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THE SLATE-COLORED SEEDEATER (*SPOROPHILA SCHISTACEA*): A BAMBOO SPECIALIST?

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The idea of constant density and stable territoriality found in some tropical birds (Greenberg & Gradwohl 1986) does not lend itself to species that rely on a short-term, unpredictable resource. One such resource is mast-seeding plants. Mast seeding is the synchronized production of seed at long intervals by a population of plants (Janzen 1976). This behavior is thought to be a reproductive strategy whereby plants satiate seed predators. The long or irregular periods between seed crops reduce predation by specialized seed predators only if the period between seeding is longer than the predator can endure (Janzen 1971, 1976; Willson 1983). This large quantity of synchronously produced seed attracts many predators, both local and nomadic. Because of its irregularity in space and time, mast is not a dependable food resource, and species that specialize on seeds from these plants must wander widely every year (Smith & Scarlett 1987).

The bamboos constitute a group of mast-seeding plants upon which many tropical species specialize (see Janzen 1976, Parker 1982, Kratter 1993). The global distribution of bamboo is primarily concentrated in the tropical, subtropical, and mild-temperate regions of the world (McClure 1966, Janzen 1976). Generally, for bamboo species an intermast period of less than about 15 years is not adequate to accumulate enough resources for predator satiation (Janzen 1976).

Many species of Neotropical birds inhabit stands of bamboo; however, most of these species are not seed specialists, but instead forage on associated arthropods (Hilty *et al.* 1979, Parker 1982, Fitzpatrick & Willard 1990, Kratter 1993, Rodrigues *et al.* 1994). The Slate-colored Seedeater (*Sporophila schistacea*) is a nomadic species that tends to breed in areas with large seed crops, especially bamboo (Willis & Eisenmann 1979, Parker 1982, Marcus 1983, Ridgely & Tudor 1989, Stiles & Skutch 1989). Previous observations of this species are anecdotal in nature and provide only qualitative evidence that the Slate-colored Seedeater is a bamboo specialist. The purpose of this study was to document the relationship between Slate-colored Seedeaters and the presence of seeding bambo.

STUDY AREA AND METHODS

We conducted our study from 15 to 25 February 1994 in Parque Nacional Soberania, Panama. From 15 to 21 February we surveyed the first 6 km of Pipeline Road and 2 km of adjacent roads for Slate-colored Seedeaters. Surveys were conducted from 06:00 to 10:30 h each day. Every 100 m we stopped for 5 min and listened for songs of ♂ seedeaters. If no songs were heard, then we conducted a 5 min playback of ♂ song. We noted all ♂ heard singing or responding to playbacks on a map. We recorded songs using a Sony Professional Walkmann® with a Sony® shotgun microphone; the same tape-recorder was used with a speaker for the purposes of playback. We also noted the presence of ♀ seedeaters, which sometimes responded to playbacks.

We color-banded 6 ♂ captured by mist netting in conjunction with playbacks. ♂ Slate-colored Seedeaters have delayed plumage maturation (Stiles & Skutch 1989); thus, we documented plumage characteristics of the ♂ we observed. Adults had bright, immaculate, yellow bills and dark gray plumage, whereas subadults had dark bills and brown, female-like plumage. The bills of the intermediate birds were yellow with a darker area on the culmen, and their plumage was duller gray than the adults.

We mapped seedeater territories by recording where banded ♂ were found singing and by observing responses to playbacks. Playbacks were initiated 25 m from where a ♂ was observed singing. After the ♂ responded (singing and perching in the vicinity of the speaker) the playback was conducted at 25 m intervals away from the first playback area in one direction until the male stopped responding. This procedure was followed for at least four compass directions from the area the ♂ was originally heard singing. Once territories were mapped, we searched this area for seeding bamboo. We determined the species of bamboo observed on seedeater territories to be *Chusquea simpliciflora* Munro (see Standley 1928). The area of bamboo was determined with a rangefinder which we used to measure the patch dimensions. In some instances we were unable to map accurately the territories because males were not responsive to playbacks. For these ♂ we sampled an area roughly equivalent to the average territory size (3500 m^2) and which encompassed the site where the bird was observed singing. We randomly chose 10 areas along Pipeline Road to survey for bamboo where seedeaters were not found. This was achieved by dividing the 6 km of road into 100 m sections and choosing 10 at random to search (sections where ♂ were heard singing were excluded). We searched these "sample areas" which were approximately 3500 m^2 (average size of seedeater territories) in the same manner as we searched the territories with ♂ known to be present.

RESULTS

We found 14 ♂ seedeaters in our study area. Their distribution was patchy (Fig. 1). Of the 6 banded ♂, 2 had full adult plumage, 2 had subadult plumage, and 2 were intermediate. We observed ♀ with 7 of the 14 ♂. Because females often did not respond to playbacks, our sightings were opportunistic, and we do not know if the other ♂ were mated.

We mapped territories of 7 ♂ (6 of which were color-banded) using playbacks. Territory size ranged from 1425 m^2 to 9800 m^2 (3834 m^2 ± 2765). This large standard deviation may be explained in part by one ♂ that appeared to have an exceptionally large territory. If we exclude this territory, mean territory size is 2840 ± 933 m^2. The area of bamboo on the 7 territoreies ranged from 130 m^2 to 975 m^2 (389 m^2 ± 327).

We obtained body masses for 5 of the banded ♂ (13.9 g ±0.91). There was no significant correlation between male body mass and area of bamboo within the territory (Spearman Rank Correlation, $r_S = 0.50$, $P = 0.39$). However, most bamboo was found on the territory of the largest ♂ (14.9 g).

