

Potential caterpillar mimicry in a tropical hummingbird

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Young animals often face heightened vulnerability to predation, a challenge that exerts strong selective pressure on phenotype and behavior. Birds have evolved a diverse array of strategies to avoid predation during the nesting phase, including concealment, camouflage, direct defense, distraction displays, communal nesting, and even migration (Humphreys & Ruxton, 2020; Ibáñez-Álamo et al., 2015; McKinnon et al., 2010). The young of tropical species are thought to be especially vulnerable (Skutch, 1985), and some (e.g., Londoño et al., 2022) have suggested that the relative lack of natural history knowledge in these regions obscures the true breadth of anti-predation strategies in birds.

Because of their small size (Unzeta et al., 2020) and uniparental care strategy, hummingbirds (Trochilidae) may be especially prone to predators as nestlings. Field measurements of nesting success have found extremely low success rates in some species, with predation as the primary culprit (Baltosser, 1986; Nuñez-Rosas et al., 2021). Despite the potential for strong selection during this life stage, there has been little attention to or description of the ways in which hummingbirds adapt to these predation pressures.

On February 22, 2024, M. Castaño-Díaz and S. G. Giraldo found a white-necked jacobin hummingbird

(*Florisuga mellivora*) incubating a nest. With photos and videos, we subsequently documented several antipredator strategies, including evidence for Batesian mimicry, a rare form of mimicry in birds. We found that newly hatched chicks of this species are covered in an unusual amount of long natal down (neossoptile) feathers that look similar to several Lepidoptera larvae in the area. Chicks also display a caterpillar-like disturbance behavior specifically in reaction to potential predation, and we recorded the use of this behavior in the successful deterrence of a predatory wasp. In this paper, we hypothesize that an exposed nest and high rates of nest predation create strong selection pressures to reduce predation, including strategies like insect mimicry. These observations shed light on the anti-predation strategies of hummingbirds, tropical birds more generally, and the evolution of Batesian mimicry in vertebrates.

Our observations took place between the dates of February 22–March 23, 2024, with a likely 18–20 day incubation period (Appendix S1: Section S1). Females of this species are polymorphic, with ~20% appearing like males while the rest look distinctly different (Falk et al., 2021, 2022). The female on this nest was one of these less common male-like females. The nest was

located along Plantation Road trail in La Soberanía National Park, Panama, approximately 6 m off the main path. It was made primarily from what appeared to be a soft seed material, most likely from nearby balsa trees (*Ochroma pyramidale*) which had opened seed capsules during the time of observation. The nest was 6.1 cm in diameter. During the observation period, we documented several potential antipredator strategies (Appendix S1: Sections S2 and S3).

Most remarkably, the freshly hatched chick appeared to be almost entirely covered in long natal down feathers, which closely matched the coloration of the nest material (Figure 1A, Appendix S1: Figure S1). Close inspection showed that these feathers emerged from the dorsal side of the bird, where they are most visible (Appendix S1: Figure S1). On the first day after hatching, as we

approached within a meter of the nest, the chick reared its head upward and began shaking its head from side to side about once per second, while the long feathers piloerected (Video S1). The chick continued to make these movements during our approach until our final visit on March 18th, though the movements were more subdued by then (Video S2). On March 12, 1–2 days after hatching, we observed and recorded the chick while the mother was away, and a carnivorous Eponime paper wasp approached the nest and appeared to investigate the nest contents. The chick began the same head-shaking movement in response to the wasp's presence, after which the wasp flew away (Video S3). We were unable to continue observations after March 23rd because the chick died (with no apparent physical damage), and the female abandoned the area.



FIGURE 1 (A) *Florisuga mellivora*, day-old hatchling in nest with unhatched egg. Photo by Jay J. Falk. (B–D) Megalopygid species found in the same region as our observations in Central Panama. (B) photo by Riley Fortier, iNaturalist ID: 50107149 (C) photo by Herschel Raney, iNaturalist ID: 149414693 (D) photo by Chelina Batista, iNaturalist ID: 114281370. Panels B–D are shared on iNaturalist under a Creative Commons (CC) License by 4.0: <https://creativecommons.org/licenses/by/4.0/>.

The color, shape, and head-shaking behavior of the nestling showed a strong resemblance to caterpillars with urticating hairs that co-occur in the region (Figure 1). For example, larvae of moths in the Megalopygidae and Saturniidae families are common in the area (Figure 1B–D), and can deliver extremely painful stings (Battisti et al., 2024; Koehler & Zaveri, 2022). Several families within Lepidoptera produce hairs or bristles as larvae, which cause varying degrees of pain and tissue damage, from mild irritation to fatality (Hossler, 2009; Villas-Boas et al., 2018). The behavior of the white-necked jacobin, when approached by humans and a predatory wasp, resembles the sudden “thrashing” or “jerking” behavior exhibited by many caterpillars in response to disturbance (Gross, 1993), including in the habitat where this bird was found. Thus, Batesian mimicry of caterpillars with urticated hairs may prevent chick predation through deception. White-necked jacobin chicks may not resemble a specific caterpillar species, but instead use a more generalized mimicry of caterpillars in the area with urticating spines (e.g., iNaturalist ID numbers: 9425948, 83504143, 114281370, 68642298, 83330695, 25069213, 111671421, 80470732, 13799024, 20496405, 222949276, 224556645).

