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Reproductive Biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*)

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ABSTRACT.—We provide a detailed report on the reproductive biology of the Red-ruffed Fruitcrow (*Pyroderus scutatus granadensis*). Eight nests were found between 2003 and 2007 in tropical montane cloud forest in Yacambu National Park, Lara, Venezuela. All nests were near streams in steep drainages. Nests consisted of twigs arranged in a cupped platform. Clutch size was a single egg and the average incubation period (n = 3) was 22.3 days. Nest attentiveness during incubation averaged [± SE] 76.3 ± 1.86% and increased only slightly across stages (early, middle, late). On-bout and off-bout durations were relatively similar across incubation stages. A nestling period of 35 days was recorded for one nest and feather pin-break was estimated to occur at day 19. Brooding attentiveness during the early nestling period averaged 62.5 ± 6.41%, and the adult ceased brooding at about feather pin-break. Food delivery rates increased with nestling age. Food provisioning consisted mostly of insects (66.7%) and lizards (25%) with fruit comprising only 8.3% of the nestling diet at early stages. Provisioning changed to mostly fruit (82.4%) and some insects (17.6%) in late stages of the nestling period. *Received 16 January 2007. Accepted 31 January 2008.*

The reproductive biology of endemic tropical birds is poorly known. Information on the life history of the Red-ruffed Fruitcrow (*Pyroderus scutatus*), despite having a broad neotropical distribution, is symptomatic of the poor knowledge of tropical endemics. *P. scutatus* is a locally rare and uncommon bird of the Cotinga family, a diverse family of passerines restricted to the Neotropics. Red-ruffed Fruitcrows are predominately frugivorous and inhabit mountainous regions of Venezuela, Colombia, Brazil, Paraguay, Peru, Ecuador, and Argentina. Most records and species accounts for *P. scutatus* are from Brazil and Colombia (Serrano 1994, Pizo et al. 2002). *Pyroderus scutatus granadensis* occurs in the Coastal Cordillera and lower Andean regions of Venezuela where it inhabits wet, humid, old growth forests (Hilty 2003). No comprehensive descriptions of the breeding biology of *P. scutatus granadensis* exist.

The Red-ruffed Fruitcrow is among the largest (300–390 g) passerines in the world (Snow 1982, Hilty 2003) and is considered rare within its range (Stotz et al. 1996). Consequently, life history data are essential for development of conservation strategies that may protect this species. The objectives of this paper are to describe aspects of the breeding biology of *P.scutatus* for the first time, and to discuss food provisioning during the nestling period. All data are from montane, wet, primary forest at Yacambu National Park, Lara State, Venezuela (09° 24′ N, 69° 30′ W; 1,750–2,000 m elevation). Data were collected from March through June 2002 through 2006.

OBSERVATIONS

Nest Locations and Descriptions.—We found eight nests of *P. scutatus granadensis* in tall forest areas of steep-sided river valleys and adjacent ridgelines within primary forest

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(canopy height = ~35 m). Nests were found by thoroughly searching throughout the forest or by following adults to the nest site. The eight nests were all on the edge of streams. This is congruent with the description of three lek sites and six nest sites in a river drainage with steep-sided valleys at Ucumari National Park, Colombia (Serrano 1994). Our study sites ranged in elevation from 1,400 to 2,000 m. Red-ruffed Fruitcrows were observed and nests located in higher elevation plots (1,650–1,850 m). Seven of the eight nests that we found occurred within an area of ~6 ha in a major river drainage; the same general area was used for nesting among years. The earliest nest building behavior was observed on 27 March and the last was on 26 May. Most breeding activity appeared to occur during April, May, and June.

Nest heights were visually estimated between 3.5 and 11 m in mid-canopy trees (5–14 m in height). Three nests were in trees (*Solanum* spp.), one was in a tree fern (Cyatheaceae), and the remainder were in unknown tree species. Nests in *Solanum* spp. were placed in horizontal, forked, mossy branches in positions where leaves provided substantial cover for the nest.

