *S. griseus* in comparison to *C. repandus*. Sosa (1991) reports an average density of 603 individuals/ha for *S. griseus* and only 82 individuals/ha for *C. repandus*.

As a result of this overlapping in the diet of birds and bats, it could be thought that there would be competition between both taxonomic groups; however, this seems highly improbable in view of the following: i) Silvius' (1995) observations demonstrate

that the fruits of this cactus open with similar frequency during the day (45%) and during the night (65%), so that the availability of the resource for both groups is guaranteed; and ii) the dimorphism in the color of *S. griseus* fruits suggests that the red morpho of this species would favor birds' attraction to them and that, on the contrary, the white morpho would not. Therefore, it is presumed that the latter would remain available for bats. The results obtained from the preference tests seem to confirm this latter assertion, since the majority of the species of birds preferred the red morpho of the *S. griseus* fruits instead of the white morpho.

Although the consumption indexes show similar values for both groups (Table 1) bats may make a greater quantitative contribution to the dispersion of *S. griseus* than birds, because seeds consumed by bats are viable when defecated, whereas some seeds are destroyed during passage through avian frugivores (Rengifo 1997, Soriano *et al.* 1999). Likewise, bats contribute more than birds to the dispersion of *C. repandus* because they consume greater amounts of pulp (Table 1) and excrete seeds without affecting their viability (Sosa and Soriano 1996, Naranjo *et al.* 2003). Furthermore, by comparing our estimations of quantitative effectiveness for birds and bats we found similar patterns to those found in other studies. For example, Godínez-Alvarez *et al.* (2002) and Fleming and Sosa (1994) reported that bats removed higher proportion of seeds and pulp from cacti fruits than birds. However, Naranjo *et al.* 2003 demonstrated that the birds *T. rufus* and *M. gilvus* and the bat *Glossophaga longirostris* (Phyllostomidae) are the most efficient disperser of *S. griseus* and *C. repandus* in the Lagunilla enclave, in terms of the quality of the treatment effected in their digestive tract that facilitates the germination of the seeds.

The product of these two components strongly determines dispersal effectiveness (Howe 1986, Debussche and Isenmann 1989, Shcupp 1993, Godínez-Álvarez *et al.* 2002), indicating whether a particular animal species is a legitimate dispersal agent for a certain plant species. Considering this,

it is possible to hypothesize that *G. longistriis* could represent a key species in the ecology of these columnar cacti because this bat plays an important ecological role not only as seed disperser but also as an effective pollinator (Soriano *et al.* 1991, Sosa and Soriano, 1996). However, seed shadows, deposition patterns, seed predation, and the establishment of seedlings, should also be evaluated. Thereby, more work is necessary to fully characterize the relationship between frugivores and plant distribution in these xerophytic systems.

Acknowledgments.—Field work was partly supported by Consejo de Desarrollo Científico, Humanístico y Tecnológico de la Universidad de los Andes (CDCHT-ULA), Consejo de Desarrollo de Pregrado (CODEPRE), Instituto Nacional de Parques (INAPRQUES), and The James Baillie Memorial Fund. The manuscript greatly benefited from comments by Richard Smith.

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