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SHORT COMMUNICATION

Granivorous birds in a stable and isolated open habitat within the Amazonian rainforest

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Granivory among birds is specially prevalent in pioneer or early stages of the ecological succession (Wiens & Johnston 1977), where plants are selected for high and rapid reproductive rates thus producing large seed crops (Leck *et al.* 1989). True granivorous birds show an array of behavioural, morphological and life-history adaptations to exploit open and unpredictable habitats, together with morphological and physiological adaptations for eating seeds (Wiens & Johnston 1977). These adaptations may allow seed-eating birds to exploit successfully rainforest openings, which are patches of open, early successional stages within dense and mature ecosystems. It has been shown that seed-eating birds are more abundant or even restricted to these openings, either natural (Levey 1988, Schemske & Brokaw 1981, Terborgh *et al.* 1990) or man-made (Karr 1976, López-Ornat 1990).

One of the main factors affecting granivorous bird abundances worldwide seems to be seed abundance (Schluter & Repasky 1991). Two main processes determine seed abundance for granivorous birds: the production and germination dynamics of plant communities, which ultimately determine the size of seed banks available to granivores (Leck *et al.* 1989), and the consumption of seeds by other granivores such as ants and rodents (Brown *et al.* 1986). Rainforest openings generally have larger seed banks than the surrounding mature forest, although there is a great deal of between-openings variation (Garwood 1989). Overall seed predation rates by rodents and ants appear to be lower in South American deserts than in comparable habitats worldwide, since rodent impact on seed resources is very low in South America (Mares & Rosenzweig 1978) and ant foraging activity does not increase to compensate for this rodent scarcity (Morton 1985).

Rainforest openings studied to date have been small gaps caused by treefalls, storms or landslides, which are ephemeral because of the fast rates of plant succession typical of tropical rainforests (see, e.g., López-Ornat 1990, Terborgh *et al.* 1990). Within the Colombian Amazon some large and isolated patches of open shrubland occur, growing on poor and shallow soils associated with the flat rocky outcrops of the Roraima formation (Estrada & Fuertes 1993, Maguire 1979). These rainforest openings appear to be permanent (Estrada & Fuertes 1993, Stiles *et al.* 1995), but the information about their basic ecological features is extremely scarce because of their extremely difficult access. In this study we examine whether or not these isolated open habitat patches could maintain stable populations of granivorous birds by measuring simultaneously bird abundance, seed abundance, vegetation structure and floristic composition, and the foraging impact of rodents and ants in one of such patches.

Field work was carried out in the Sierra de Chiribiquete, a range of palaeozoic sandstone outcrops of the Roráima formation (Maguire 1979) located in the Caquetá–Guaviare departments of the Colombian Amazon (0° 56′ N, 72° 42′ W), during a Spanish–Colombian expedition in November–December 1992, just at the end of the rainy season. The outcrops form an extensive plateau (*c.* 1300 km^2) up to 800 m asl, isolated within intact basal rainforest at 300 m asl. The hill tops, on which the study was carried out, are mainly covered by open, low-tree and shrub communities growing in small fissures filled with shallow sandy soils (see Estrada & Fuertes 1993 for a full description). Shrubs and trees are arranged as a mosaic of patches of *Bonnetia martiana* Maguire (Bonnetiaceae), *Tepuianthus savanensis* Maguire & Steyerm. (Tepuianthaceae), *Decagonocarpus cornutus* Cowan (Rutaceae) and *Clusia* spp. (Clusiaceae), between which can be found areas with very shallow soil covered by herbaceous plants (*Vellozia phantasmagorica* R. E. Schult. (Velloziaceae), Xyridaceae, Eriocaulaceae, Burmanniaceae, Cyperaceae, Graminae) and rocky outcrops partially colonized by bromeliads (*Navia garcia-barrigae* L. B. Smith, *Aechmea* sp. (Bromeliaceae)).

We censused and trapped birds over 15 days. Censuses were made during our daily visits to the lines of mist nests we set up to study the bird communities inhabiting the study area (Stiles *et al.* 1995), as well as during checkings of the feeding stations installed to study seed predation rates by ants and rodents. We only considered the time spent and the observations made in the open vegetation of the hill tops around our permanent camp site. Mist-netted granivorous birds were weighed and treated with an emetic (apomorphine) to obtain diet samples (Díaz 1989). The stomach contents of some birds, collected for taxonomic studies, and casual observations of foraging individuals were also used as sources of data on granivorous bird diets. The seeds found were weighed to the nearest 0.1 mg, and the remains of arthropods were identified following Moreby (1988).

