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BREEDING BIOLOGY OF THE RED-BELLIED GRACKLE (*HYPOPYRRHUS PYROHYPOGASTER*): A COOPERATIVE BREEDER OF THE COLOMBIAN ANDES

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ABSTRACT.—We document the breeding behavior of the Red-bellied Grackle (*Hypopyrrhus pyrohypogaster*: Icteridae) from monitoring seven breeding groups during 4 consecutive years (2006–2009) in the central cordillera of the Colombian Andes. All nests were attended by three to seven individuals, representing family groups composed of adult males and females, as well as immatures from previous generations. Clutch size ranged from two to four eggs and was positively correlated with family group size. The incubation period was 15–17 days and nestlings left the nest when 16–18 days of age. Nestling success was relatively low (0.39), and mortality was caused by predation and harsh environmental events; however, groups attempted to breed after nest failures. The Red-bellied Grackle has a cooperative breeding system and individuals delay dispersal by remaining in natal territories. *Received 15 July 2011. Accepted 14 April 2012.*

About 9% of bird species scattered across the avian evolutionary tree, from rheas (*Rhea* spp.) to passerines (Skutch 1987, Hatchwell 2009, Cornwallis et al. 2010), are now thought to exhibit cooperative breeding (Cockburn 2006). This behavior has been reported in Icteridae for no fewer than 14 species (Fraga 2008), including 13 members of the South American quiscaline clade (i.e., grackles and allies *sensu* Johnson and Lanyon 1999, Lanyon and Omland 1999). Red-bellied Grackles (*Hypopyrrhus pyrohypogaster*) are a member of this assemblage (Cadena et al. 2004, Eaton 2006) and have recently been observed breeding in groups of three or more individuals (Betancur 1994, Ochoa and Cuervo 1998). These observations suggest Red-bellied Grackles have a cooperative breeding system, contrary to historical accounts reporting breeding by solitary individuals (Sclater and Salvin 1879, Hilty and Brown 1986).

Hypopyrrhus is a monotypic genus endemic to the humid montane forests of the Colombian Andes. Its restricted, disjunct distribution spans the northern sections of the western and central Andes, as well as the base of the eastern Andes in southern Colombia (Hilty and Brown 1986, Cuervo 2002, Cuervo et al. 2008). Red-bellied Grackles are currently categorized as endangered using IUCN criteria (Cuervo 2002, BirdLife International 2011), mainly due to habitat loss (Renjifo 1999). However, Red-bellied Grackles are known to thrive in fragmented and disturbed habitats (Ochoa and Cuervo 1998, Cuervo 2002, Cuervo and Restrepo 2007). Red-bellied Grackles are highly mobile, gregarious birds that form flocks of up to 30 individuals when not nesting (AMC, pers. obs.), similar to other cooperative-breeding icterids (R. M. Fraga, pers. comm.). Large non-breeding flocks in the non-breeding season imply the small reproductive flocks (3–7) have great potential for fusion and rearrangement and suggest complex social and behavioral interactions are important in the cohesiveness of breeding groups, hierarchical dominance, and kinship.

The nests and eggs of Red-bellied Grackles were described >130 years ago (Sclater and Salvin 1879). However, little is known about other aspects of their breeding biology (Webster 1992, Ochoa and Cuervo 1998, Jaramillo and Burke 1999). This information should serve as a basis for understanding the intrinsic biological traits involved in differential fates of populations to disturbance (i.e., to thrive or decline to local extinctions), and for informing conservation strategies. Our objective was to examine the breeding biology and behavior of Red-bellied Grackles in a suburban landscape in northwestern Colombia.

