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Natural History Note

Morphological and Behavioral Evidence of Batesian Mimicry in Nestlings of a Lowland Amazonian Bird

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ABSTRACT: Because predation is the main cause of avian nest failure, selection should favor strategies that reduce the probability of nest predation. We describe apparent Batesian mimicry in the morphology and behavior of a *Laniocera hypopyrra* nestling. On hatching, the nestling had a distinctive bright orange color and modified feathers all over its body, and 6 days after hatching, it started to move its head very slowly from side to side (in a "caterpillar" movement) when disturbed. These traits gave it a resemblance to a hairy, aposematic caterpillar. This species has a long nestling period for its size (20 days), perhaps due to slow provisioning rates (about one feeding per hour). We argue that the slow growth rate, combined with high nest predation, favors the evolution of antipredation mechanisms such as the unique morphological and behavioral characteristics of *L. hypopyrra* nestlings.

Keywords: Batesian mimicry, *Laniocera hypopyrra*, life history, incubation, tropical nesting.

Introduction

Most failures of bird nests are caused by nest predation (Ricklefs 1969; Martin 1993; Robinson et al. 2000), presumably resulting in selection for nesting strategies that reduce its likelihood. Selection should be strongest in areas where nest predation is especially high, such as in lowland Neotropical rain forests (Skutch 1985; Martin 2004; Martin et al. 2006). There is strong evidence that tropical birds have adaptations to cope with high nest predation (e.g., small clutch sizes; Skutch 1985; Martin et al. 2006). On the other hand, the long nesting cycles characteristic of tropical birds would seem to increase the risk of nest predation (Martin et al. 2007; Robinson et al. 2010). This apparent contradiction might be explained if tropical birds employed compensatory strategies, such as increased nesting attempts or longer nesting seasons (Roper et al. 2010). Recent field evidence, however, suggests that at least some tropical birds do not have longer breeding seasons or more nesting attempts per year (Gill and Haggerty 2012). Thus, tropical birds could be using unrecognized nesting strategies to increase their nesting success in areas with high nest predation pressure, such as lowland humid forests. Here we describe an unusual suite of morphological (e.g., modified downy feathers) and behavioral (e.g., unusual begging behavior) traits in a tropical lowland nestling bird, *Laniocera hypopyrra* (cinereous mourner), that we hypothesize to be antipredator adaptations that could increase nesting success.

Based on museum specimens in a recent study, D'Horta et al. (2012) suggested that the strikingly different plumage coloration of a juvenile nestling and an old nestling—bright orange—compared with the plumage coloration of adult *L. hypopyrra* and *Laniisoma elegans*—dull gray—could be associated with chemical defense or Batesian mimicry. They proposed that the bright orange coloration and hairlike feathers of nestlings and juveniles resemble characteristics of a large, hairy (aposematic) caterpillar. They concluded that this explanation was more plausible than an alternative proposed by Snow (1982) that the nestlings resembled moss-covered fruit, which might provide crypsis for nestlings on otherwise exposed nest sites. However, D'Horta et al.'s (2012) hypotheses on the functions of the contrasting plumage of nestlings were based on two museum specimens, providing few insights into natural history.

In this study, in addition to presenting detailed morphological and behavioral traits during the entire nestling cycle of *L. hypopyrra*, we provide information on a local toxic caterpillar that has astonishing morphological and behavioral similarities to the *L. hypopyrra* nestling during its early stages. Our observations on the morphology and behavior of a nestling of *L. hypopyrra* support D'Horta et al.'s (2012) hypothesis of Batesian mimicry, particularly during the early stages of nestling development. Furthermore, we suggest

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that the orange coloration can also be cryptic, providing some support for Snow's (1982) hypothesis.

Methods

This study was conducted in a lowland Amazonian rain forest located along the upper Madre de Dios River at the Pantiacolla Lodge (lat. 12°39′362″S, long. 71°13′900″W; 400 m), Madre de Dios, Peru. The area encompasses a mix of foothill, terra firme, and flooded forests, with an average canopy height of 30 m. We found the nest described here on August 13, 2012.

