

BREEDING BIOLOGY OF THE COLLARED INCA (*COELIGENA TORQUATA*) IN EASTERN ECUADOR

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Resumen. – **Biología reproductiva del Inca acollarado (*Coeligena torquata*) en el este de Ecuador.** – Presentamos datos sobre la reproducción del Inca acollarado (*Coeligena torquata*) recolectados entre 2003 y 2011 en el Ecuador. Aparentemente, la anidación coincide con las épocas secas en la mayoría de su rango. Los nidos tienen la forma de una copa nítida, construidos de materiales suaves, tejido con telaraña, y decorado externamente con musgos verdes. La mayoría están fijos por un lado a ramitas delgadas y verticales. Los nidos estaban un promedio de 1.7 ± 0.3 m sobre el suelo. Las puestas completas contaron con dos huevos blancos, depositados con 48 horas entre cada huevo, pero los pichones nacieron sincronizadamente después de 18 días de incubación. Realizamos observaciones detallada sobre el comportamiento de incubación y cuidado parental en un solo nido. Durante el desarrollo de los pichones, los índices de alimentación variaron entre 1.3 a 5.2 visitas por hora. Las visitas estaban distribuidas uniformemente durante el día y el número de visitas aumento significativamente con la edad de los pichones. El promedio (de promedios diarios) del intervalo entre visitas fue de 28.5 ± 11.30 min. La duración de visitas disminuyo significativamente con el aumento de la edad de los pichones. La hembra demora de 8–92 s (promedio de promedios diarios 32.5 ± 11.53 s) por visita. Los pichones de dos a tres días de edad fueron incubados un 56% del día, pero después de 6 días de edad, la incubación disminuyo drásticamente. Encontramos una correlación significativamente negativa entre la edad de los pichones y el tiempo dedicado a la incubación.

Abstract. – We present data on the nesting biology of Collared Inca (*Coeligena torquata*) gathered between 2003 and 2011 in Ecuador. Nesting appears to peak during the drier periods across its Ecuadorian range. Nests are tidy cups built principally of soft materials bound together with spider web, decorated externally with green moss, and affixed predominantly by one side to thin, vertical, hanging branches. Nests were built at a mean height above the ground of 1.7 ± 0.3 m. Complete clutches consisted of two immaculate white eggs, laid c. 48 h apart, but which hatch synchronously after 18 days of incubation. We made detailed observations on incubation behavior and nestling care at a single nest. Across the developmental period, daily feeding rates ranged from 1.3 to 5.2 visits per hour. Provisioning visits were evenly distributed during the day. The number of feeding visits/h increased significantly with nestling age, and the mean (of daily means) interval between visits was 28.5 ± 11.30 min. The female spent 8–92 s (mean of daily means 32.5 ± 11.53 s) per visit feeding. Average feeding duration became significantly shorter with nestling age. Two to three-day-old nestlings were brooded during 56% of the day; after day 6, brooding diminished sharply. There was a significant negative correlation between nestling age and time devoted to brooding. *Accepted 29 June 2012.*

Key words: Collared Inca, *Coeligena torquata*, cloud forest, Ecuador, egg, nest, nestling, parental care, Trochilidae.

INTRODUCTION

One of 12 species in the genus (Züchner 1999), the Collared Inca (*Coeligena torquata*) is common throughout much of its range. It inhabits upper subtropical and temperate zones, from 2100–3000 m a.s.l. (exceptionally down to 1500 m a.s.l.), in the Andes from north-western Venezuela to southern Peru, predominantly associated with the understory and borders of montane forest and in adjacent clearings (Hilty & Brown 1986, Züchner 1999). In Ecuador, populations east of the Andes belong to the nominate subspecies (Züchner 1999, Ridgely & Greenfield 2001). Apart from the brief nest descriptions and scant additional information provided by Sclater & Salvin (1879) and Wiedenfeld (1985), little information has been published on the breeding biology of the Collared Inca (Züchner 1999). Here we present the first detailed account of its reproductive biology from nests studied in eastern Ecuador.