METHODS

Breeding groups of Red-bellied Grackles were observed at Alto San Miguel, along the upper

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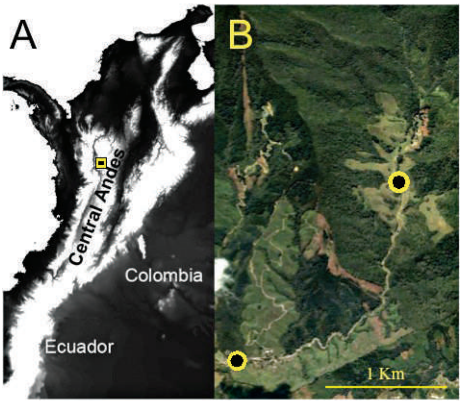

FIG. 1. (A) The Alto San Miguel in the northern central Andes, Department of Antioquia, Colombia (06° 02′ 05″ N, 75° 36′ 58″ W). (B) Aerial photograph depicting the end-points of our 2-km transect along the upper Medellín River at Alto San Miguel where seven groups of Red–bellied Grackles (*Hypopyrrhus pyrohypogaster*) were nesting co-operatively for at least 4 consecutive years (2006–2009).

watershed of the Medellín River in the northern central cordillera of the Andes, Department of Antioquia, Colombia (Fig. 1). The region is in the 'lower montane wet forest' life zone at an elevation of 1,800 to 2,100 m; the mean annual temperature and precipitation is 16 °C and 4,000 mm, respectively (Espinal 1992). The upper watershed of the Medellín River has a long history of human disturbance due to the influence of small urban settlements and conversion of forest to pastures for cattle ranching and for forest plantations. The current landscape is dominated by second growth, pastures with isolated trees, semi-open areas at different stages of succession, and *Eucalyptus* and pine (*Pinus patula*) plantations. Patches of native montane forest remain in the upper hills and the Alto San Miguel Nature Reserve. Red-bellied Grackles have been observed nesting at this location since at least 1999 (AMC, pers. obs.). We describe the nests and behaviors of seven groups observed along the river.

We followed individuals along a 2–km transect from January through July 2006–2009 along the Medellín River that exhibited nesting or parental behavior and searched for nests and nesting groups following Martin and Geupel (1993). We recorded nest stage (under construction, incubation, nestling, or inactive), the species of tree or shrub, and height for each nest. We measured nests whenever possible (inner and external diameters, depth, and height) after nestlings fledged or nests were depredated, and eggs (length, width, fresh mass at day 0); we weighed eggs every 2 days for one nest to estimate mass loss rate during incubation. We measured nestlings' body mass every day until they fledged, and estimated nestling growth rate following Martin et al. (2011) using the logistic growth curve based on the equation: $W(t) = A/(1 + e^{(-K^{*}(t-ti))})$, where $W(t)$ denotes body mass of a nestling at time t, A is the asymptotic mass that nestlings approach, t_i is the inflection point of the curve, and K is a constant scaling rate of growth (Ricklefs 1967, Ricklefs 1968, Remeš and Martin 2002). All measurements were taken on site with an accuracy of 0.05 g (FlipScale F2) for mass and 0.1 mm for external measurements with a caliper.

We monitored nests every 1 to 3 days during incubation, or until the last egg in the clutch hatched, and during the nestling period from clutch hatching until nestlings fledged. Every monitored nest was observed for 1 hr in the mornings within the 0900–1100 hrs period, and from distances ≥15 m. We recorded brooding behavior, nest attentiveness (proportion of time adults were on the nest over total time of observation), provisioning rate (food deliveries/hr), and type of food items (e.g., arthropods, fruits and flower parts, and small vertebrates) given to nestlings by direct observation. We estimated the proportion of eggs that hatched (hatching success) and the proportion of young that fledged (fledgling success) based on observations of 21 nests. We calculated daily survival rate and nesting success using the Mayfield estimator (Mayfield 1961), but used exposure days in incubation and nestling periods combined because we did not have information on the exact hatching day for a number of clutches. We assumed nestlings fledged successfully when nests were empty and fledglings remained in the group territory. We observed the first and subsequent hatchings of the clutch of two nests allowing us to ascertain if all eggs of the clutch hatched synchronously (within a 24-hr period).

