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OBSERVATIONS ON THE BREEDING BIOLOGY OF BRONZY INCA (*COELIGENA COELIGENA*) IN NORTHEASTERN ECUADOR

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Resumen. – Observaciones sobre la reproducción de la Inca bronceado (*Coeligena coeligena*) en el noreste de Ecuador. – Observamos un nido del Inca Bronceado (*Coeligena coeligena*) encontrado durante el periodo de pichones, a una altitud de 2050 m s.n.m., 5 km al oeste de Cosanga (provincia de Napo), Ecuador. El nido estaba ubicado a 1,2 m sobre el suelo, en la Y de un árbol pequeño de bosque primario. La puesta fue de dos huevos, completada cerca del 15 Noviembre 2007. Describimos el comportamiento del adulto y el cuidado parental durante 15 días de observaciones, comenzando un día después del nacimiento, y culminando cuando ambos pichones volaron del nido, 22 días después de la eclosión de ambos huevos en el mismo día. La frecuencia de alimentaciones a los pichones por hora fue 1,1 a 2,0. Las alimentaciones se distribuyeron equitativamente durante el día. El número de alimentaciones por hora no cambió significativamente durante nuestras observaciones. El promedio (del promedio diario) de la duración entre visitas fue 40,2 ± 7,19 min. La hembra permaneció en el nido 9–55 s (promedio de promedios diarios = 28,4 ± 6,83 s) por visita. La duración de visitas disminuyó significativamente con la edad de los pichones. Pichones de 1–3 días de edad fueron empollados > 50% del día, pero después de 5 días de edad, el empollamiento fue significativamente menor. Encontramos una relación significativamente negativa entre la edad de los pichones y el porcentaje diario de empollamiento.

Abstract. – We observed care of two nestlings of the Bronzy Inca (*Coeligena coeligena*), at an altitude of 2050 m, 5 km west from Cosanga (Napo Province) in Ecuador. The nest was built 1.2 m up in the vertical fork of a small sapling inside mature forest. The clutch (two eggs) was completed around 15 November 2007. We describe adult behavior and parental care during 15 days of observations began the day after hatching and ended upon fledging, 22 days after both eggs hatched synchronously. Daily feeding rates ranged from 1.1 to 2.0 visits per hour. Provisioning visits were rather evenly distributed during the day. The number of feeding visits/h did not change significantly with nestling age, and the mean (of daily means) interval between visits was 40.2 ± 7.19 min. The female spent 9–55 s (mean of daily means = 28.4 ± 6.83 s) per visit feeding. Average feeding durations became significantly shorter with nestling age. One to three-day-old nestlings were brooded during > 50% of the day and, after day 5, brooding diminished sharply. There was a significant negative correlation between nestling age and time devoted to brooding. *Accepted 23 August 2008*.

Key words: Nest, eggs, hatching, nestling provisioning, Bronzy Inca, *Coeligena coeligena*, Ecuador.

Bronzy Inca (*Coeligena coeligena*) is a widespread Andean hummingbird (Züchner 1999, BirdLife International 2004), one of 12 species in the genus (Schuchmann 1999). This

common species inhabits cloud forests or open terrain at 1400–2600 m from Venezuela to Bolivia (Hilty & Brown 1986, Züchner 1999, Ridgely & Greenfield 2001, Hilty 2003). It is generally found inside mature cloud forest but also locally in clearings open terrain with scattered trees (Züchner 1999, Ridgely & Greenfield 2001). In Ecuador, this species occurs only east of the Andes, with Ecuadorian birds assigned to the subspecies *obscura* by some authors (Zimmer 1951, Ridgely & Greenfield 2001), and *columbiana* by others (Züchner 1999). The breeding biology of Bronzy Inca is poorly studied. Schuchmann (1977, 1989) describes one nest (ssp. *ferruginea*) from Mares, 19 km west of Cali, South Colombia, at 2000 m altitude), and provides details of nestling development. A few additional data concerning foraging and social communication are also given in Schuchmann (1975) and short nest description in Ridgely & Gaulin (1980).