MATERIALS AND METHODS

Our detailed observations on the reproductive habits of the Collared Inca were made at a single nest (subsequently referred as nest no. 1), from October to December of 2009, at the Yanayacu Biological Station and Center of Creative Studies (00°35'S, 77°53'W), 5 km west of Cosanga, Napo Province, north-eastern Ecuador, at an altitude of 2160 m a.s.l. (for a more complete site description see Valencia 1995). At this nest, we gathered direct observational data during the incubation and nestling periods by watching the nest from a hide placed c. 10 m from the nest using 10x40 binoculars. We also used video data from tripod-mounted camera placed c. 8 m from nest. 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). Significance values

($P = 0.05$) were calculated using Spearman's Rank Correlation tests (r_s). We gathered additional data on nesting from seven nests found from 2003 to 2011 at Yanayacu and from 3 nests found at the Tapichalaca Biological Reserve (2400–2700 m a.s.l., 04°30'S, 79°10'W), north of Valladolid, and adjacent to Podocarpus National Park, in south-eastern Zamora–Chinchipec Province, Ecuador.

RESULTS

Nests, eggs, and seasonality. All of the nests we observed ($n = 11$) were tightly woven cups of soft, cotton-like, red-brown fibers, predominantly from tree-ferns and bromeliads. Nests were bound together with ample spider webs and decorated on the outside with light-green moss which often formed a loose skirt or tail below the nest (Fig. 1). Nests were attached by the side to thin, vertical (or nearly vertical) stems or branches, always very close to the end and usually partially supported from below by one or several small, laterally-projecting stems or petioles. Mean nest height ($n = 8$) was 1.7 ± 0.3 m above the ground. Mean measurements (cm) of three nests were: outer diameter, 7.1 ± 0.8 ; outer height, 7.5 ± 0.5 ; inner diameter, 3.5 ± 0.1 ; inner depth, 2.7 ± 0.2 ; tail of moss below bottom of nest, 12.7 ± 4.2 . The mean diameter of supporting stems (at the attachment point) was 4.1 ± 1.9 mm.

All eggs ($n = 15$) were immaculate white and clutch size at six nests was two eggs. Mean measurements of nine eggs were: length, 16.5 ± 0.8 mm; width, 10.0 ± 0.2 mm; fresh mass ($n = 5$), 0.90 ± 0.06 g.

We found seven additional nests of the Collared Inca at Yanayacu. Using the duration of the nesting cycle observed at our focal nest (see below), we calculated that eggs were laid on the following dates: 1 November 2003, 15 September 2004, 18 September 2005, 3 December 2007, 25 December 2008, 23 August 2009, 7 September 2009. Three nests



FIG. 1. Female Collared Inca incubating (photo: R. Mikusek).



FIG. 2. Collared Inca female and two nestlings at 19 days of age (photo: R. Mikusek).

TABLE 1. Incubation constancy in the nest no. 1 of the Collared Inca with two eggs in 2009 at the Yanayacu Biological Station, Napo Province, Ecuador.

Day after clutch completion	Observation time (h)	Range of incubation periods (min)	Range of absences (min)	Incubation constancy (%)
4	6.5	3–51	2–26	71
5	6.5	2–29	1–12	68.5
13	4	2–14	1–8	63
14	6	3–28	2–9	74
15	5	1–106	1–10	75
16	3	1–16	1–8	64

at Tapichalaca were estimated to have initiated laying on 20 October 2004, 29 July 2005, and 7 August 2005.

Incubation. In nest no. 1, the first egg was laid on 9 November and the second one after two days (11 November). In spite of considerable asynchronous laying both eggs hatched within c. 12 h which suggests that female started real incubation after laying second egg. Incubation lasted 18 days, from the laying of second egg to the hatching of that egg. Daily incubation constancy ranged from 63–75% (Table 1).