Nests were large, untidy structures consisting of leafless twigs forming a shallow cup. On one occasion an individual brought sticks to the nest while another adult observed the nest from nearby. All other observations of nest building efforts were of solitary individuals. We prepared a detailed description of one nest. The nest was circular to elliptical in shape with an external diameter of 21.5–22.5 cm and an inner diameter of 14.8–15.6 cm. It was close to the trunk of the tree and supported by one main branch with a few large sticks spanning the gap to other branches. The main branch had a diameter of 3.0 cm. The nest was composed of two types of sticks. The outer part of the nest was composed of ~45 large, dark brown, dead sticks arranged to form a platform; the sticks were 30–60 cm long and averaged 4–5 mm in diameter. Some sticks had lichen, moss, or black rootlets growing on them. The inner sticks were light reddish-brown and flexible. The longest pieces were 25 cm in length, but most were ~10 cm with a diameter of 1–1.5 mm. The flexible sticks were woven to form a distinct cup placed on and woven into the large stick platform. The cup was tightly woven and more dense on the side closest to the tree trunk; it was not possible to see through it. The other side was more loosely woven. Nests measured in Colombia had an external diameter of 37.0 ± 7.5 cm and were lined with leaves (Serrano 1994, Snow 2004). The nest that we measured differed in external diameter and had no inner lining of leaf litter.

Clutch Size and Nest Success.—Each active nest had one egg. Six of eight nests were depredated; four during incubation and two during the nestling stage. One nestling fledged from one nest and the other nest was still active with a 20-day old nestling when we stopped monitoring at the end of June. Overall daily mortality (±SE) rate at these eight nests calculated using the Mayfield method was 0.032 ± 0.013 (exposure days = 190) (Hensler and Nichols 1981).

Laying and Incubation Behavior.—Red-ruffed Fruitcrows delayed laying eggs following nest completion; the time between nest completion and laying was 8 days at one nest checked daily and 6–8 days at two other nests. We measured incubation periods as the number of days between the last egg laid and last egg hatched (Briskie and Sealy 1990) based on visual inspection of nests. One of three nests where both laying and hatching were observed had an incubation period of 21 ± 1 day and two had an incubation period of 23 ± 1 day each.

Nest attentiveness (percent time spent on the nest incubating eggs) during incubation was measured by video-taping nests at early (day 1 to 3 of the incubation period), middle (day 8 to 13 of the incubation period), and late (day 17–22 of the incubation period) stages. The camera ran for 6–8 hrs and started within 1 hr of sunrise (Ghalambor and Martin 2001, Martin 2002). Only the female incubated, as males were not recorded attending the nest. Nest attentiveness remained similar across stages with a slight increase through incubation (Fig. 1A). Nest attentiveness averaged 76.3 ± 1.86% (n = 13) across all nests and stages. Duration of incubation on-bouts was similar across stages of the incubation period and averaged 60.0 ± 5.51 min (n = 13) across all nests and periods (Fig. 1B). Off-bout duration also was similar among periods (Fig.

