Breeding biology of Speckled Hummingbird Adelomyia melanogenys in eastern Ecuador

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El Colibrí Jaspeado Adelomyia melanogenys se encuentra comúnmente en los bosques nublados andinos entre Venezuela y Argentina, pero se conoce poco sobre su biología básica de anidación. Grabamos en video un nido entre el 23 de octubre y el 21 de noviembre de 2012 en el noreste de Ecuador, con el objetivo de cuantificar las actividades de empollación y alimentación. El ave empolló del día 1–7 después de la eclosión. Durante este periodo, el adulto gastó un promedio de 52% del tiempo total atendiendo el nido o cerca de él. La actividad de empollar cesó el día 8. A partir de ese día, las visitas de alimentación fueron breves, bajando al 5% del tiempo total observado. El adulto hizo una media de 2,5 visitas por hora, que estuvieron repartidas de forma regular durante todo el día y durante todo el periodo de anidación. Este estudio presenta el primer análisis cuantitativo de la biología de anidación del Colibrí Jaspeado.

Descriptions of nesting behaviour for Neotropical hummingbirds remain incomplete^{6,11,17,18}. Speckled Hummingbird Adelomyia melanogenys inhabits Neotropical montane cloud forests, at elevations of 1,000–2,500 m, from Venezuela to Argentina^{9,14}. Monomorphic, it is the only species in its genus, although recent evidence suggests populations either side of the Andes are genetically distinct⁵ and eight subspecies have been described⁴. The species is typically solitary and does not gather with others to feed, even at flowering trees¹³. Speckled Hummingbirds feed on the nectar of flowers, often near the ground, either from short-tubed flowers or holes at the base of long-tubed flowers^{3,19}.

Incomplete descriptions of the nest⁹ and eggs²⁰, including two nests in captivity^{7,27} are available in the literature. Although nests have long been present in collections¹⁵, a complete description of the species' nesting biology is lacking.

Methods

All observations were made at the Yanayacu Biological Station and Center for Creative Studies (00°36'S 77°53'W), Napo prov., north-east Ecuador. For more complete descriptions of the area, see Greeney et al. 11 and Guayasamin et al. 12. We observed behaviour of one adult hummingbird at a nest, located at an elevation of 2,050 m and sited 4.6 m above ground. We recorded 17 days of video footage between 23 October and 21 November 2012 using a video camera placed on a tripod 10 m from the nest. There was a gap in recording between 8 November and 17 November. We recorded between c.06h00 and 18h00 for a total of 85 hours, beginning during late incubation (23 October-31 October), hatching, into the brooding stage (1-7 November) and ending prior to fledging on 21 November. The adult laid two eggs, but a single nestling hatched. We believe hatching occurred between 31 October and 1 November based on subsequent measurements of nestling size and development, as well as nest visitation patterns.

While Speckled Hummingbird is monomorphic and not readily sexed using plumage, given that only one individual was observed incubating and feeding, we assumed this was an adult female. Males are not known to participate in nesting in any Trochilidae²⁰, and females construct the nest, incubate and rear the nestlings alone.

We recorded frequency and duration of each visit. Nest attentiveness was calculated as the total time the adult spent in the nest incubating, feeding or brooding. Nest attentiveness did not include time spent near the nest. During visits, unique behaviours were noted, when possible. Time spent perched outside the nest was also recorded, as well as entry and exit from the nest. Observations of nestling behaviours were limited by camera angle and nest construction, but some were noted and reported. Waste removal was quantified by marking the time of each observed defecation.

Quantification of visitation rates and duration was made via video analysis using VLC software (www.videolan.org) for playback. Index of Dispersion was calculated using methods outlined in Fowler *et al.*¹⁰. All other statistical analyses were performed using SPSS²⁵. Results of two-tailed tests were considered significant at the 0.05 level and means presented ± standard deviation (SD).

