Nesting biology of the Long-wattled Umbrellabird *Cephalopterus penduliger*. Part II: nestling provisioning

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Presentamos la segunda parte de un estudio sobre un nido del Pájaro Paraguas Longuipéndulo *Cephalopterus penduliger* en el suroeste de Ecuador, detallando el cuidado parental durante el crecimiento del pichón. Solo la hembra atendió al nido, empollando el pichón principalmente durante los primeros diez días. El pichón fue alimentado principalmente con invertebrados grandes a lo largo del estudio, pero su dieta también incluyó lagartijas, ranas y culebras. El pichón voló del nido después de 32 días.

This paper is the second in a two-part study of the breeding biology of Long-wattled Umbrellabird *Cephalopterus penduliger* in south-west Ecuador[10]. Long-wattled Umbrellabird (Fig. 1) is considered a globally Vulnerable[2,4,13] inhabitant of foothill and lowland humid forests west of the Andes from Colombia to southern Ecuador[20,24]. Prior to recent studies of its nesting habits[10,15], few data were available apart from unsubstantiated reports of nests[2,8,11]. Both recent studies confirmed that only the female participates in nesting activities, as expected in a lekking species[12]. Both also found that the clutch comprises one egg, and each provided a description of a nest and nest site. Greeney *et al*.[10] expanded on the brief observations of Karubian *et al*.[15] regarding incubation behaviour. Karubian *et al*.[15] made detailed but limited observations on nestling care during the early stages of development. Here we supplement these data based on video observation of a nest during the entire nestling period.

Study site and Methods

We videotaped a nest of the Long-wattled Umbrellabird at the Buenaventura Biological Reserve (03º39'S 79º46'W), 20 km north of Piñas, in prov. El Oro, south-west Ecuador. In addition to the 226 daylight hours (06h00–18h30) reported on for incubation[10], we recorded 336 hours of behaviour during the nestling period. Details of our methods are given in Greeney *et al*[10]. During subsequent review of the video we recorded all behaviours at the nest of both the adult and the nestling.

Chronology of nest and observations

On 23 February 2004 at 14h30, after 27–28 days of incubation, the single egg hatched[10]. At 12h45 on 26 March, the nestling moved to the rim of the nest and began vigorously flapping its wings. At this point it toppled over backwards out of the nest, quickly righting itself then flying down and away from the nest. While its departure appeared awkward, it flew well, and we consider that fledging was not accidental. Thus, the nestling period was 1.75 hours less than 32 days.

Brooding

The female spent much of the first days of the nestling period brooding, but this daily proportion decreased steadily throughout the nestling period (Fig. 2). By the time the nestling was ten days old, the female was never observed to brood for longer than 40.5 minutes, and then only during hard rains. During periods at the nest, the female spent a sizable amount of time engaged in nest maintenance such as rapid probing, where the bill is jabbed into the nest substrate[9]. As an example, on 24 February 2004, during an 86.9-minute brooding bout, the female spent 5.8% of that time engaged in such behaviour. In addition, even when brooding, the female regularly preened and yawned. These behaviours, however, were executed very quickly (e.g. 2–3 seconds per preening bout, with six such bouts spread over four minutes) and the female generally maintained a very high level of vigilance at the nest.

Nestling diet and feeding rates

We recorded a total of 342 feeding visits by the adult female (Fig 3). Of these, we were able to identify 172 items, the majority of which were invertebrates (Fig. 4). Invertebrate prey (n = 146) included: 84 adult cicadas (Heteroptera, Cicadidae); 32 larval Lepidoptera; 14 katydids (Orthoptera, Tettigoniidae); nine adult Lepidoptera; three undetermined Orthoptera; one cockroach (Blattodea, Blaberidae, *Blaberus* sp.); one adult beetle (Coleoptera, Cerambycidae); one dobsonfly (Megaloptera, Corydalidae); and one unidentified arthropod. Vertebrate prey (n = 22) included: 13 lizards (most appeared to be Iguanidae), six frogs and three snakes. The four fruits that were fed to the nestling appeared to be all of the same type: round, c.4–5 cm in diameter, and orange, probably belonging to the family Solanaceae or Arecaceae. Prey items ranged in size from 2–3 cm unidentified

Figure 1. Adult male Long-wattled Umbrellabird *Cephalopterus penduliger*, Buenaventura, El Oro, Ecuador (Murray Cooper)