Size, age, and gender (M/F) composition of each breeding group was based on counts of the number of adult and immature individuals. Adults were recognized by their scarlet bellies and shiny black plumage, and their bicolored irides (pale yellow with a bright red outer margin). First–year birds were recognized by their pale red belly, dull brownish-black plumage, and dark brown to grayish-yellow irides. Adults were classified as males or females in the field from behavioral differences and the larger size of males (135 vs. 97 g in body mass; AMC, unpubl. data); (~30 vs. 27 cm total length) (Hilty and Brown 1986). However, gender of first-year birds could not be identified in the field. We marked captured birds with two plastic color bands to identify individuals, one colored band to recognize breeding group and the other, individuals in the group. All fledglings from five nests were banded to examine if first–year birds act as helpers in the next breeding season and if they remain in natal groups. We used a general linear mixed model (GLMM) to examine the variation in clutch size as a function of group size where we specified group identity as a random-effect variable. We had 18 observations from six groups. We used the glmmPQL function implemented in the R package MASS to fit the GLMM (Venables and Ripley 2002). This function used pseudo- and penalized quasi-likelihood to estimate the parameters of the model (Bolker et al. 2009). Values are presented as means ± SD.

RESULTS

Most breeding events occurred from March to June ($n = 35$). All seven breeding groups located every year exhibited a cooperative breeding system. Groups varied in size from three to seven individuals in each breeding event (5 ± 1.3, $n = 27$), not including nestlings, and also varied by gender and age class composition (e.g., 1–2 adult males, 1–3 adult females, and 1–3 first–year birds or subadults). We observed two adult males (by size) in one breeding event; one was much more active vocalizing from a high perch and delivering vocalizations that have solely been observed for dominant males, suggesting primary and secondary males in that group. Individual colored bands placed on 13 nestlings in five nests indicated breeding groups raise the helpers of the following years, and that groups have high fidelity to breeding territories across years. Nine of 13 marked fledglings remained in their group and spatial territory for at least 2 consecutive years. We did not re-encounter the remaining four fledglings and they may have been depredated or dispersed to another area.

Nests.—We found 38 nests attended by seven groups. Nests averaged 4.6 ± 2.1 m above ground ($n = 34$), but four were at a height of 15 m. Most were on bifurcations of lateral branches of a variety of trees or tall shrubs of 11 species in Clusiaceae, Melastomataceae, Monimiaceae, Rutaceae, Solanaceae, and Tiliaceae. Introduced trees including *Eucalyptus camaldulesis* (Myrtaceae), *Pinus patula* (Pinaceae), and *Cupressus lusitanica* (Cupressaceae) were also used for nesting. Nests were in trees and tall shrubs at the edge of forest fragments ($n = 16$), or in isolated trees in pastures at a mean distance of 12.5 m (range = 5–81 m, $n = 22$) from the nearest forest edge. The mean distance of nests to the river edge was 13.8 m (range = 0–66 m, $n = 38$).

Nests of Red-bellied Grackles were ovoid open–cup structures of two layers of sticks and roots that had different diameters (internal layer = 0.5 ± 0.2 mm, $n = 85$ items; external layer: 1.0 ± 0.3 mm, $n = 75$ items; $n = 3$ nests). Nests were lined with dry leaves. There appeared to be little variation in materials used, although one group added an extra external layer of an epiphyte (*Tillandsia usneoides*, Bromeliaceae). Mean measurements were based on a subset of eight nests: inside cup depth = 77 ± 14 mm, outside cup depth = 155 ± 22 mm, inside opening = 103 ± 7 × 112 ± 8 mm, outside opening = 152 ± 15 × 182 ± 24 mm. We observed construction of only one nest, and this nest was completed between 4 and 8 days; we only observed one adult female building it. Nest materials were collected in the surrounding area (<100 m^2) by the female and other members of the group, which also supplied her with food. We did not quantify the rate of delivery of nest materials or food items to the female. The male did not participate actively in construction of this nest.