Seed abundance was estimated by measuring seed numbers only in the top soil layer, since close examinations of plants in the area revealed that they were not bearing seeds during the study period. Fifty sampling points were placed

at *c.* 18 m intervals along a line transect established across the open vegetation around our permanent camp site. Samples of 15 cm × 15 cm of the top 1 cm soil layer were taken every two sampling points in a 2 m radius around each point. A sample of unvegetated sandy soil and another of soil covered by herbs or lichens was taken from each circle whenever possible. Bare rocks and soil covered by a thick (5–10 cm) litter layer were not sampled because seeds in these locations (if any) were considered not available to birds. The soil collected was air-dried in the laboratory and washed through sieves after treatment with a soil disperser, and seeds retained were then sorted and counted under a dissecting microscope (see Díaz 1992a,b for a full explanation). Samples of intact, air-dried seeds of each of the species detected were weighed to the nearest 0.1 mg and identified to the lowest taxonomic level possible. Vegetation and soil structure at the ground level was characterized by measuring the lineal cover (to the nearest 10 cm) of litter, bare rock, sand, small-seeded herbs (Velloziaceae, Bromeliaceae, Xyridaceae, Eriocaulaceae), large-seeded herbs (Cyperaceae, Graminae) and lichens. A 10 m measure mark was made every five sampling points, thus totalling 10 cover samples.

Seed predation rates by rodents and ants were measured by means of feeding stations (Díaz 1992a,b; Morton 1985). Two trays were placed at each of the 50 sampling points, one being only accessible to ants (a plastic 9 cm diameter Petri dish with four opposite entrances 1.5 cm wide cut in the sides, and covered with a 1 cm plastic mesh box), and the other only to vertebrates (a plastic Petri dish glued to the top of a plastic cup 12 cm high, pushed upright 5 cm into the soil, and with an adhesive strip put directly beneath the dish to deter ants). In each tray, 9 g of canary seeds (*Phalaris canariensis* L.) were put out at dawn and replenished at each following dusk and dawn for two consecutive night–day periods. Seed remains were air-dried and weighed in the laboratory to the nearest 0.5 g to determine the amount of seeds taken. No removal in the trays for vertebrates during daylight (attributable to birds) was detected. Night removal in these trays was attributed to rodents (Díaz 1992a,b, Morton 1985). Seed predation rates were standardized to g $tray^{-1}$ 12 h^{-1}, averaged for the two consecutive sampling days or nights, and log-transformed before analysis (Díaz 1992a,b; Morton 1985).

Only two *Zonotrichia capensis* (Emberizidae) were detected foraging in the open vegetation 1 km around our permanent camp site during the 22 h we spent censusing birds there. Mist-net captures also shown an extreme scarcity of granivorous birds, since only six out of 61 birds (9.8%) captured with a sampling effort of 298 h net^{-1} were granivorous birds belonging to two species (three *Zonotrichia capensis* – 19.3 g body mass; SD = 0.29 and three *Dolospingus fringilloides* – Fringillidae; 13.0 g body mass; SD = 0.50) (Stiles *et al.* 1995). The abundance index of granivorous birds obtained for the open hill tops of the Sierra de Chiribiquete was then 0.09 birds h^{-1} (1.74 g h^{-1}) of only one species, a very low figure as compared with the results reported by Schluter & Repasky (1991) for continental finch communities worldwide. These authors found 1.77–78.04 g h^{-1}

of granivorous birds of 2–12 species in 17 communities from Kenya, Brazil, Argentina and California, and 16–502 mg m^{-2} of edible seeds at the same localities. The regression model relating these finch and seed data predicts 2.86 g h^{-1} of granivorous birds from the observed seed abundances at Chiribiquete (8.02 mg m^{-2}), a figure close to our results. Unfortunately, the statistical significance of this result cannot be estimated, since the observed seed abundances fell outside of the range of values used to compute the regression model (Zar 1984).

Seed abundances for seed-eating birds in the Chiribiquete hill tops were ascertained by combining the data on bird diets and the measurements of vegetation structure and seed density (see Schluter & Repasky 1991). Two stomach contents and one foraging observation of *Zonotrichia capensis* and two stomach contents of *Dolospingus fringilloides* show that they are mainly granivorous but also feed on insects. Out of the 212 food items identified, 171 (80.7%) were seeds of six species, plus one more species detected in foraging observations (only one *Zonotrichia capensis* was seen feeding on the seeds of two herbaceous plants). The average fresh seed weight of the seven seed species (five unknown, one Melastomataceae sp. and one *Selaginella* sp.) was 0.67 mg (range 0.07–2.60). The remaining food items were ants (10.8%), grasshoppers (3.3%), beetles (1.9%), caterpillars and small hymenopterans (1.4% each), and spiders (0.5%).