Results

Eggs.—We found two eggs, the first measured 12.4 \times 8.7 mm and weighed 0.48 g, and the second 12.6 \times 8.6 mm, 0.47 g. The first was found undeveloped, presumed infertile, and did not hatch. The second was approximately one-quarter developed at the time of measurement and subsequently hatched. These eggs are slightly smaller than those in the

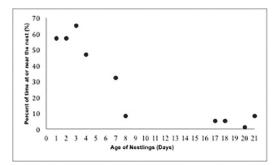


Figure I. Amount of time spent in or near the nest during the nestling period in Speckled Hummingbird Adelomyia melanogenys as a percentage of the total observed. Each point represents the percent of time the adult was observed in or near the nest on each day. Days without observations represent days in which nest activity was not recorded.

collection of the Western Foundation of Vertebrate Zoology (14.02×8.91 mm, collection no. 162.892-2) from Ecuador but are within the range reported by Schuchmann²⁰.

Incubation.—Nest attentiveness during the day averaged $54\% \pm 7$ (n = 34 hours 15 minutes). Frequency of visits averaged 2.44 ± 0.67 /hour/day (n = 94) and were consistent throughout the period (Index of Dispersion¹⁰). Duration of incubation visits averaged 12 minutes one second \pm one minute 52 seconds (n = 94).

Brooding and nest attentiveness after hatch.— During the first seven days following hatching, the adult spent a mean $52\% \pm 13$ of time observed (n = 21 hours 59 minutes, ten seconds) in or perched near the nest. Time spent in or near the nest peaked on day 3 (Fig. 1). On day 8, the adult only visited the nest to feed the hatchling. By days 17-21, visits consisted of brief feeding bouts and time perched on a nearby branch. Prior to each feed, beginning on day 8, the adult perched on the branch before proceeding to feed the nestling. Instead of entering to feed, the adult perched on the nest rim, placed its head inside and regurgitated food into the nestling's gape. The adult would then leave the area. This behaviour was not observed on days 1-7 and was only recorded once on day 8, but was observed consistently on days 17-21.

Compared to the first seven days after hatching, time spent at the nest in the later stages of the nestling period (days 8–21) declined significantly to 5.4% (n=30 hours 32 minutes 33 seconds, range = 1–65% of time observed; two tailed t-test, P < 0.001).

Duration of visits.—During the nestling period, nest attentiveness averaged five minutes 19 seconds \pm five minutes one second (n=153), but declined with nestling age. After hatching and until brooding ceased (days 1–7), nest attentiveness

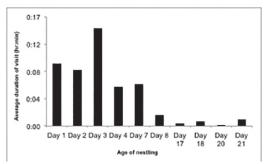


Figure 2. The average visit duration by the adult for each day after hatch. For days 1–7, both brooding and feeding were included, as separation of these behaviours was not possible. Days 8–21 represent mean feeding duration for each day. The time the adult spent on a nearby branch is excluded.

averaged nine minutes 26 seconds \pm three minutes 44 seconds (n=74) and did not differ significantly compared to incubation visits (two tailed t-test, P=0.14). Duration of attentiveness decreased significantly with development of the nestling to a mean of one minute 12 seconds \pm 29 seconds once brooding ceased (n=79 visits; two tailed t-test, P=0.001; Fig. 2). Time observed near the nest was not included in overall nest attentiveness. Length of feeding visits averaged 37 seconds \pm 24 during the post-brooding period (Fig. 2). Exact feeding time was not observable in the brooding stage, because feeding occurred in the nest and out of view.

Nestling provisioning rates averaged 2.5 ± 0.5 visits/nestling/hour (n=153). The frequency of visits showed no significant change throughout the period, though visit frequency had a near-significant change from brooding to post-brooding stages (two tailed t-test, P=0.06). Throughout the period, visits were regularly dispersed (Index of Dispersion¹⁰). Nest visit frequency was also quantified for each hour of each day. Visits were regularly dispersed throughout the day.

Nestling defecation.—After feeds, the nestling was observed defecating outside the nest entrance in a projectile manner. On average, this behaviour occurred 12 minutes 54 seconds \pm eight minutes 27 seconds after each feed (n=30). Defecations were first observed on day 3, and occurred while the adult was present at the nest until day $7 \ (n=7)$. Beginning on day 8, this behaviour was observed more frequently, usually after feeds (n=23), and while the adult was not in the nest.

