ORNITOLOGIA NEOTROPICAL

Volume 17 | 2006 | No. 3

ORNITOLOGIA NEOTROPICAL 17: 321–331, 2006

BREEDING BIOLOGY OF THE GREEN-FRONTED LANCEBILL (*DORYFERA LUDOVICAE*) IN EASTERN ECUADOR

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Resumen. – Reproducción del Pico de lanza mayor (*Doryfera ludovicae*) en el este del Ecuador. – Breves recuentos sobre la biología de reproducción del Pico de lanza mayor (*Doryfera ludovicae*) han sido publicados anteriormente, pero aún no han sido realizados estudios detallados. Se observaron 36 nidos del Pico lanza mayor entre Septiembre del 2001 y Marzo del 2002 en el este de Ecuador. Los huevos presentaron una forma elíptica, fueron de color blanco inmaculado, y con medidas de 14,9 x 9,6 mm. El promedio del tomaño de anidada fue de 1,92 y del éxito del nido fue de 42,1% (0,58 juveniles volantones por nido). El período de incubación fue de 20–21 días y el período de empollamiento fue de 29 a 30 días. Se encontraron nidos a lo largo de los riachuelos exclusivamente, predominantemente en bosque maduro, desde los 0,8 hasta los 6 m sobre el nivel del suelo. Las hembras alimentaron a los polluelos que se encontraron en crecimiento medio, con una dieta basada en "canarias" (Ephemeroptera) y otros insectos pequeños.

Abstract. – Brief accounts of the breeding biology of the Green-fronted Lancebill (*Doryfera ludovicae*) have been published, but detailed studies are lacking. We observed 36 nests of the Green-fronted Lancebill between September 2001 and March 2002 in eastern Ecuador. Eggs were elliptical, immaculate white, and measured on average 14.9 x 9.6 mm. Mean clutch size was 1.92 and nest success was 42.1% (0.58 young fledged per nest). The incubation period was 20–21 days and nestling period was 29–30 days. All nests were along streams, predominantly within mature forest, from 0.8 to 6 m above the ground. Adult females fed half-grown nestlings a diet that included mayflies (Ephemenoptera) and other small insects. *Accepted 28 February 2006.*

Key words: Natural history, nesting seasonality, egg, nestling, nest placement, clutch size, Green-fronted Lancebill, *Doryfera ludovicae.*

INTRODUCTION

The two *Doryfera* hummingbirds, Green-fronted Lancebill (*D. ludovicae*) and Blue-fronted Lancebill (*D. johannae*), although formerly placed in the subfamily Phaethornithinae (e.g., Peters 1945), are currently thought to be part of the basal radiation of the Tro-

FIG. 1. Typical cylindrical nest of Green-fronted Lancebill suspended by rim from a sheltered portion of a fallen log, November 2001, 2100 m a.s.l., Yanayacu Biological Station, Napo, Ecuador. Photo by H. F. Greeney.

chilinae (see Schuchmann 1999, Stiles 1999). The Green-fronted Lancebill ranges from Costa Rica to northwestern Bolivia, while the Blue-fronted Lancebill is confined to the eastern Andes of Colombia, Ecuador, Peru, and, disjunctly, the tepui region of northern South America. The Blue-fronted Lancebill occurs primarily at lower elevations (400–1600 m; Stotz *et al.* 1996) than the Green-fronted Lancebill (1200–1800 m; Stotz *et al.* 1996), with

FIG. 2. Adult female Green-fronted Lancebill incubating in nest partially supported by a small, sheltered rock ledge, December 2001, 2100 m a.s.l., Yanayacu Biological Station, Napo, Ecuador. Photo by H. F. Greeney.

some overlap in the eastern Andes of Colombia, Ecuador, and Peru (Hilty & Brown 1986, Ridgely & Greenfield 2001). Both species are confined to humid forests, are hover-feeding trapliners, and construct cup-shaped nests of moss, plant fibers, and spider webs, which are suspended from hanging roots or vines (Stiles 1999). In Ecuador, Green-fronted Lancebills are encountered most commonly along fast-moving forest streams and are rarely seen outside of mature forest.