Eggs and Clutch Size.—Eggs were elliptical in shape and light blue in color with purplish brown spots and stripes that were denser towards the wider end (Fig. 2). Fresh egg mass averaged 7.0 ± 0.3 g ($n = 12$, from 4 nests), and their external measurements averaged 28.8 ± 1.0 mm × 21.0 ± 0.4 mm ($n = 35$, from 11 nests). Females laid one egg per day, and clutch size averaged 3.1 ± 0.5 (range = 2–4, from 21 nests). Breeding group size and clutch size were positively correlated (slope = 0.25 ± 0.09 (SE), $P = 0.03$).

Incubation Period.—Incubation periods lasted 16 ± 1 days (15, 15, 17 days, respectively; $n = 3$). Eggs lost up to 11.9% of their weight during this period at a rate of 0.07 ± 0.01 g per day ($R^2 = 0.92$, $n = 4$; Fig. 3). Nest attentiveness averaged 69 ± 18% during incubation of the total

FIG. 2. Nest, eggs, and hatchling of Red-bellied Grackles at Alto San Miguel. Photograph by M. Camila Estrada-F.

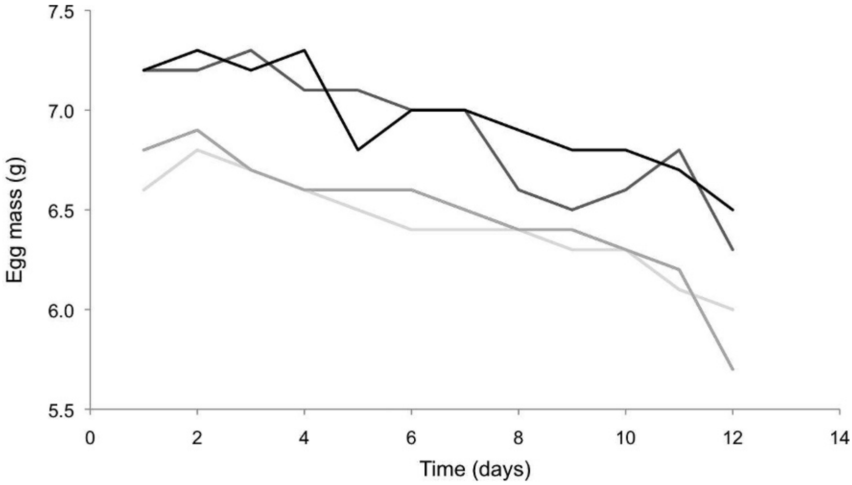

FIG. 3. Egg mass loss during the incubation period for four eggs in one nest of the Red-bellied Grackle. Lines connect daily weight loss values for each individual egg.

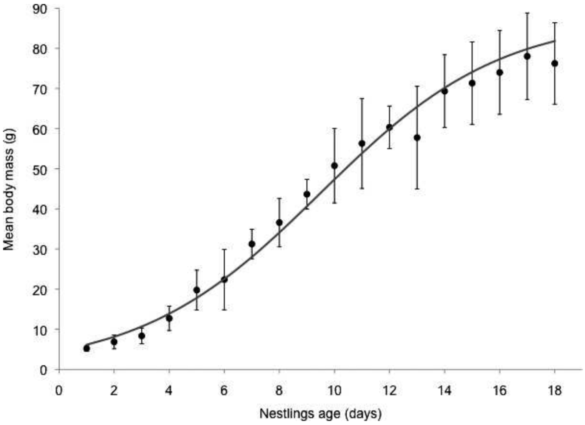

FIG. 4. Mean ± SD body mass of Red-bellied Grackle nestlings during development at the nest (n = 11, from 4 nests), the gray line shows the logistic growth curve ($R^2 = 0.98$) based on the equation $W(t) = A/(1 + e^{(-K*(t-ti))})$.