MATERIALS & METHODS

All observations of Bronzy Inca were carried out, at altitudes ranging from 1950 to 2200 m, in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (00º35'S, 77º53'W) 5 km west of Cosanga (Napo Province, northeastern Ecuador). For a more complete site description, see Greeney *et al.* (2006). Feeding observations were made opportunistically, and thus likely do not properly represent this species flower preferences. On 27 November 2007, Oscar G. Manzaba B. showed us a nest of Bronzy Inca containing two eggs. We began observations on 2 December, when nestlings were 1-day old, and ended on 23 December, when both 22-day old nestlings successfully left the nest. We gathered direct observational data by watching the nest from a concealed position, c. 10 m from the nest, using 10 x 40 binoculars. Data were collected on 15 days, with observation periods per day ranging from 3 (5 days) to 6 h (6 days; two 3-h sessions per day). On 4 days the observation time was 3.5–5 h. Mean observation time across all observations was 4.7 h (SD = 1.347). We began observations soon after sunrise (3 h) and continued them in the afternoon for the final 3 h of daylight (18:15 h, EST). Across the entire period, we watched the nest for 70.5 h. Using a stopwatch, at each arrival of the female we recorded the amount of time spent feeding nestlings (bill in contact with that of the nestlings) and the total amount of time the female perched on the rim of the nest. Significance values were calculated using Spearman's Rank Correlation tests (r_s).

RESULTS

Nest. The nest was 1.2 m up in the vertical fork of a 1.9 m tall *Nectandra* (Lauraceae) sapling, on a steep bank c. 1.5 m from a 1.5 m wide stream in mature forest. The supporting sapling was 8 mm in diameter just below where it forked, with the supporting arms of the Y measuring 6.5 and 3 mm in diameter. The nest was a tightly compacted cup of soft, light brown seed down and tree-fern ramenta, bound together with spider webs. The exterior of the cup was heavily decorated with long strands of pale green moss which, along with spider webs, bound the nest to the sapling. Externally, the nest was 62 mm wide, and 77 mm tall, with a 190 mm tail of moss hanging below. Inside, the egg cup was 34 mm wide and 29 mm deep.

Eggs. Both eggs were immaculate white. They measured 14.9 x 9.8 mm (0.69 g) and 14.8 x 10.1 mm (0.70 g). As both eggs hatched on 1 December, and the incubation period is 15–16 days (Züchner 1999), we estimate the clutch was completed around 15 November.

Nestling provisioning and adult behavior. Before

TABLE 1. Length of female feeding visits in the nest of the Bronzy Inca with two nestlings.

Nestling age (days)	Time in seconds (medians)	No. of records
2	28	4
3	26	12
5	37.5	4
6	44	7
8	28	9
10	26	9
12	27	9
14	25.5	10
15	31.5	6
16	31	4
18	25	4
19	18	3
21	22	5
22	16.5	6

landing on the nest, the female hovered 2–3 times in different places close to the nest, zigzagging rapidly between locations. During every visit with food, she sat on the rim of nest, fed both nestlings one after the other. She fed by inserting her bill into the mouth of the gaping nestling and regurgitating. After leaving the nest she usually sat briefly (2–217 s) on one of two preferred perches (c. 2 and 3 m) from the nest, and preened her plumage. Perches were nearly horizontal, slender twigs, in relatively open area of the understory (c. 2 and 3.5 m up, respectively). The female spent 9–55 s (mean of daily means = 28.4 s ± 6.83) per visit feeding. Average feeding durations became significantly shorter with nestling age ($r_s = -0.654$, n = 14, $P = 0.019$) (Table 1).

Provisioning visits were rather evenly distributed during the day (Fig. 1). On 7 of 15 observation days, the distribution of visits during the day was regular, and in remaining days it was random, but the distribution of visits was never clumped (Index of dispersion; Fowler *et al.* 1998).

In comparison to many small Passerines (see Discussion), the rate of nestling provisioning in Bronzy Inca was low. Daily feeding