Discussion

Nestling provisioning rates averaged 2.5 ± 0.5 visits/hour, a rate slightly higher than most other hummingbirds, which often visit the nest <2.5 visits per hour (e.g. White-crested Coquette *Lophornis*

adorabilis, 2.4 per hour²²; Purple-throated Carib Eulampis jugularis, 1–2 per hour²⁸; Glittering-bellied Emerald Chlorostilbon aureoventris, 1–2 per hour¹⁶; Swallow-tailed Hummingbird Eupetomena macroura, 1–2 per hour¹⁷; Bronzy Inca Coeligena coeligena, 1.1–2.0 per hour⁶). Feeding rates do not appear to increase with age, as reported for passerines^{6,8}. Skutch²³ noted that, in general, parents that regurgitate, such as hummingbirds, feed less frequently than those that carry food in the bill. This may be a result of higher calorific content of food brought to the nest, or of high energetic demands of hummingbird metabolism, precluding more frequent nest visits⁶.

Although the precise incubation length at the nest we studied is unknown, an incubation period of 17-20 days has been reported for Speckled Hummingbird²⁰, in accordance with other tropical hummingbird species, which average 20 days⁸. Nest attentiveness during incubation (54%) was lower than that reported for many tropical hummingbirds (62–77%). However, a lower percentage of attentiveness was found in some species including White-crested Coquette Lophornis adorabilis, although the exact stage of incubation in that study was not specified^{8,22}. This is also significantly lower than temperate hummingbirds, probably because in tropical climates, eggs remain warm for longer while the adult is away from the nest^{2,8,26}. Less frequent nest visits permit more time away from the nest, presumably to collect food. This is beneficial to Speckled Hummingbird, as the species often travels several km to forage alone, to avoid competition 7,24 .

During the late incubation and brooding periods, the adult was observed picking at the nest with its bill on multiple occasions. While the purpose of this behaviour is unclear, other researchers have suggested that it is to collect insects caught in the nest.¹⁸ or to maintain the nest. This may include pushing sphagnum moss and spiders' webs into the roof to reinforce the structure⁷.

Time spent brooding began to decline seven days after hatching. Brooding behaviour has not been described in detail for closely related genera such as Oreonympha and Aglaiocercus. However, other hummingbirds have been recorded to decrease brooding time at a similar rate^{20,22}. For Bronzy Inca, Dyrzc & Greeney⁶ reported a decline five days after hatching. Brooding behaviour in this study ceased in the middle of the nesting period, which is typical of other tropical hummingbirds⁸. Once brooding ceased, the duration of feeding visits decreased significantly, which may be a result of the nestling's developed ability to swallow food quickly, necessitating less time at the nest⁶. Furthermore, as the nestling gained the ability to thermo-regulate, the adult no longer needed to enter as frequently to brood. This may be an important survival mechanism, as reduced visit length may lower chances of predation⁶.

Once brooding ceased, the adult often remained perched near the nest prior to feeds. Due to the angle of the camera, we could not confirm the zigzag and erratic approach flight observed in other hummingbird species, which may serve to distract predators from a nest's true location^{6,21}. However, it is interesting to note the regular presence of the adult near the nest, potentially alerting predators to its location. Swallow-tailed Hummingbird has been reported exhibiting similar behaviour¹⁷.

Continued research on Speckled Hummingbird is encouraged, especially behaviour away from the nest, before or after the nesting period. Although basic nesting information is presented here, our data come from just one nest. Future studies are required to better understand Speckled Hummingbird and closely related species' breeding ecology and their role in Andean cloud forest ecosystems. Previous studies suggest that hummingbird diversification may be linked to angiosperm floral specialisation¹. Further understanding the foraging and reproductive ecology of species such as Speckled Hummingbird may help further elucidate this and other interesting questions in Andean cloud forest ecology.

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