Measurements and nest monitoring. Egg and nestling mass were measured to the nearest 0.05 g with a pocket scale (Flipscale, Phoenix, AZ); nestling mass was measured daily. Egg, nestling, and nest dimensions were recorded to the nearest 0.1 mm with calipers. We used a logistic equation (Ricklefs 1967) to estimate the nestling's growth constant, K.

Two different techniques were used to obtain behavioral data. First, we placed two thermistors, one under the eggs and another on an adjacent branch (to obtain nest and ambient temperatures, respectively); these were attached to a Hobo U12 data logger (Onset Computer, Bourne, MA) that stored temperature data every minute. Next, we placed a motion sensor camera ~70 cm from the nest (RM45 RapidFire; Reconyx, Holmen, WI). The camera took 1 photo every minute and 10 photos per second every time there was movement in the nest. Incubation behavior was obtained from temperatures recorded by the thermistor under the eggs. Rapid and sustained temperature decreases (1°C/min) indicated trips departing from the nest (off bouts), and rapid temperature increases (1°C/min) and sustained high temperature indicated incubation periods (on bouts). This technique was validated with images from the motion sensor camera. Due to battery failure, no images were obtained for 6 days (August 31–September 5). We also made video recordings during two 1-h sessions on September 5 (10:23–11:23) and September 5 (13:42–15:17).

Results

At hatching, the *Laniocera hypopyrra* nestling was covered with orange down (fig. 1*a*), a very different plumage coloration compared to that of gray adults. Each downy feather had 1–10 elongated orange barbs (fig. 2), each of which had a bright white tip (figs. 1, 2). These plumage characteristics are unique among the 120 species of nestlings we have observed at this study site. Unlike most altricial nestlings, the *L. hypopyrra* chick did not beg immediately when the parent arrived at the nest with food. Similarly, when we took the nestling out of the nest for measuring, it did not beg for food as other nestlings do. In another uncommon behavior among altricial birds, the parent spent long periods of time at the nest rim after arriving with food but before delivering the food to the nestling. The time spent at the rim of the nest before offering the food to the nestling was longer (mean ± SD = 64 ± 27 s) during the first 7 days after hatching; and although it decreased to 30 ± 25 s after day 7, it remained long (see video 1, also available at http://youtu.be/mkRmMQ-xBuo). During three video-recorded feeding visits, we detected vocalizations by the parent while it waited on the nest rim, and almost immediately after these vocalizations, the nestling began to beg.

The nestling moved its head slowly from side to side ("caterpillar" movement; video 1) while the parent was on the nest rim with food, before raising its head and opening its bill to beg for food, and when being handled for the purpose of our study (although it never begged for food during handling). This behavior was first observed on day 6 after hatching and was not observed after day 16, during nestling measurements. We could not quantify the frequency of adult vocalization while the parent was on the nest rim or the caterpillar movement of the nestling during most feeding visits, as the motion sensor camera was not equipped with a microphone or video. As nestlings aged, cessation of the caterpillar movement after day 16 coincided with the decline in their resemblance to caterpillars, as feathers were substantially emerged and the downy feather with elongated barbs started to drop from the feather tips (fig. 1*f*).

In both appearance and behavior, young nestlings of *L. hypopyrra* bear a striking resemblance to large caterpillars. We encountered at the study site a caterpillar with aposematic coloration and irritating hairs that belongs to the Megalopygidae family (fig. 2*f*; Greeney et al. 2012) and can be placed in either the *Megalopyge* or *Podalia* genera (M. Epstein, personal communication). Caterpillars of the Megalopygidae family are well known for their high toxicity (Dyar and Morton 1895; Lamdin et al. 2000; Deml and Epstein 2001; Hossler 2009; Greeney et al. 2012). The caterpillar we encountered measured 12 cm, which closely matches the size of the *L. hypopyrra* nestling (14 cm during the first 14 days); but the striking morphological similarity is the caterpillar's orange "hairs" with white tips, which match almost exactly the nestling's elongated orange downy feather barbs with bright white tips. The morphological appearance of an aposematic caterpillar was reinforced by behavior: the caterpillar-like head movements of nestlings (when disturbed) closely resembles the movements of the aposematic caterpillar (see video 2, also available at http://youtu.be/IakXyq7zz5Y).