Few details on the breeding biology of Green-fronted Lancebill are available in the published literature, which is limited to brief accounts in field guides and short notes based on 1–2 nests. Here we present data on 36 Green-fronted Lancebill nests in eastern Ecuador and compare our observations with previous descriptions of the species' nesting habits, thus significantly expanding knowledge of its breeding biology. We also place this information within the wider context of lancebill taxonomy and hummingbird life history.

MATERIALS & METHODS

We made observations at elevations ranging from 2000 to 2200 m a.s.l. on the privately owned reserve of the Bustamante family, Hacienda San Isidro, and the Yanayacu Biological Station & Center for Creative Studies (00°35'S, 77°53'W), Napo Province, northeastern Ecuador. While logging and dairy farming pressure have caused recent deforestation, large tracts of intact forest remain on the preserve and in the adjacent Sumaco and Antisana reserves. All nest observations were

TABLE 1. Range of dimensions (cm) of Green-fronted Lancebill nests in eastern Ecuador.

Nest stage	Inside cup diameter	Inside cup depth	Outside nest diameter	n (nests)
Early incubation	3.5–4.0	3.0–4.0	8.0–9.0	4
Late nestling	3.5–4.5 x 5.0–7.0	3.0–4.5	6.5–10.0 x 8.5–11.5	5

made in a roughly 600 ha area of primary forest bordered by the Cosanga River on the east and the Las Caucheras road to the west. This area is relatively flat by Andean standards, extends roughly 2.5 km west of the Cosanga River, and is dominated by tree genera such as *Vismia* (Clusiaceae), *Solanum* (Solanaceae), *Nectandra* (Lauraceae), *Miconia* (Melastomataceae), *Ficus* (Moraceae), *Bunchosia* (Malphigiaceae), *Myrica* (Myricaceae), and *Alchornea* (Euphorbiaceae). The canopy is occasionally disrupted by *Chusquea* (Poaceae) *Cecropia* (Moraceae), *Tibouchina* (Melastomataceae), *Baccaris*, and *Vernonia* (Asteraceae). The understory is dominated by *Cyathea* (Cyatheaceae), *Piper* (Piperaceae), *Cestrum* (Solanaceae), *Siparuna* (Monimiaceae), *Monina* (Polygalaceae), *Weinmannia* (Cunoniaceae), and various Rubiaceae. Rainfall ranges from 2500 to 3500 mm per year, with the driest period generally being from August to January. Rainfall during the study averaged 123 mm per month, with the heaviest amounts in September and March.

From September 2001 to March 2002, we observed 40 nesting attempts. As four nests were reused for a second brood, this represents a total of 36 individual nests. We determined clutch size by observing the contents of the nest at least three days after the laying of the last egg and for a period of at least three days. Only nests with incubating adults were used to determine clutch size. We marked eggs with a small black dot at one end using an indelible marker to determine order of laying and hatching. Nests were checked once per day. We measured incubation period from the laying of the second egg to the hatching of that egg. We measured nestling period from the hatching of the first egg to the fledging of the first young. We observed 51 eggs and measured 18 to the nearest 0.1 mm. We measured or estimated nest height to the nearest 10 cm from the bottom of the nest to the ground or stream, and measured nest dimensions to the nearest 0.5 cm at 10 nests.