The predatory Epiponine wasp that approached the nest appeared to immediately trigger head-shaking behavior from the chick, whereupon the wasp subsequently left the nest (Video S3). It is difficult to know the wasp's intention and the precise reason it fled, but it certainly could have posed a lethal threat to an exposed day-old chick. Wasps of the same family (Vespidae) are known to prey on bird nestlings, including hummingbirds (e.g., Fu et al., 2016; Gorosito & Cueto, 2024; Lyons, 2018; Moller, 1990), and Epiponine wasps, in particular, were found to have fatally predated one or more Lined Seedeater chicks in Brazil (Frankhuizen et al., 2020). Besides preventing predation and parasitization from insects (Gross, 1993; Kageyama & Sugiura, 2016; Sugiura & Yamazaki, 2014), urticating hairs on caterpillars can also deter birds (Barbaro & Battisti, 2011; Lindstedt et al., 2008), such that mimicking caterpillars might also provide protection from understory avian predators.

There are several nonexclusive alternatives to the mimicry hypothesis. First, the long natal feathers may have evolved as a form of crypsis by matching the appearance of the nest. The white-necked jacobin natal down coloration is remarkably similar to the nesting material texture and coloration (Figure 1A) and it is possible that the extensive natal down coverage in this species is also used for crypsis. Another possible alternative is that caterpillar larvae and *Florisuga* chicks have convergently evolved a physical barrier (hairs or feathers) to prevent

predators like the wasp we observed from accessing the soft-bodied parts of the animal (Sugiura & Yamazaki, 2014). We suspect this would be most effective against smaller invertebrate predators. The crypsis and barrier hypotheses alone cannot account for head-shaking behavior, although they may be relevant in some contexts or act in tandem. For example, crypsis and a physical barrier may be used as a first line of defense against predation, and head-shaking could be used as a startle mechanism in case of detection and approach by a predator. Long hairs can act as movement sensors in caterpillars (Castellanos et al., 2011) and long feathers may play a similar role. Long feathers may also play a role in thermoregulation.

By explaining both appearance and behavior, the mimicry hypothesis is perhaps more parsimonious than alternatives. Mimicry should also be effective against the many different types of predators known to predate hummingbirds, both vertebrate and invertebrate. However, none of these hypotheses is mutually exclusive. They may play roles toward different predators (Fabricant & Herberstein, 2015), during different phases of a predation sequence (Endler, 1991), and may have multiple functions. For example, barriers may be more effective against insect predators, but crypsis and mimicry may be important deterrents for birds.

The presence of head-shaking behavior at hatching is unusual among birds. In passerines and groups more closely related to hummingbirds, such as swifts, the detection of a nearby presence instinctually elicits begging behavior (i.e., chicks lift their heads while vocalizing and opening their mouths), even if that presence is a nest predator (e.g., Budden & Wright, 2001). Yet hummingbirds have lost this behavior, presumably to reduce detection from eavesdropping predators (Schuchmann, 1989). The type of head-shaking behavior we observed was never mentioned in a study of chick behaviors in 14 hummingbird species across the phylogeny (Schuchmann, 1989), suggesting it has only evolved in specific lineages.

Like the head-shaking behavior, the degree of natal down coverage of white-necked jacobin hatchlings is unusual among hummingbirds. We compared the nest and hatchling appearance of white-necked jacobins and closely related species by searching for photographs of newly hatched hummingbird chicks on ebird.org (filtering for nest tags). All species in the Topaz (including *Florisuga*) and Hermit groups were searched, along with a few other species from other more distantly related clades (Appendix S1: Table S1, following the phylogeny from McGuire et al., 2014). In most species with hatchling photos, we found scant or absent natal down. Only white-necked jacobins and the closely related black

jacobins (*Florisuga fusca*) showed open cup nests on top of understory leaves and the presence of long natal down with little skin exposure.

If this morphology and behavior are uncommon in hummingbirds, why has it evolved in the *Florisuga* lineage? Comparison to another potential evolution of bird-caterpillar mimicry allows for speculation. The natal feathers in nestlings of the cinerous mourner (*Laniocera hypopyrra*) are conspicuously orange (D'Horta et al., 2012) and show a strong resemblance to a Megalopygidae species in the same range (Londoño et al., 2015). Like the white-necked jacobin, chicks of the cinerous mourner did not beg until prompted by specific parental signals and instead made caterpillar-like movements after nonspecific disturbances (Londoño et al., 2015). Londoño et al. (2022) hypothesized that birds with long fledging periods might be especially prone to predation and that this might be the cause of mimicry in the cinerous mourner. Though we do not know the full nesting timeline of the white-necked jacobin, the black jacobin has a fledging timeline of 22–25 days (Schuchmann et al., 2020). While longer than the cinerous mourner period, this is not an especially long time for hummingbirds (Winkler et al., 2020). Instead, we propose that specialized antipredator strategies in the genus *Florisuga* may have evolved in response to the high nest depredation rates found in hummingbirds (e.g., Baltosser, 1986; Nuñez-Rosas et al., 2021) and in tropical regions (e.g., McKinnon et al., 2010). In *Florisuga*, this may be rendered even higher because of their exposed nesting strategy: while many tropical hummingbirds nest under leaves, in caves, or on small tree branches, both *Florisuga* species use open cup nests on top of large, flat leaves in the forest understory.

If true, this begs the question of why they use such an exposed strategy to begin with. Furthermore, the lack of total natal feather coverage in closely related species suggests a cost to the strategy, but specifics are unknown. While the iridescent and flight feathers of hummingbirds typically receive the most attention from researchers, our findings demonstrate that variation in their natal feathers may be yet another fascinating avenue for further research in this family of birds. Experiments using models with potential predators, as well as fine-scale temperature logging at nests, will likely reveal further insights into the diversification of antipredator strategies in hummingbirds and other avian taxa.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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