During the 2 days in which we continuously monitored incubation, the parent made 4 ± 1.4 trips per day

Figure 1: *Laniocera hypopyrra* nestling development in lowland Amazonian forest in southeastern Peru. *a*, Day 1, nestling with long orange barbs with white tips. *b*, Day 4, nestling in nest next to unhatched egg. *c*, Day 9, nestling feathers have started to emerge and eyes have started to open. *d*, Day 14, most of the body feathers have completely emerged, eyes are completely open, and wing feathers are emerging. *e*, Day 18, all body feathers have completely emerged, and the wing feathers are ~90% emerged. *f*, Caterpillar (Megalopygidae) in the area that matches the nestling's plumage characteristics. See also videos 1 and 2, available online. Photo credits: Duván A. García (*a*–*c*), Santiago David (*d*, *e*), and Wendy Valencia (*f*). Credit for video 1: Dano Grayson, wildlife photographer/videographer, danograyson.com; and Artists for the Amazon, Amazon Aid Foundation, amazonaid.org. Credit for video 2: Matt Dickinson.

Figure 2: Close-up of the elongated barbs that remained attached to the tips of feathers as they developed. Also shown is the variation in the number of barbs that emerged from a single feather track. Photo credits: Santiago David.

(mean ± SD) with a mean duration of 65.8 ± 30.8 min. Incubation bouts averaged 143.8 ± 60.3 min, resulting in daytime nest attentiveness of 61.1%. Nestling feeding behavior was observed over 132 h, and we registered 129 feeding events. We could identify the food brought by the parent in 60 trips, and all but one event included at least one caterpillar; the exception included an unidentified insect. Feeding trips changed through the nestling stage, from shorter feeding trips during the first 5 days (0.63 ± 0.9 trips per hour) to almost doubling between days 6 and 11 (1.1 ± 1.9 trip per hour) and decreasing to 0.75 trips per hour the day before abandoning the nest. To reduce variance, we included only days in which we had continuous daytime observation (05:00–18:00); days 12–18 were excluded. Overall, the parent made, on average, one trip per hour. On day 18, the nestling's morphological measurements were as follows: mass = 41.15 g (adult measurement = 48.1 g; nestling relative development compared to adult = 85.6%), flight feathers = 74.3 mm (106.5 mm; 69.8%), and tarsus = 21.9 mm (21.95 mm; 99.8%; fig. 2*e*). On average, the tarsus grew 1.2 mm per day and the wing 5.0 mm per day once feathers started emerging. The nestling gained 2.2 g per day ($K=$ 0.28 days; fitted asymptote = 40.30 g).

Finally, the cup-shaped nest of *L. hypopyrra* was found in a 3-m-high tree in an area of flooded forest 2.5 m above ground. The nest was composed exclusively of thick, dry leaves. One egg failed to hatch, the other hatched on August 20 (8 days after it was found), and the nestling fledged on September 8 (20 days after hatching) at 06:51, after the adult appeared to prompt it.

Discussion

We believe that the unique appearance and behavior of *Laniocera hypopyrra* nestlings is best explained as Batesian mimicry of a noxious caterpillar model that could increase nesting success. As shown in figure 1, the *L. hypopyrra* nestling during the early stages bears an astonishing resemblance in size, morphology, and behavior to a caterpillar encountered in our study that belongs to the family Megalopygidae. This family is well known for its toxicity (Dyar and Morton 1895; Lamdin et al. 2000; Deml and Epstein 2001; Hossler 2009), and there is even a report that these toxins can be lethal to humans in unique circumstances (Pinson and Morgan 1991). The close match in size, morphology, and behavior between the nestling and the caterpillar supports the hypothesis of Batesian mimicry being used by the nestling, possibly to reduce nest predation. Therefore, nestling morphological and behavioral characteristics could have evolved as a result of the combination between the slow life-history nesting strategy observed in *L. hypopyrra* (e.g., long nestling period) and the high nest-predation pressures observed at the study site. Preliminary data from a long-term study indicate that ~80% ($n = 230$) of the cup nests at the study site are depredated (G. A. Londoño, unpublished data), supporting previous reports of high nest predation in tropical birds (Skutch 1985; Robinson et al. 2000; Martin et al. 2006).