RESULTS

Nest material, form, and location. All nests were constructed entirely of dry mosses, liverworts, and spider webs. There was no apparent lining. All were attached to the substrate with a tough lip consisting of a thick mat of spider webs. Most were tall and cylindrical (Fig. 1) with a small cup at the top and often with a poorly formed "tail" of material hanging from the bottom. All nests were located in dark, moist, sheltered situations immediately adjacent to, or directly over, 2–5 m wide streams. With one exception, all were located within primary forest and ≥ 1 km from human disturbance. Most nests (23 of 36) were pendant, and hung free from the substrate or rested lightly against it. Of these, 19 nests were attached to rock or clay banks or overhangs. Two nests were in similar situations, but were attached to live moss hanging over rock edges and were "reversed" in orientation such that the nest faced the rock cliff rather than away. One nest was attached to a small rootlet forming a U below a rock outcrop and one was attached to the inner lip of a rain culvert running under a road. The 13 remaining nests were in similar situations, but

TABLE 2. Mean (± SD) measurements (mm) of Green-fronted Lancebill eggs.

References	Length	Width	n (eggs)
Ruschi 1961	16	11	2
Snow & Gochfeld 1977	15.7 (± 0.1)	11.1 (± 0)	2
This study	14.9 (± 0.5)	9.6 (± 0.2)	18

rather than hanging free, the cup was partially supported by a small ledge of substrate (Fig. 2). Small rock ledges supported 12 nests, and one nest was partially supported inside a cavity under a fallen log. Nests with partially supported cups tended to have shorter cylinders but longer, partially formed "tails." Nest height ranged from 0.8 to 6 m.

Nest dimensions show that nest cups were round early in incubation or before the onset of incubation, but that cups and nest cylinders stretched as incubation continued, and especially during the nestling period, resulting in nests with distinctly oblong cup and rim shapes (Table 1). For all nests (n = 36) the entire structure ranged from 9.0 to 15.0 cm in total height (i.e., bottom of nest to nest rim), but often had an additional 4–8 cm of hanging material below the nest cylinder.

Nest construction behavior. We observed seven nests during construction. On all occasions only the female participated. During one observation, a second adult, whose more glittering frontal patch suggested a male, was seen to swoop repeatedly in and chase the female that was building. On three of seven chases this resulted in the loss of the nesting material being carried. At three separate nests, females were observed adding material to the rim of the nest during incubation.

We found one nest as the adult brought in the first piece of moss. It appeared that there was already a thick mat of spider web attached to the rock. The moss, an approximately 4-cm long piece, was hung from this lip. Four days later a loose, hanging cylinder was formed which approximated the size of the finished nest but lacked any well-formed cup. Two days later the cup was well formed and the female was observed entering the nest and wiggling around inside the cup, apparently using her body and tail to further shape the cup. Twelve days from the original observation, the first egg was laid. These and other observations suggest a 12–16 day building period.

At all of the nests except for those with running water directly below, we found dry moss, indistinguishable from that used in nest construction, in clumps below the nest. The amount found ranged from a few scraps to that nearly equal to a completed nest. This extra material, was often a good indication of an otherwise hidden nest.

Eggs and incubation. Of three nests where laying date was determined, one female laid on subsequent days and two skipped a day between eggs. Females spent the night on the nest after laying the first egg, but it was not determined exactly when incubation began.

All 51 eggs were elliptical and immaculate white. Linear measurements of eggs ranged from 14.1–15.7 mm in length and 9.1–10.0 mm in width (n = 18; see Table 2 for mean ± SD). Mean clutch size was 1.92 (n = 26 nests). Modal clutch size was two. At 24 nests where clutch size was two, six were nests that were reused, in which a clutch was subsequently laid in the same nest, or nests that were rebuilt in the same location after removal of a successful nest. One nest, in which two successive clutches were laid, contained only one egg per clutch. At two nests, both with a

FIG. 3. One to three-day-old Green-fronted Lancebill nestlings begging, January 2002, 2100 m a.s.l., Yanayacu Biological Station, Napo, Ecuador. Photo by H. F. Greeney.

clutch of two, the incubation period was 20 and 21 days, respectively. Only females incubated. Females left the nests as early as 05:48 h and were never seen to leave the nest after 18:15 h. During the last hours of daylight (17:30–18:15 h), females were often observed leaving the nest every 1–2 min to forage for insects over the stream for periods of 1–4 min.