observation time for the three nests monitored from egg laying to hatching (37 hrs). The individual incubating the eggs was a female, which was fed an average of 1.9 ± 1.1 times/hr ($n = 3$ nests) by other members of the group during 41 hrs of observations (data from 12 of the 14 days of the incubation period). The incubating duties on the nest were alternated between females ($n = 3$ events), and were followed by a provisioning event. We directly observed all eggs hatch at two nests, both with a clutch size of four eggs and, in all cases, the entire clutch hatched within 24 hrs. Adult males did not participate in brooding but remained perched in the surrounding trees, often vocalizing.

Nestlings.—The nestling period was 17.3 ± 1.3 days ($n = 5$). Nestlings weighed 5.2 ± 0.7 g ($n = 5$, from 2 nests) at hatching. Nestlings had light orange skin, black downy feathers, white claws, a whitish bill with a darker tip, and a bright yellow gape (Fig. 2). Nestling growth rate (K) was 0.304 ($n = 11$ from 4 nests; Fig. 4). These 12 nestlings opened their eyes on the sixth or seventh day. The eyes were dark brown, and the bill was black at this point. Nestlings were covered by a dull black plumage by day 15 except in the naked area around the eyes, and on the lower breast and belly where the feathers were reddish orange. Nestlings were active at that age and able to exercise their wings and perch by themselves. Nestlings fledged when 16 to 18 days of age with a mean mass of 76.3 ± 10.1 g ($n = 4$ from 2 nests). Their flight ability was limited, the tail was <50% of full length, and flight feathers were still growing. Fledglings continued to be fed by members of the group.

Eight fledglings were still fed by the group 2 weeks after leaving nests, their tails were still growing, and their overall plumage was brownish black with orange or dull red bellies. Ten fledglings ~6 weeks of age were able to forage more or less independently along with the group and were clearly distinguishable from older birds. Six juveniles still had dull plumages after 12 months but they had dark–yellow irides, were similar in size to subadults and females, and started to participate as helpers in the group (observations from 4 breeding groups). Individuals ($n = 4$) at 22 months of age, and probably after completing a second molt, had bicolored irides and reached the plumage brightness and coloration of adults, and continued to serve as helpers in their group.

The brooding adult remained the first 5 days of the nestling period at the nest ($n = 3$; Fig. 5) and was fed by helpers, during which time the provisioning rate of the nestlings averaged 15.8 visits/hr (55 hrs of observation; Fig. 5). Some food was delivered by regurgitation ($n = 47$; 3 groups) but, after the fifth day, it was progressively passed from helpers to nestlings as parts or whole items. Helpers occasionally passed food items to the brooding individual at the nest that in turn delivered food to nestlings. Provisioning of young decreased gradually within the last few days of the nestling period (Fig. 5). We identified 450 prey items during 95 hrs of observations at three nests. The nestlings' diet consisted mainly of arthropods (72%, $n = 353$), fruits and flower parts of melastome (*Tibouchina lepidota*, 9.4%, $n = 44$), and small vertebrates (3 unidentified frogs, and 4 *Anolis mariarum* lizards). Provisioning was