Most of the ground in the open areas of the hill tops was covered by a thick layer of *Bonnetia* and *Tepuianthus* leaf litter and by bare rocks (mean ± S.E., 47.5 ± 10.9 and 24.2 ± 7.9%, respectively; N = 10 cover samples), two kinds of substrates which do not provide seed sources for avian granivores. Herb communities were dominated by small-seeded perennials such as *Navia garcia-barrigae* and *Vellozia phantasmagorica*, together with ephemeral Xyridaceae, Burmanniaceae and Eriocaulaceae (20.4 ± 5.5%), whereas large-seeded herbs such as Cyperaceae and Graminae were much scarcer (5.2 ±1.6%; see also Estrada & Fuertes 1993). Lichen and sandy patches were minor substrates (1.8 ±1.2 and 0.9 ±0.9%, respectively).

As a result of these floristic and physiognomic characteristics, the production of seeds edible to granivorous birds in the study area would be very low as compared to other open areas worldwide (Schluter & Repasky 1991; see also Leck *et al.* 1989 for a review). Seeds from six species were found in the top soil layer, whose average fresh seed weights varied between 0.015 and 1.28 mg. Seeds weighing less than 0.05 mg (*Paepalanthus* sp. (Eriocaulaceae), 0.015 mg on average, N = 20; *Xyris* sp. (Xyridaceae), 0.018 mg, N = 50; *Abolboda* sp. (Xyridaceae), 0.05 mg, N = 50) are seldomly eaten by granivorous birds (see the diet results above, and Schluter & Repasky 1991), so that we only considered the seed species larger than this size (*Selaginella* sp. (Selaginellaceae), 0.17 mg on average, N = 7; Graminae sp., 0.3 mg, N = 1; and Cyperaceae sp., 1.28 mg, N = 10). The abundances of these large seeds were 25.9 ±14.1 mg m^{-2} in sandy patches (N = 14) and 28.4 ±12.7 mg m^{-2} in vegetated ground

(covered by small-seeded herbs, large-seeded herbs or lichens; N = 16), thus giving an average abundance of 8.02 mg m^{-2} of edible seeds when seed abundances in each substrate (sandy patches, vegetated ground, and litter and rocky outcrops) were weighted with their average percentage cover.

Additionally, an important part of this low seed production appears to be consumed by other granivores, as measured by removal rates of canary, a relatively large seed species (6.6 mg; Díaz 1990). Both ant (*Solenopsis* sp., among others; F. Fernández, *pers. comm.*) and rodent (*Olygoryzomis* sp.; A. Cadenas, *pers. comm.*) predation rates were much larger than those reported for South American deserts by Mares & Rosenzweig (1978), a type of habitat where granivores usually are important primary consumers (Brown *et al.* 1979). Ant removal rates at Chiribiquete were 0.52 ± 0.19 g $tray^{-1}$ 12 h^{-1} (average ± S.E.) as compared with the average value of 0.08 g $tray^{-1}$ 12 h^{-1} measured in November and December in the Monte Desert of Argentina ($t = 3.281$, $df = 49$, $P = 0.002$; t-test on log-transformed data; Zar 1984). The corresponding values for rodents were 0.07 ± 0.03 for Chiribiquete and 0.03 for the Monte Desert ($t = 2.346$, $df = 49$, $P = 0.023$). The granivorous rodents and ants found in Chiribiquete are generalist species which rely on a wide array of plant and animal food (see Carroll & Risch 1984 for *Solenopsis*, and Emmons 1990 for *Olygoryzomis*). This fact could explain their survivorship in the study area, where they probably exploit seed resources opportunistically.

The results presented here are probably affected by the seasonality of the study area. Our measurements were made at the end of the rainy season, when most seeds have probably germinated and no new seeds have yet been produced (Garwood 1989, Leck *et al.* 1989). It is very likely that seed resources will be larger at other times of the year, especially at the end of the dry season (Garwood 1989), so that larger bird populations would be expected at these more favourable times. The degree to which granivorous bird populations of Chiribiquete could track the seasonality of their food resources would depend on their reproductive potential, the potential for immigration from near-by open areas, or both. This information, which is still lacking, will thus be of paramount importance to understand the role of these stable forest openings for the maintenance of granivorous bird populations in mature rainforest areas.

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