Nestlings. Of five nests where hatching dates were determined, the eggs hatched one day apart in three and on the same day at two. The nestling period was 29 days (two nests with two young each) and 30 days (one nest with a single nestling).

At hatching, nestlings were completely naked and dark grayish pink with pale creamy yellow bills. Within 24–48 h the dorsal surface turned dark gray to black (Fig. 3). Bills, and especially the gape, became bright yellow to yellow-orange. As the bill lengthened it darkened to black, except for the base which remained yellow. Black pin feathers developed over the entire body and feather sheaths broke at ≈6–8 mm in length. Wing pin feathers broke sheaths around days 8–10. Just prior to fledging, dorsal plumage was green, ventral plumage was pale gray, crowns and napes were dull bronzy, and an indistinct white post-ocular spot was present.

We examined the crops of two dead, 10-day-old nestlings found in mid-March. The crop of one contained 81 small (6–9 mm) mayflies (Ephemeroptera) and one 4-mm long fungus gnat (Sciaridae, Nemotocera, Diptera). The crop of the other nestling contained 74 mayflies, 9 fungus gnats, and one moth fly (Psychodidae, Diptera).

The female was almost always observed

brooding when nestlings were ≤ 10 days old. Nests with no adult present contained nestlings that were frequently cold to the touch. Females brooded less frequently once nestlings were ≥ 10 days old, and nestlings were always warm to the touch. These observations suggest that nestlings begin thermoregulation sometime around 10 days of age. For additional photographs of nests, eggs, and nestlings, see Sheldon & Greeney (2005).

Nesting success. Seven of 17 nests with two-egg clutches hatched only one egg. Of 19 nests where nest fate was determined, two failed during incubation, eight failed during the nestling period and one failed during building. Eight of 19 nests fledged at least one young (42.1% nest-success), with five of these fledging one young and three fledging two young (0.58 young per nest, or 1.38 young per successful nest).

Of two nests that failed during incubation, one was destroyed by a waterfall as it expanded during a rain storm, and a second collapsed under the weight of the incubating female. A nest that failed during building fell to the ground near completion, possibly due to faulty construction. Each of these nests were among those with a great deal of fallen material below. Two of the eight nests that failed during the nestling period are thought to have done do as a result of predation of the female away from the nest. Both nests were intact. In one the nestlings appeared unharmed and in the other the nestlings appeared partially eaten, but the damage was likely that of insects or snails. The remaining 6 nests were damaged and empty, and are presumed to have been destroyed by a predator.

Nesting seasonality and nest reuse. We discovered the first lancebill nest two days prior to laying on 8 September 2001. Subsequently, throughout September, we found nests during building and incubation. Nestlings were not observed until late September and early October. Nests in all stages were found from October through December. Most nesting activity had ceased by the end of January. Adult presence along streams was greatly reduced by this time and by mid-February only an occasional adult was encountered. A single exception, a nest that had been rebuilt after successfully fledging two young and then having been removed, was found with a third clutch of two eggs in mid-February. The nestlings were found dead in the nest on 18 March and it is estimated they would have fledged in early to mid-April. We thus estimate that breeding activity began in late August to early September and continued to late March or early April with the majority of breeding occurring from mid-October to mid-December.

Three nests were collected after successful fledging. At each of these sites, a second active nest was later discovered in the same location. At an additional four nests, a second clutch was laid after fledging of the first brood. It is not known whether old nests were removed and rebuilt or if they were reused, but the short period (< 1 month) elapsing before the appearance of a new clutch suggests that nests were reused. Thus, seven successful nest sites were reused; no failed nest sites were reused.