Figure 3. Adult female Long-wattled Umbrellabird *Cephalopterus penduliger* feeding 25-day-old nestling, Buenaventura, El Oro, Ecuador (Murray Cooper)

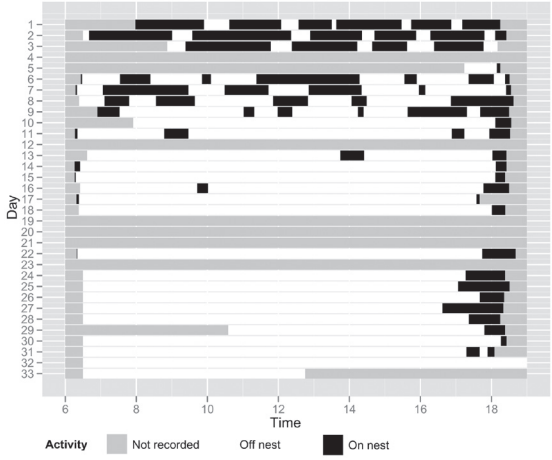

Figure 2. Brooding rhythms of an adult female Long-wattled Umbrellabird *Cephalopterus penduliger*. Each row represents an entire day, and rows are numbered according to the day of the nestling period (1 = day of hatch). Time of day is on the x-axis, and runs from 06h00 to 18h30. The rows are coloured according to the activity of the female at that time.

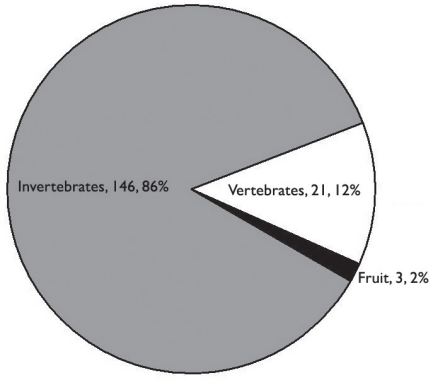

Figure 4. Pie chart showing relative percentage of dietary items brought to the nest by a female Long-wattled Umbrellabird *Cephalopterus penduliger* in southern Ecuador.

items (probably small invertebrates) to several of the lizards that were c.50 cm in total length. The identified larval lepidopterans included several 4–6 cm silk moth species (Saturniidae) with strongly urticating spines (HFG pers. obs.). In all cases they appeared to be dead upon arrival, perhaps partially masticated. Adult Lepidoptera included large (8–10 cm wingspan) Sphingidae and Saturniidae, which were probably gleaned from foliage or tree trunks while roosting. These were generally delivered still alive, often flapping vigorously. The three snakes brought to the nest were all 25–40 cm long and all appeared to be non-venomous Colubridae. All of the snakes and lizards showed no signs of life when brought to the nest.

Daily feeding rates varied from 0.4 to 1.9 feeds / hour (mean = 1.0) and exhibited a significant positive increase with nestling age (r^2 = 0.559). Feeds were distributed evenly across daylight hours, however, and across the entire observation period the nestling was fed at the following rates: 06h00–11h00, 1.2 feeds / hour; 11h00–16h00, 0.8 feeds / hour; 16h00–18h30, 1.0 feeds / hour.

Adult and nestling behaviour

Perhaps the most striking behaviour exhibited by the adult was its extreme vigilance on arriving at the nest. Flights to the nest were generally long and direct, most often from >20 m away. After landing on the nest's rim, the adult froze for several seconds and then slowly swayed in both directions, peering out intently. This period of vigilance lasted between two seconds and 8.4 minutes (mean ± SD = 37 ± 42 seconds). At the end of this vigilant period the bird began to vibrate as if making a call. Our equipment could not detect any sound, but we presume that some type of soft call was made. Until this point the nestling remained absolutely still with its head down. Only after the adult called did the nestling, slowly and silently, lift its head and open its bill.

After passing food to the nestling, if not remaining to brood, the adult generally left after pausing 3–6 seconds. When transferring larger prey (e.g. lizards), the adult often aided the nestling several times by shoving the prey deeper into its mouth. Whenever it delivered snakes and lizards, however, the adult left the nest before the entire tail of the animal had disappeared inside the nestling.

All faecal sacs were produced by the nestling in the presence of the female, generally in the 3–6 seconds immediately following food delivery. Production of a faecal sac was preceded by a vigorous wiggling of the nestling's rump, usually eliciting an expectant forward lean by the female. During the entire observation period the nestling produced 0.8 sacs / hour, showing only a slight increase in production, from 0.6 / hour to 1.0 / hour, between the first and second half of the period. Most (80%) faecal sacs (n = 268) were consumed at the nest. Only 14% were carried away from the nest and 6% were apparently accidentally dropped or missed by the adult. In each case where the faecal sac fell from the nest the adult went after it. We presume that all of these were eaten or carried away, as we found no evidence of faecal sacs below the nest.