The possibility that *L. hypopyrra* nestlings might mimic toxic, hairy caterpillars was first suggested by D'Horta et al. (2012), based on examination of a juvenile specimen that had lost many of the characteristics resembling those of caterpillars (the elongated barbs did not have white tips and were present only on the crest; see fig. 1 in D'Horta et al. 2012). To our knowledge, this is the first bird species for which Batesian mimicry has been proposed for nestlings (Caro 2014). D'Horta et al. (2012) also described a well-developed nestling of *Laniisoma elegans* (Brazilian laniisoma) that retained most of the elongated barbs, suggesting that this type of mimicry may be present in closely related species. Batesian mimicry is widespread among many invertebrate groups (Guilford 1990; Mallet and Joron 1999) and, to a lesser extent, in vertebrate groups including snakes (Cox and Rabosky 2013), amphibians (Kuchta et al. 2008; Cummings and Crothers 2013; Twomey et al. 2013), and fishes (Randall 2005; Cheney 2010; Dudgeon and White 2012). While there is little evidence of Batesian mimicry in birds (Cott 1940; Caro 2014), there are examples of warning coloration. For example, the hooded pitohui (*Pitohui dichrous*) has aposematic plumage (black and orange) and contains toxins (Dumbacher et al. 1992; Dumbacher and Fleischer 2001). It is possible that *L. hypopyrra* nestlings contain toxins, in which case their characteristics would be best described as Müllerian mimicry. However, we think this is unlikely. Most food items brought for the nestling were caterpillars, while prey consumed by other vertebrates to obtain toxins from food consists mainly of ants and beetles (Santos et al. 2003; Dumbacher et al. 2004).

Unlike most nestling birds that are cryptically colored, presumably to blend with the environment and reduce predation (Kilner 2006), the bright orange coloration of *L. hypopyrra* juveniles and nestlings is highly conspicuous. D'Horta et al. (2012) suggested that the function of the bright coloration would apply both in the nest and after fledging. However, we cannot discard an early hypothesis proposed by Snow (1982), in which he suggested that *L. elegans* nestling coloration had evolved as a cryptic coloration to resemble moss-covered fruits. Similarly, the orange coloration of the *L. hypopyrra* nestling may serve as a cryptic coloration, as it matches the light color of the dry leaves used as nest material (see fig. 1*b*). Thus, *L. hypopyrra* nestling coloration could serve simultaneously as a warning and as cryptic coloration, which could detract more predators.

Because we observed a reduction in the behavioral (disappearance of the caterpillar movement) and morphological (drastic reduction in the density of the elongated orange barbs with white tips throughout the body) traits that enhanced the *L. hypopyrra* nestling's resemblance to caterpillars, we suggest that nestling traits in this species evolved primarily to cope with high nest predation during the early stages of the nestling period. At this time, altricial nestlings are particularly vulnerable, as they have little ability to move, their eyes are closed, and their tarsi and wings are not well developed. Thus, they cannot escape when a predator approaches, compared to at later ages near fledging, when nestlings are more active and noisier and can potentially "force fledge" if at risk. The nestling period in *L. hypopyrra* is long, and the growth rate is slow ($K = 0.28$ day) for a cup-nesting tropical passerine (Martin et al. 2011), which is probably linked to a low feeding rate (less than one feeding per hour). Nestling growth rate could be even slower and nestling period even longer if the nest had two nestlings.

The low number of incubation and feeding trips could be a response to high nest predation (Ghalambor and Martin 2002), but the long nestling period could increase the overall probability of nest predation. Our study reports a novel nesting strategy previously unrecognized (Batesian mimicry) in a tropical bird, which could increase nesting success in bird species that inhabit areas with high nest predation and have long nesting cycles. We present significant evidence that demonstrates the striking similarities in morphology and behavior between a *L. hypopyrra* nestling in its early stages and a local toxic caterpillar (Megalopygidae), reinforcing the idea of Batesian mimicry.

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Laniocera hypopyrra nestling, day 8. Photo credit: Duván A. García.