DISCUSSION

Green-fronted Lancebill nesting activity in northeastern Ecuador began in late August–early September and continued through late March–early April. The peak in activity appeared to be from mid-October to mid-December. These breeding dates roughly correspond to the dry season and are similar to those reported for Green-fronted Lancebills in Costa Rica (August–January; Stiles & Skutch 1989), Colombia (May–January; Hilty & Brown 1986, Ramirez & Arias 1994), Peru (September; Snow & Gochfeld 1977), and northwestern Ecuador (June–January; Ruschi 1961, Greeney & Nunnery 2006). Our data on the duration of nest building (12–16 days) and incubation (20–21 days) in Ecuador are very consistent with the 12 day nest-building and 20–21 day incubation periods documented at a single Green-fronted Lancebill nest in Colombia (Ramirez & Arias 1994). The nestling period at our study site (29–30 days) was shorter than the 36 day nestling period observed at the Colombian nest, but this difference could be due to human activity patterns near the Colombian nest, which was located at a human dwelling (Ramirez & Arias 1994). Our data on nestling periods are based on a larger sample size (n = 3) and none of our nests were near human activity. Our egg size data are also based on a much larger sample size than data previously available, which may explain our slightly smaller average egg dimensions (Table 2).

Nest form (bulky, pendant cup) and nest location (dark sheltered situations associated with streams) of Green-fronted Lancebills in our study area were similar to those reported elsewhere (Snow & Gochfeld 1977, Hilty & Brown 1986, Stiles & Skutch 1989). Nest material and attachment to the substrate, however, show some variation. Snow and Gochfeld (1977) reported a nest resting on a rock ledge, and Ruschi (1961) described a nest partially supported by and partially suspended from a low branch. We also found that, while most nests were completely pendant, some received partial support from the substrate (see Fig. 2). Although Stiles and Skutch (1989) reported Costa Rican nests to be usually attached to a rootlet or twig and to include tree fern scales, nests in our study area were made exclusively of moss and spider webs and were almost always suspended, attached by the nest rim, from a solid substrate such as a rock. It is difficult to assess the importance of this apparent variation because previous reports were based on very few nests, and thus have no measure of variation. If nest material and nest substrate do vary geographically, this may simply reflect variation in availability of nest materials and substrates. Documentation of nest reuse and nest site reuse in Colombia (Ramirez & Arias 1994) are consistent with our observations, and suggest that nest and nest site reuse are common occurrences with Green-fronted Lancebills.

The systematic relationships of the *Doryfera* lancebills have long been uncertain. The genus has traditionally been placed next to the monotypic genus *Androdon* (Tooth-billed Hummingbird, *A. aequatorialis*) in checklists, apparently due to similarities in bill morphology (bill serrations of *Androdon* notwithstanding), and both genera have been included within the hermit assemblage, subfamily Phaethornithinae (e.g., Cory 1918, Peters 1945). Systematic work based on osteological characters (Zusi & Bentz 1982) and molecular techniques, including protein electrophoresis (Gill & Gerwin 1989, Gerwin & Zink 1998), DNA hybridization (Sibley & Ahlquist 1990, Bleiweiss *et al.* 1994, 1997), and DNA sequencing (Altshuler *et al.* 2004), however, consistently show that *Doryfera* and *Androdon* are not hermits. Based on similarities in song structure, shape and coloration of rectrices, and hindneck musculature, Schuchmann (1995, 1999) suggested that the two genera may even constitute a separate subfamily, Doryferinae. On the other hand, recent molecular phylogenies indicate that *Doryfera* and *Androdon* both belong in the primitive "mango" clade of the Trochilinae (Bleiweiss *et al.* 1997, Altshuler *et al.* 2004). Among the mango-types, which also include *Heliactin*, *Heliothryx*, *Antracothorax* and *Eulampis*, *Doryfera* appears to be most closely related to the *Colibri* violet-ears and the *Augastes* visor-bearers (Bleiweiss *et al.* 1997, Altshuler *et al.* 2004; see also Gerwin & Zink 1998).