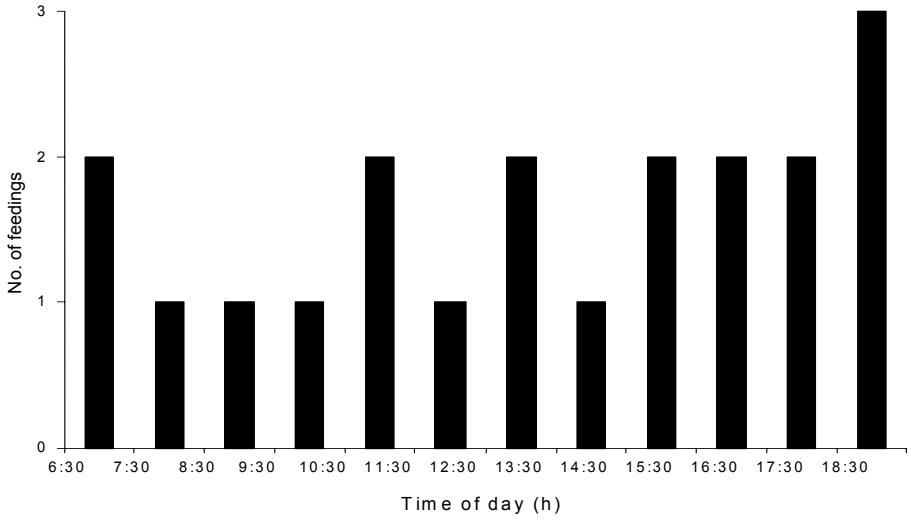

FIG. 1. Daily pattern (sum of three days) of provisioning rates at a nest of the Bronzy Inca (*Coeligena coeligena*) containing two nestlings 1–3 days old.

TABLE 2. Pattern of provisioning rates in the nest of the Bronzy Inca.

Nestlings age (days)	No. of visits	No. of hours (observed)	Visits/h
1	8	6	1.3
2	4	3.5	1.1
3	15	8	1.9
5	6	5	1.2
6	8	6	1.3
8	9	6	1.5
10	10	6	1.7
12	9	6	1.5
14	11	6.5	1.7
15	6	4.5	1.3
16	4	3	1.3
18	5	4	1.2
19	4	3	1.3
21	5	3	1.7
22	6	3	2.0

TABLE 3. Time devoted to brooding for nestlings 1-8 days old in the Bronzy Inca.

Age of nestling (days)	No. of observation hours	Brooding time (%)
1	6	56.1
2	3.5	53.8
3	8	42.9
5	5	27.7
6	6	2.0
8	6	0.0

rates ranged from 1.1 to 2.0 feedings/h (Table 2). Note that, as in most hummingbirds (e.g., Skutch 1931, DuBois 1938, Wagner 1945, Haverschmidt 1952, Skutch 1961), both nestlings are fed on every visit so this rate is equivalent to rates reported as feeds per nestling/h. Surprisingly, the number of feeding visits/h did not change significantly with nestling age (r_s = 0.299, n = 15, P = 0.234).

Intervals between feeding visits ranged from 8 to 95 min, and mean of daily means was 40.2 ± 7.19 min, and there was a slightly significant, negative correlation between nestling age and the duration of between-feed intervals (r_s = – 497, n = 15 days, P = 0.063).

Brooding. One-two day old nestlings were brooded during > 50% of the observation periods. After 5 days of age, brooding diminished sharply (Table 3). There was a significant negative correlation between nestling age and percent of observation time devoted to brooding (r_s = – 0.991, n = 6, P = 0.017). Brooding bouts of 1-day old nestlings lasted 4–30 min (mean = 11.0 ± 6.37, n = 17), and periods of absence ranged from 3–16 min (mean = 8.4 ± 3.67, n = 17). Nestlings of the following ages were brooded and unattended for the following ranges of and mean durations of, respectively. For nestlings 2-day old, periods on the nest were 5–14 min (mean = 9.1 ± 3.24, n = 11), and periods off were 4–13 min (mean = 8.4 ± 2.66, n = 11). For nestlings 3-day old, on bouts lasted 3–15 min (mean = 8.1 ± 3.02, n = 23), and off periods lasted 2–34 min (mean = 11.9 ± 7.72, n = 22). For the later case there was a significant difference between length of attentive and inattentive periods (t = 2.13, df = 43, P = 0.039). For nestling 4-days old, on bouts lasted 4–12 min (mean = 7.9, ± 2.98, n = 11), and off periods lasted 2–34 min (mean = 20.5, ± 10.79, n = 10); difference between length of attentive and inattentive periods was significant (t = 3.53, df = 19, P = 0.002).

As we observed the female brooding 3-day old nestlings for at least an hour after sunset, at which point it was completely dark, it is likely she spent the entire night on the nest. She spent the night on the nest until the nestlings were at least 5-day old. When we checked the nest 1.5 h after sunset when the nestlings were 17 days old, however, we found no female on the nest.