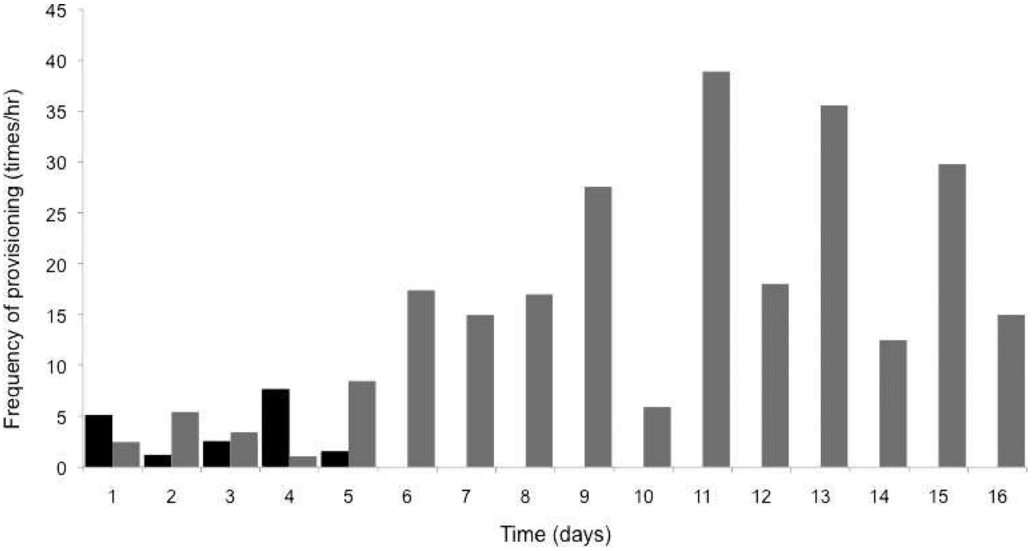

FIG. 5. Nest attentiveness of helpers during the nestling period of the Red-bellied Grackle depicted as the hourly provisioning frequency to nestlings (gray) and to brooding frequency (black). Data are from two breeding events.

mostly by immature helpers and females (94%) and less by adult males (6%), based on 627 visits at three nests.

Fledgling Survival.—The daily survival rate was 0.97 and nesting success was 0.39 ($n = 24$ nests), hatching success was 92%, and 86% of these nests were depredated during the nestling period. The cumulative fledgling survival over four breeding seasons (2006–2009) was 29%, corresponding to 19 fledglings (from 8 nests) from 65 eggs laid (21 total nests) that ultimately integrated into their family groups. Nests were also lost to harsh environmental events such as heavy rainstorms or to unknown factors. All groups that lost their nest reinitiated breeding during the same season, and there were three double-brooding events in 2010 (unpubl. data).

DISCUSSION

Red-bellied Grackles exhibited a cooperative breeding system with juveniles staying in natal territories and assisting with subsequent breeding efforts of their family group. Nest construction, brooding, and nestling care was mostly by females and young helpers, while adult males remained in the territory often vocalizing, which we interpret as involved in social cohesion and defense. Cooperative breeding at Alto San Miguel is consistent with previous casual encounters with nesting groups of Red-bellied Grackles not only at this study site, but elsewhere across its disjunct, restricted range where nests were also attended by three or more individuals (Ochoa and Cuervo 1998, Cuervo 2002; J. J. León and S. Vargas Troncoso, pers. comm.). We demonstrated by color-banding juveniles, that they become helpers at the nest (Skutch 1935) of their own family group in subsequent years. However, behavioral and genetic studies are needed to understand juvenile dispersal and kin structure in this population. Family groups in the disturbed landscape of Alto San Miguel were cohesive throughout the year, but this may not be the case in populations from less disturbed habitats where large flocks are observed outside the breeding season (AMC, pers. obs.). Unknown social interactions and the ecological conditions of undisturbed habitats could be involved in fusion and division of groups during non–breeding and breeding seasons, respectively.

The breeding activity of Red-bellied Grackles in our study area was concentrated between March and June, which agrees with previous anecdotal information of breeding in this species (Hilty and Brown 1986, Ochoa and Cuervo 1998, Jaramillo and Burke 1999). We did not detect any indication of breeding during four visits to the same transect from August to December.