The pendant form of Green-fronted Lancebill nests is similar to that of the phaethornithine hermits, and is unique within the Trochilinae. Yet, Green-fronted Lancebill nests also show some affinities to the sturdier, bottom-affixed nests typical of the majority of trochiline species. That is, Green-fronted Lancebill nests are often not completely pendant, but may receive partial support from the substrate (see also Ruschi 1961) or a ledge of the substrate (see Fig. 2) to which they are affixed. Thus, while lancebill nests are clearly pendent, the degree to which they receive support from below varies and appears to be intermediate between the truly pendent nests of hermits and the typically non-pendent nests of non-hermits. Our data, therefore, further supports the idea that nest form in *Doryfera* lancebills represents a transition between subfamilies Phaethornithinae and Trochilinae. Note that, while the nest of the single *Androdon* species, to which *Doryfera* is traditionally allied, remains undescribed, species in all other genera of the mango clade (following Altshuler *et al.* 2004) construct small compact cups that are saddled on horizontal branches or attached to vertical branches (see Schuchmann 1999).

Development periods for Green-fronted Lancebills are remarkably long compared with those documented to date for hermits and most other trochilines (Schuchmann 1999). The incubation period for Green-fronted Lancebills was 20–21 days, which is substantially longer than the 16–19 day incubation period typical for most hummingbirds (Schuchmann 1999). Among other mango-types (following Altshuler *et al.* 2004), incubation periods range from 15–18 days in *Anthracothorax*, *Augastes*, and *Colibri*, to 17–19 days in *Eulampis* (Schuchmann 1999). The nestling period for Green-fronted Lancebills was 29–30 days, also notably longer than the 23–26 day nestling periods typical of other hummingbirds and, more specifically, the 17–25 day nestling periods documented for other mango-types (Schuchmann 1999). Incubation and nestling periods of the Green-fronted Lancebill are intermediate between those of species thought to be closely related to lancebills and species that inhabit extremely high-elevations (e.g., Andean Hillstar, *Oreotrochilus estella*) (Schuchmann 1999). However, consistent with observations that inclement (i.e., cool, wet) weather often prolongs nestling development time in hummingbirds (see Skutch 1973), the relatively long incubation and nestling periods of the Green-fronted Lancebill may simply be due to the environmental conditions characteristic of its habitat and microhabitat.

Green-fronted Lancebill nestlings lacked the dorsal neossoptiles (natal down) characteristic of the vast majority of hummingbird species (Collins 1978, Schuchmann 1989). Schuchmann (1989) proposed that dorsal neossoptiles function to stimulate begging behavior in older nestlings, and represent an adaptive response to nest predation pressure, replacing begging vocalizations. He argued that air currents from an adult female hummingbird's wings, created as she hovers near the nest prior to feeding, are perceived by the neossoptiles, which elicits gaping (begging) behavior. Schuchmann (1989) showed experimentally that nestlings with neossoptiles removed ceased to respond by gaping to a female's arrival near the nest. One prediction of Schuchmann's hypothesis is that nestling begging vocalizations should be more prevalent in hummingbird species that lack dorsal neossoptiles. In Ecuador, we did not hear nestling begging vocalizations at Green-fronted Lancebill nests at any stage of nestling development. We note, however, that stream noise was characteristic of all Green-fronted Lancebill nests that we observed and we can not say with absolute certainty that nestlings did not give begging vocalizations. We encourage field biologists in the Neotropics to carefully note the presence (and configuration of) or the absence of dorsal neossoptiles and begging vocalizations in hummingbird nestlings.

ACKNOWLEDGMENTS

We are indebted to C. Bustamante and M. Lysinger for allowing access to the San Isidro preserve. For logistical support we thank the owners of the Magic Roundabout Lodge and Cabañas, Baeza. We thank C. Torres S. for help with Spanish translation. For critically reviewing earlier versions of this manuscript we thank P. R. Martin and M. Lysinger. This study was supported by the generous donations of Ruth Ann and John V. Moore through the Population Biology Foundation. Additional funding was provided by a Pamela & Alexander F. Skutch Award and a Rufford Small Grant. Preparation of the manuscript was greatly facilitated by the generosity of Tim Metz, Jay Peltz, and the Humbolt crew. This work was inspired and aided by the PBNHS and is publication number 16 of the Yanayacu Natural History Research Group.

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