During all of our observations of the incubation phase, continuing through two days after hatching, the female added material to the nest on many of her arrivals at the nest. She most frequently brought green moss and incorporated it into the nest rim (28 times during 37 h of observation, mean = 1 time/1.3 h). Less frequently (eight cases), she brought soft brown material, most likely from *Tillandsia* sp. (Bromeliaceae) and incorporated it into the inner layer of the nest. On an additional 26 arrivals, the female brought no visible material, but after sitting she made wiping movements with her bill along the edge of the nest. Based on detailed observations at the nests of other hummingbirds (HFG pers. observ.), we interpret this behavior as the addition of spider webs to the nest. Indeed,

spider webs are clearly visible in several photos taken from the nest (cf. Figs 1, 2). We observed these nest maintenance activities only in morning. In total, the female added material (green moss, brown material and webs) to the nest 62 times (1 time/1.7 h), and 37% of visits included nest maintenance.

Nestling provisioning. During every visit with food (nest no. 1), the female (Fig. 2) sat on the rim of nest and fed both nestlings, one after the other. She fed by inserting her bill into the mouth of the gaping nestling and regurgitating. The female spent 8–92 s (mean of daily means = 32.5 ± 11.53 s) per visit feeding. Average feeding duration became significantly shorter with nestling age ($r_s = -0.534$, $n = 18$, $P = 0.022$).

Provisioning visits were regularly distributed during the day (Fig. 3, Index of dispersion; Fowler *et al.* 1998), and daily feeding rates ranged from 1.3 to 5.2 feedings/h (Table 2). Note that, as in most hummingbirds, both nestlings are fed on every visit so this rate is equivalent to rates reported as feeds per nestling/h. Number of feeding visits/h increased with nestling age (Table 2, $r_s = 0.953$, $n = 18$, $P < 0.001$). Intervals between feeding visits ranged from 1–96 min, and mean of daily means was 28.5 ± 11.30 min, with a significant negative correlation between nestling age and the duration of

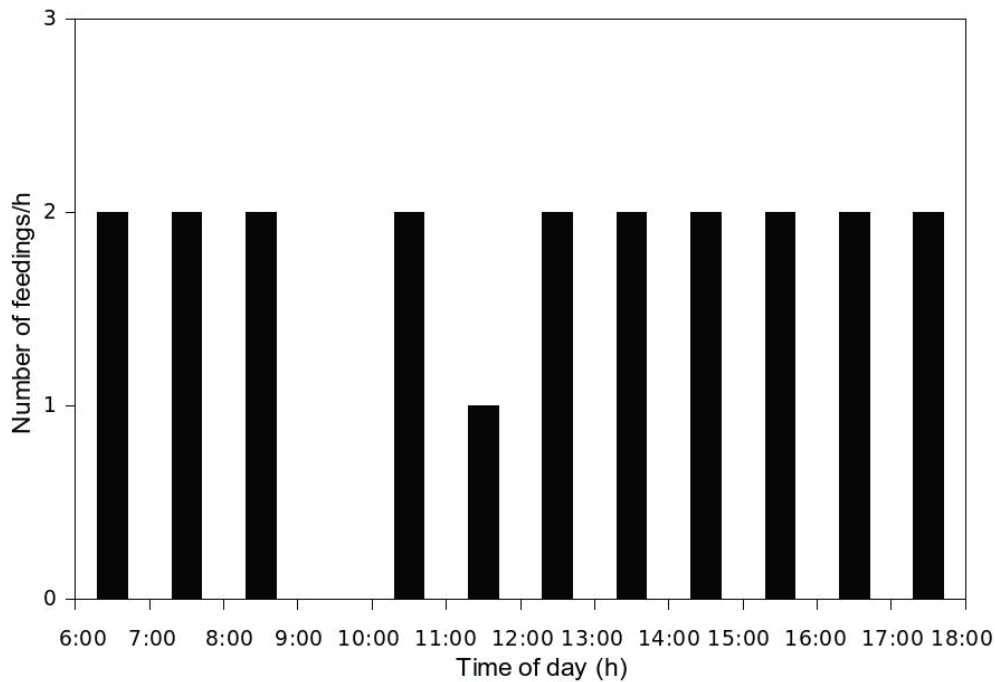


FIG. 3. Daily pattern (two days combined) of provisioning rates at a nest no. 1 of the Collared Inca containing two nestlings 7–8 days old.

between-feed intervals ($r_s = -0.938$, $n = 18$, $P < 0.001$).