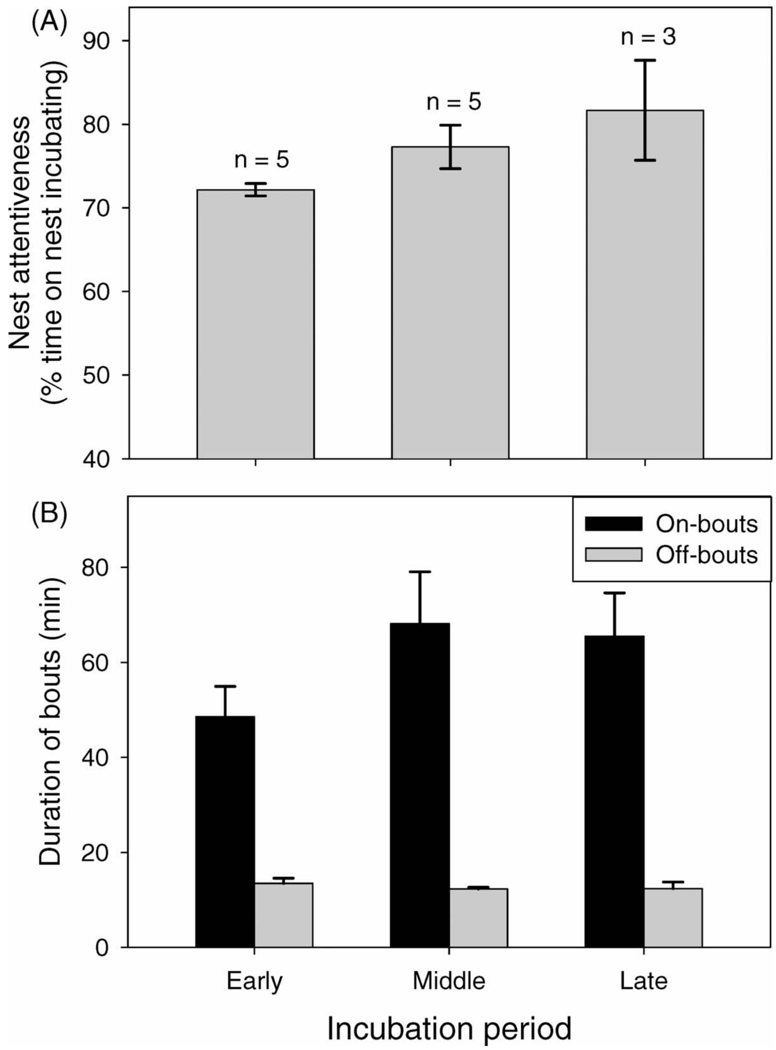

FIG. 1. Behaviors during early (day 1–3), middle (day 8–13), and late (day 17–22) stages of the incubation period for the Red-ruffed Fruitcrow: (A) nest attentiveness and (B) duration of on and off-bouts. Sample sizes (n) represent numbers of nests sampled and error-bars represent ± SE.

1B) and averaged 13.4 ± 0.59 min (n = 13) across all nests and periods.

Nestling Development.—Nestling development was documented by video taping a single nest in 2004. The nestling remained covered in thin feathery yellow-orange down from day 2 through day 15. Black feathers first developed on the wings, and pin feathers broke their sheaths about day 19 (±1 day) of the nestling period. The nestling had lost almost all of the down by day 21 and was standing and flapping in the nest. Only residual down remained on the eyebrow region by day 24 and the nestling had a well developed bill. The nestling at day 31 had adult-like black plumage and was about three quarters the size of the adult; the 'Red Ruff' throat plumage that is most distinctive in adults was extremely faint and almost non existent in the nestling at this stage. Serrano (1994) noted the 'Red Ruff' does not develop until the fledgling is 2 months of age. Video analysis indicated the nestling did not appear to vocalize and begging displays were infrequent and subdued. Serrano (1994) reported a soft 'mooing' vocalization between adult and nestling. We fol-

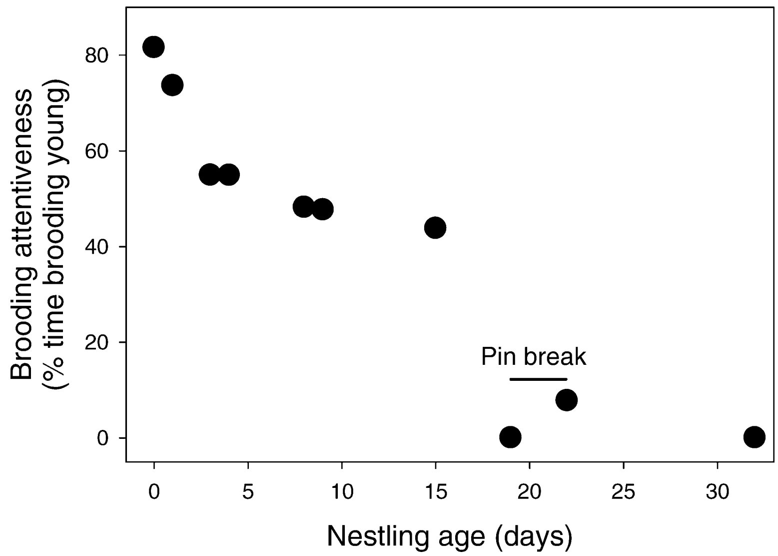

FIG. 2. Brooding attentiveness of the Red-ruffed Fruitcrow as a function of age of the nestling based on repeated video observations at two nests.

lowed one nest through to fledging with a nestling period of 35 days.

Brooding attentiveness (percent time spent brooding the nestling) during the nestling period was recorded by video-taping two nests starting on day 0 (hatching) and repeated once a week for 6–8 hrs per recording event. Brooding attentiveness decreased with age of the nestling and appeared to stop about the time of feather pin-break (Fig. 2). Adults provisioned nestlings an average of 0.18 ± 0.42 times/hr with little variation by age, varying from 0.14 to 0.22 visits/hr across stages.