The nests and eggs of the Red-bellied Grackle described here match the illustrations and descriptions by Sclater and Salvin (1879) and Ochoa and Cuervo (1998), although we found one group that consistently built its nests with an outer layer of an epiphyte. The closest relatives of the Red-bellied Grackle are the Oriole Blackbird (*Gymnomystax mexicanus*) and the Velvet-fronted Grackle (*Lampropsar tanagrinus*) (Cadena et al. 2004, Eaton 2006). The bulky cup nest of the Red–bellied Grackle is more similar to the nest of the Oriole Blackbird (Jaramillo and Burke 1999) but not to the hanging basket nest of the Velvet-fronted Grackle (Maillard and Herrera 2007). Egg coloration (but not size) is similar among the three species, all having pale blue or greenish eggs with dark brown or purplish spots (Skutch 1967, Maillard and Herrera 2007).

Cooperative breeding likely evolved independently in the Icteridae, but is most pervasive in South American species of grackles (Orians et al. 1977, Jaramillo and Burke 1999, Fraga 2008). The Oriole Blackbird, among Red-bellied Grackle relatives, is a solitary breeder (Jaramillo and Burke 1999) and the Velvet-fronted Grackle has apparently been observed breeding cooperatively (J. A. Tobias cited by Fraga 2008), but published information is inconclusive (Jaramillo and Burke 1999, Maillard and Herrera 2007). The scarcity of breeding ecology data and missing taxa in the phylogeny of the Icteridae make unclear if occurrence of cooperative breeding in the Red-bellied Grackle is phylogenetically or ecologically constrained. Observation of solitary breeding individuals of Red-bellied Grackles (Hilty and Brown 1986) reported prior to our study, if true, would imply either plasticity or temporal or geographic variation in breeding strategies. We suspect those reports resulted from incomplete observations. Recently, helpers attending a nest of Red-bellied Grackles have been observed in Huila in the southern part of its range (J. J. León and S. Vargas Troncoso, pers. comm.).

Nest attentiveness across the incubation period was variable, similar to that reported for other neotropical montane birds (Martin et al. 2007). The weight loss of eggs during incubation (11.9%) is surprisingly small in comparison to the ~18% loss documented for 475 species (Rahn and Ar 1974) or the known estimates for other neotropical birds (e.g., Greeney 2006). Hatching in our study was roughly synchronous (i.e., all eggs hatched within 24 hrs irrespective of their laying time) in two cases, contrary to the asynchronous hatch reported by Ochoa and Cuervo (1998), who inferred the presence of nestlings from observations of adults carrying food to the nest. However, feeding the incubating individual in the nest is rather common and could be mistaken for provisioning of young.

We do not know if eggs of a single clutch were laid by one or more females, or the extent of extra–group matings. Nestling development (i.e., during incubation) ranged from 16 to 18 days, similar to other neotropical icterids of similar size (Skutch 1996, Jaramillo and Burke 1999). Nestling growth rate was slightly lower than in other neotropical birds of similar nestling period length (~0.33; Martin et al. 2011). This comparatively lower growth rate for Red-bellied Grackles may be due to the overall smaller body size of species included in that analysis as slower growth is expected for larger species of comparable nestling duration (Case 1978, Starck and Ricklefs 1998).

Juveniles in at least two groups stayed up to 3 years in their natal territory and delayed dispersal to help their group in provisioning nestlings. There are a number of ecological and fitness benefits of delayed dispersal in juveniles. We recorded the first breeding attempt of a 5 year-old female, banded as a nestling in 2006 during more recent observations (2010–2011, unpubl. data). It is possible that sexual maturation of Red-bellied Grackles is achieved after several years. We have not found any individual banded as young that have reached the size of dominant adult males. All fledglings captured during the first years of the study exhibited a size similar to that of adult females. Thus, it is difficult to ascertain whether there is a pattern in failure to disperse with respect to gender of fledglings.

It remains to be confirmed if breeding is concentrated along the relatively short stretch of habitat along the river watershed, where a maximum of seven groups was breeding at any given time. Group territories were maintained year after year (unpubl. data); juveniles, by remaining with their group, could eventually occupy their natal territory as their reproductive territory in following generations.

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