Discussion

Greeney *et al*.[10] already provided comparative details of the nesting biology of Long-wattled Umbrellabird versus that of its two congenerics, Bare-necked Umbrellabird *Cephalopterus glabricollis* and Amazonian Umbrellabird *C. ornatus*. With respect to parental care of the nestling, nothing has been published to date concerning this aspect of the breeding system of Amazonian Umbrellabird[16], and the only report of nesting in Bare-necked Umbrellabird ended in predation when the nestling was just one week old[6]. Consequently, at present we are unable to determine how nestling diet, brooding behaviour, etc., might compare among these species. The only other detailed study of reproductive behaviour in *C. penduliger*[15], however, gives us the opportunity to make direct comparisons of parental care and nestling diet. In respect of patterns of feeding and brooding, our results mirror those of the nest studied in north-west Ecuador[15], including a sharp reduction in daily brooding around age 10–12 days. Similarly, nestling diet was remarkably similar, with both young fed a predominance of invertebrate prey, but also a selection of vertebrates dominated by lizards. The only apparent difference, in fact, was that we observed no instances of regurgitation by the parent (as opposed to 20% of feeds observed by Karubian *et al*.[15]). Further detailed studies are needed to investigate the possible significance of this.

The apparent predominance of invertebrates in the nestling's diet is mirrored in other cotingas with sufficient comparative data. For example, at the only nest of Cinnamon-vented Piha *Lipaugus lanioides* studied to date[26], the young were apparently fed solely invertebrates until circa halfway through the nestling period, whereupon fruit was introduced into the diet. The congeneric Rufous Piha *L. unirufus* takes at least some insects and spiders, and these are apparently also fed to young[21] (GMK pers. obs.). For Capuchinbird *Perissocephalus tricolor*, Snow[22] reported very few fruits in the diet of the young, which was principally insectivorous at two nests studied. At a single nest of Red-ruffed Fruitcrow *Pyroderus scutatus* in Brazil[7], insect prey was considered to constitute at least c.30% of nestling diet. Likewise, at nests of *P. s. granadensis* studied in north-west Venezuela[17], provisioning consisted mostly of insects (66.7%), with fruit comprising just 8.3% of diet during the early stages. These proportions changed to mostly fruit (82.4%) and some insects (17.6%) in the later stages of the nestling's growth. For Purple-throated Fruitcrow *Querula purpurata*, nestling diet appears to be largely insect-based as well (including larvae; cicadas, mantids and moths being some of those recognised during nest observations), with fruit only introduced from *c*.12 days of age[23]. Given the preponderance of insects in the diet of adult Crimson Fruitcrows *Haematoderus militaris*, it might be assumed that young are fed similarly, but to date we lack any proof of this[16,24].

Snakes, frogs and lizards have only rarely been recorded in the diets of other nestling Cotingidae. Notable examples include Red-ruffed Fruitcrow, which were fed a substantial proportion of small lizards (25%) in the early stages of their growth[17], and Whittaker[25] even speculated that an adult Capuchinbird that he observed seize a roosting bat had a nest with young. To some extent, this may reflect the lack of detailed studies using video cameras at the nests of other large cotingas such as *Perissocephalus*, *Pyroderus*, *Haematoderus*, etc. For example, we still know nothing concerning the nestlings' diet for large species such as Bare-necked Fruitcrow *Gymnoderus foetidus*, though their nests have been discovered on multiple occasions[16]. It should be remarked that both species of *Rupicola* also take large prey items and feed their nestlings vertebrates, including lizards, as well as insects, although fruit appears to be the most important dietary constituent, at least in Guianan Cock-of-the-Rock *R. rupicola*[1,3,5,18,19].

Other cotingas have also been observed to assist their young to consume large prey, and such behaviour is presumably common but rarely documented. For example, GMK (pers. obs.) witnessed a female Rufous Piha aid its nestling consume an unidentified beetle, which it gave to the young 14 times, grasping the prey afresh and crushing it in the bill between attempts; eventually

she 'gave up' and ate the beetle herself. The second time, the prey was an unidentified winged insect, which the chick managed to consume, with assistance, on the 11th attempt[16].

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