Nestling Diet.—Food items brought by parents for nestlings were identified by viewing videos in two nests filmed at early (day 0–16), middle (day 17–22), and late (day 23–35) nestling stages. The diets of both nestlings were combined to characterize food type (Fig. 3). Food type was recorded if it was positively identifiable and was used to estimate the relative abundance of foods brought to nestlings at different ages. The incidence of fruit in the nestling's diet increased strongly from early to middle to late nestling stages (Fig. 3). Correspondingly, the incidence of insects in the nestling's diet decreased from early to late in the nestling stages (Fig. 3).

DISCUSSION

Male Red-ruffed Fruitcrows form communal leks (Hilty 2003) and do not help with parental care at any stage, leaving females to raise the young alone. Many species with female-only nest care are frugivorous or nectivorous (Beehler 1986, Cockburn 2006). A coevolutionary interaction between food plant and avian disperser has been proposed by Snow (1976) to be a causal factor influencing male emancipation from nesting duties (Beehler 1986, Cockburn 2006). Snow (1976) uses the Cotingas as exemplary subjects because the female appears to rear the nestling on lipid rich lauraceous fruits unassisted by the male. However fruit may not provide sufficient protein to allow rapid growth (Morton 1973). Data presented here and by Serrano (1994) indicate Fruitcrow nestlings do not have a significant fruit diet until late in the nestling period. Serrano (1994) reported that nestlings were fed only insects until day 10 of the nestling period and only fruit thereafter. In our study, insects were part of the nestling's diet throughout the nestling period in decreasing amounts with nestling age. The high protein diet of *P. scutatus* nestlings does not yield rapid growth but may be essential for development. Brietwisch et al. (1984) reported that nestling frugivory only becomes profitable as nestlings develop endothermy. *P. scutatus* adults may feed nestlings an optimal mixture of animal protein for growth, and fruit car-

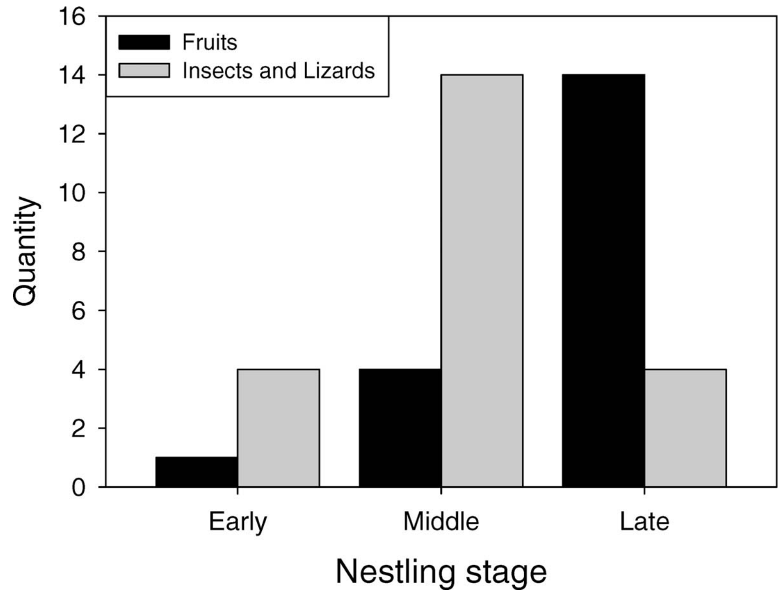

FIG. 3. Foods provided to Red-ruffed Fruitcrow nestlings during early (day 0–16), middle (day 17–22), and late (day 23–35) stages of the nestling period. Two nests were sampled in each period.

bohydrates for other energetic needs, despite adults being almost solely frugivorous. Extremely low provisioning rates may prolong the nestling period but may also reduce risk of nest predation (Skutch 1949). Development rate of nestlings may represent a compromise among energy delivery, physiological trade-offs, and predation risk.

The Red-ruffed Fruitcrow is a rare neotropical endemic and it is essential that its ecological requirements and reproductive biology be better understood. Further study into the life history and habitat requirements of the Red-ruffed Fruitcrow is clearly needed.

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