Nestlings. At 1–3 days of age, the nestlings remained coiled onto one another at the bottom of nest. Young nestlings were dark skinned, with pink bellies and pale yellow bills. They had 2 rows of 10 pale beige mesoptiles. Two-day old nestlings weighed 1.17 and 1.23 g. By 6 days of age nestlings weighed 4.15 and 4.57 g. Older than 6 days nestlings sat in the nest side by side. We observed nestlings to be able to lift their heads above the nest rim for the first time at the age of 10 days. At the age of 12 days, both nestlings were visible above the rim even with their heads lowered, and at the age of 18 days, their entire heads were visible. Nineteen-day old nestlings showed begging behavior similar to passerines (Dyrcz pers. observ.), with their orange gapes visible at a distance. At the age of 21 days (one day before leaving the nest) we first observed the nestlings preening their plumage with semi-open wings, and also scratching their heads. On this same day, both nestlings began to exercise, vigorously flapping with their wings. Both nestlings left the nest around noon, 22 days after hatching.

Adult nectar sources. We made 8 observations of Bronzy Incas foraging. We recorded them feeding on *Guzmania* (Bromeliaceae, n = 3), *Cavendeshia* (n = 1), *Psamisia* (Ericaceae, n = 1), *Elleanthus* (Orchidaceae, n = 1), *Alloplectus weirii* (Gesneriaceae, n = 1), and once on cultivated *Impatiens* (Balsaminaceae).

DISCUSSION

The nest and its location described here (ssp. *obscura*) was very similar to that described by Schuchmann (1977; ssp. *ferruginea*). Similarly, most of the details of Bronzy Inca's breeding biology conform to those of other hummingbirds. For example, the female's erratic zigzag maneuvers when approaching the nest, have been described for other hummingbirds (DuBois 1938, Skutch 1958), and likely serve to distract predators from the true location of the nest (Schuchmann 1999).

We feel it is likely that the reduction in the duration of feeding visits, as the nestlings aged, may be a result of more efficient (probably faster) food swallowing by older nestlings. This would be beneficial, as shorter visits to nest (because of reduced feeding time) likely result in lowered chances of predation. The rate at which Bronzy Inca provisioned nestlings (1.1–2.0 times/h) is typical for hummingbirds, which generally feed at rates < 2.5 times/h (DuBois 1938, Skutch 1961, 1964, Schuchmann 1986, Wolf & Wolf 1971, Oniki & Antunes 1998; but see Baltosser 1996, Fierro-Calderón & Martin 2007), but low in comparison with passerines. According to Gill (1990) normal rates of food delivery by small and medium-sized landbirds average 4 to 12 times per hour. Recorded extremes in small insectivorous birds such as the Great Tit (*Parus major*) are 60 feeding visits per hour, and 33 visits per hour in the case of the Pied Flycatcher (*Ficedula hypoleuca*) (Welty & Baptista 1988). In general, parents that regurgitate feed far less frequently than those that bring food in the bill (Skutch 1976). Like other species that regurgitate (i.e., Columbiformes), these differences likely reflect the fact that Bronzy Incas and other hummingbirds bring more food during each visit, than most passerines. It may, however, reflect the female hummingbirds' high metabolism, and thus the need for more foraging for self-nourishment, which results in longer periods of absence from the nest. While data are scarce, it appears that, like Bronzy Inca, feeding rates in most hummingbirds do not significantly change with nestling age (e.g., Skutch 1961, 1964; Fierro-Calderón & Martin 2007).

According to our observations, after nestlings are 5-day old, brooding diminishes sharply. This is rather early in comparison to other hummingbirds (e.g., Orr 1939, Skutch 1961, Fierro-Calderón & Martin

2007). Schuchmann (1999) mentions that most species show this decline in brooding around 7–12 days after hatching, and his summary included at least 3 species breeding at the same or lower elevations than Bronzy Inca.

Interestingly, while most of the above observations point to the uniformity of breeding behavior within the Trochilidae, synchrony of hatching is one character which does seem to vary between species. Bronzy Inca eggs both hatched on the same day, and we observed very little difference in weight between the two nestlings. Most species of hummingbirds, however, appear to hatch asynchronously (e.g., Wagner 1945, Haverschmidt 1952, Skutch 1964, Baltosser 1996, Schuchmann 1999, Caldrerón-F. 2005). Seemingly fewer, but at least some species hatch synchronously (e.g., Skutch 1931, Orr 1939, Greeney *et al.* 2006, Fierro-Calderón & Martin 2007). Only with more detailed descriptions of the natural history of Bronzy Inca and additional species can the potential adaptive significance of such variation be elucidated. As pointed out recently by Fierro-Calderón & Martin (2007), we still know very little about the breeding biology of tropical hummingbirds. We encourage others to publish their observations in order to provide more data for comparative and conceptual studies on the breeding of these and other poorly known tropical birds.

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