Brooding. Nestlings (nest no. 1) were brooded for some portion of the day while they were 2–7 days old (no observations of day 1). The nestlings were not brooded during any of our observations after their 7th day. There was a significant negative correlation between nestling age and percent of observation time devoted to brooding ($r_s = -0.943$, $n = 6$, $P = 0.017$) (Table 3). Brooding bouts of two-day-old nestlings lasted 2–32 min (mean = 8.52 ± 6.77 min, $n = 15$).

Nestlings. The first egg hatched in the evening of 27 November (c. 17:00 h) and the second one in the morning of 28 November. We made assumption that both nestlings were one day old on 28 November. Nestlings were

born dark-skinned and with two rows of ten pale, red-brown neossoptiles.

At 14 days of age, we first observed nestlings flapping their wings and scratching themselves. By 17 days of age, nestlings occasionally perched on the rim of the nest (Fig. 2). On its 21st day (on 19th December), one of the nestlings was observed sitting on the branch above the nest and later half walking, half flying, along a branch while the second nestling sat on the rim of the nest. Later, nestling were seen out of the nest exercising their wings. The next day they disappeared from the vicinity of nest. Probably both nestlings left the nest successfully (Fig. 4).

DISCUSSION

Results of the present study on the Collared Inca allow comparison with the results of a

TABLE 2. Provisioning rates at nest no. 1 (two nestlings) of the Collared Inca in 2009 at the Yanayacu Biological Station, Napo Province, Ecuador. Most observations started at 07:00 h.

Nestling age (days)	Female visits	Observation time (h)	Visits/h
2	8	5.8	1.4
3	8	6	1.3
4	5	3.5	1.4
6	9	6	1.5
7	10	6.3	1.6
8	11	6	1.8
9	13	6.5	2.0
10	13	6	2.2
11	15	5.5	2.7
12	15	5.5	2.7
13	13	6	2.2
14	17	7	2.4
15	14	5.5	2.5
17	28	8	3.5
18	43	12	3.6
19	16	3.5	4.6
20	14	4	3.5
21	21	4	5.2

similar study of the Bronzy Inca *Coeligena coeligena*, carried out one year earlier in the same area (Dyrce & Greeney 2008). The two species are closely related (Parra *et al.* 2009) but we found some differences between their nesting biology. The daily patterns of nestling provisioning of the Bronzy Inca were less regular. According to Züchner (1999), the incubation period of the Bronzy Inca is 15–16 days, while we found a period of 18 days for the Collared Inca. In the former species we never observed the addition of nest material during the incubation or nestling periods as with the Collared Inca. Schuchmann (1999) stated that (in hummingbirds) “females repair nest regularly, especially during the incubation period,” and we have found this to also be the case with several other species studied in both tropical and temperate regions (HFG unpubl.), making its absence in the Bronzy Inca somewhat puzzling, though sample size is admittedly low.

The length of female feeding visits was similar in both species (Bronzy Inca: mean 27.6 ± 7.11 s, range 16.5–44 s, $n = 14$; Collared Inca: mean 32.5 ± 11.53 s, range 14.5–61.5 s, $n = 18$; $t = 1.37$, $df = 30$, $P = 0.18$). In both species, average feeding duration decreased significantly with nestling age. Provisioning rate, however, was significantly higher in the Collared Inca (mean 2.6 ± 1.13 , range 1.3–5.2, $n = 18$) than in the Bronzy Inca (mean 1.5 ± 0.27 , range 1.1–2.0, $n = 15$; $t = 3.56$, $df = 31$, $P = 0.001$). The rates at which the Bronzy Inca provisioned nestlings (1.1–2.0 times/h) are closer to published information for other hummingbirds, which generally feed at rates < 2.5 times/h (Skutch 1961, 1964; Schuchmann 1986, 1999; Wolf & Wolf 1971, Oniki & Antunes 1998), while rates for the Collared Inca (1.3–5.2 times/g) are generally higher. This difference may be a result of larger food quantities per visit in the Bronzy Inca, though this remains to be quan-