In addition to the 7 ♂ for which we mapped territories, we also assessed the presence of bamboo for 5 ♂ where we estimated their territory boundaries. Of the 12 territories, 11 had patches of bamboo greater than 100 m^2. Of the 10 randomly sampled areas, 6 had no bamboo, 3 had only a few strands of bamboo, and 1 had 2 small patches of sparse dead bamboo (approximately 10 m^2). A comparison of presence/absence of bamboo shows a significant difference between territories and sample areas (Fisher exact test, $P = 0.0147$). However, if we assume that bamboo must be seeding and must occupy an area of at least 10 m^2, then the differences are more extreme (Fisher exact test, $P = 0.00002$).

DISCUSSION

In *S. schistacea* local distribution was strongly associated with the presence of seeding bamboo. Bamboo was present on 92 % of ♂ territories, whereas all randomly selected areas contained insignificant amounts of bamboo or none at all. ♂ territories appeared to be clumped in close proximity to rivers or clearings (Fig. 1) where bamboo is more common (Ridgely & Tudor 1989, Fitzpatrick & Willard 1990). ♂ territory size was similar among individuals, with the exception of one ♂ that had an exceptionally large territory. This ♂ was extremely responsive to the playback and may have continued to respond past his territorial boundary.

Our data lends strong support for the hypothesis that this species is a bamboo specialist. Further evidence linking this species to the mast seeding of bamboo comes from its irruptive behavior. Slate-colored Seedeaters were observed in association with seeding bamboo in the years 1961—1962, 1975 and 1977—1978 at Barro Colorado Island, Panama (Willis & Eisenmann 1979). We observed seedeater ♂ singing in seeding

bamboo on Barro Colorado Island during this study. Our study site in Parque Nacional Soberania is close to Barro Colorado Island (~ 20 km), and we expect similar seeding patterns of bamboo in these two areas. These sightings of Slate-colored Seedeaters occurred approximately every 15 years. This coincides closely with the intermast period (15—23 years) of four related South American species of bamboo (*C. culeou*, *C. quila*, *C. ramosissima*, *C. tenella*; Janzen 1976). Other evidence comes from Stiles & Sktuch (1989), in which sightings of Slate-colored Seedeaters in Costa Rica were associated with bamboo seeding.

Our data on the territoriality of Slate-colored Seedeaters in conjunction with the correlation between bamboo seeding and bird irruptions would suggest that this species is a bamboo specialist. Species that specialize on a single food tend to be more prone to extinction than "generalist" species because a change in conditions is more likely to move outside a narrow tolerance range than a broad one (Brewer 1988). A familiar example of a species specializing on mast is the now extinct Passenger Pigeon (*Ectopistes migratorius*). One of the contributing factors in the decline of this species was a shortage of mast resulting from severe deforestation following European settlement in the eastern United States (Bucher 1992). In contrast, the clearing of Neotropical forests may result in an increase of bamboo from creation of forest gaps (see Janzen 1983, Marcus 1983). Marcus (1983) documented the forst sighting of Slate-colored Seedeaters in Honduras in 1980. This range expansion is likely the result of the spread of introduced bamboo (*Bambusa* sp.; Marcus 1983, Stiles & Skutch 1989). The flourishing of bamboo due to introductions and deforestation may have much affect on reproductive strategies and life history variables of Slate-colored Seedeaters.

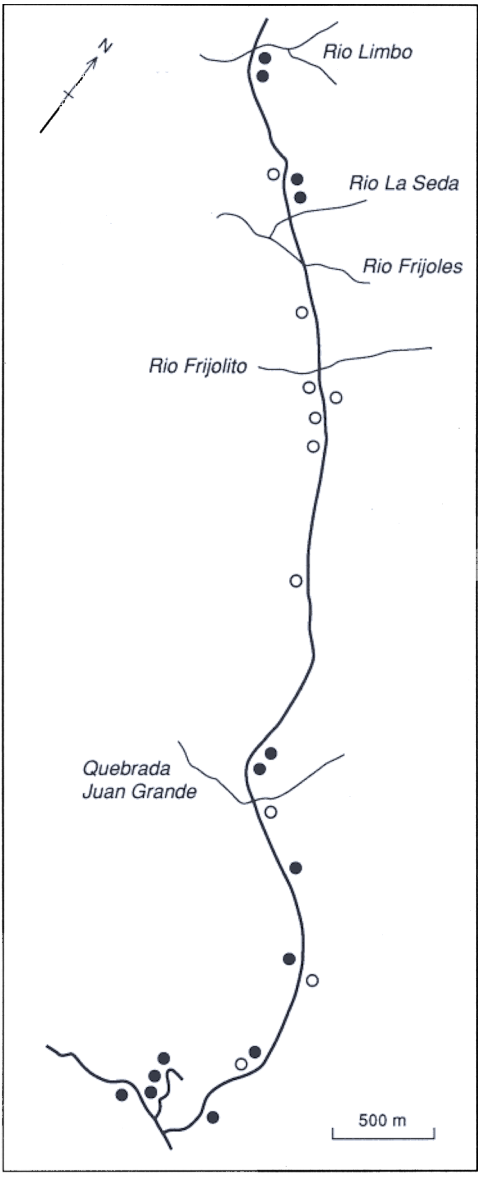

FIG. 1. Map of study area indicating territories of Slate-colored Seedeaters (*Sporophila schistacea*; ●) and 10 randomly sampled areas (O).

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