TABLE 3. Time devoted to brooding and nestling age in nest no. 1 of the Collared Inca.

Nestling age (days)	Observation time (h)	Brooding time (%)
2	5.8	56.3
3	6	56.4
4	3.5	35.7
6	6	29.4
7	6.3	6.6
8	6	0.0

tified. In the Bronzy Inca, the number of feeding visits/h did not change significantly with nestling age (which seems typical for hummingbirds, Schuchmann 1999) while in the Collared Inca the number of feeding visits/h increased with age.

Pattern of brooding were similar in both species: during the first two days after hatching nestlings were brooded during > 50% of the day, and stopped when nestlings were 7–8 days old. Schuchmann (1999) also found that other hummingbird species show a decline in brooding around 7–12 days of age.

Nest situation and nest construction were similar in both species. Additionally, the nest architecture reported here is congruent with the original description of the nest of the Collared Inca given by Sclater & Salvin (1879; as *Bourcieria torquata*): “the nest of this species is composed outwardly of moss and thickly lined with fine pubescence from the bases of fern-fronds.” Our egg measurements are also similar to those given by Oates & Reid (1903; as *Helianthea torquata*). Though not explicitly indicated, these are presumably from the nest described by Sclater & Salvin (1879) from Antioquia, Colombia.

There are few data concerning the seasonality of breeding for the Collared Inca. According to Züchner (1999), breeding in Colombia lasts from November to March. The eight nests described here from north-eastern Ecuador suggest that clutches are ini-

tiated from late August to late December, coinciding with the drier months in this region (Greeney 2010), and matching the seasonal reproductive activities of the sympatric Green-fronted Lancebill (*Doryfera ludoviciae*) (Greeney *et al.* 2006). Our three nests observed in southeastern Ecuador, combined with other records from this region (Greeney *et al.* 2010), suggest a similar or perhaps slightly earlier nesting season in that region, but similarly coinciding with drier months. The only other than in this study, available on seasonality are an active nest in March in northwestern Ecuador (Greeney & Nunnery 2005) and two nests with eggs in March in the Peruvian Andes (Wiedenfeld 1985). It seems likely that, though across its range the Collared Inca may breed year-round, in any given region breeding coincides with drier months.

No significant differences were found between the breeding biology of the Collared Inca and other than Bronzy Inca hummingbird species. Mean incubation period in twelve species listed in Fierro-Calderon & Martin (2007) was c. 17.5 days while in our study incubation lasted 18 days. In our case, incubation periods lasted from 1–106 min (mean = 21.3 ± 30.87 min), and absences from 1–26 min (mean = 6.75 ± 7.35 min) (Table 1). Similar figures were obtained for the Scaly-breasted Hummingbird (*Phaeochoera cuivierii*), with 1–103 min (mean 14.3 min) for incubation and 1–23 min (mean 6 min) for absence times (Skutch 1964). Mean incubation constancy for ten hummingbird species was 68 % while in our study it was 63–75 %. The nestling period of the Collared Inca (21–22 days) was similar to the average nestling period (ca 23 days) of 12 other hummingbird species (Fierro-Calderon & Martin 2007). However, in some species this period is much longer; e.g., in the Green-fronted Lancebill *Doryfera ludoviciae* it lasts 29–30 days (Greeney *et al.* 2006).



FIG. 4. Collared Inca nestling at 20 days of age, 1 day prior to fledgling (photo: R. Mikusek).

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