BREEDING ECOLOGY OF THE SMOKE-COLORED PEWEE (CONTOPUS FUMIGATUS) IN NORTHEASTERN ECUADOR

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Resumen. – Ecologia reproductiva del Pibí ahumado (*Contopus fumigatus*) en el noreste de Ecuador. – Estudiamos la biología reproductiva del Pibí ahumado (*Contopus fumigatus*), una especie bastante común en áreas montañosas de Sudamérica, en al noreste de Ecuador desde 2001–2008. Econtremos nueve nidos, los que fueron actives durante las meses de septiembre hasta siciembre, sugiriendo un periodo de reproducción durante las meses más secas del ano. Nidos eran copas abiertas de poco profundidad y construido de musgos, con el interior de la copa hecho de licenes y fibras pálidas, y ubicados sobre las ramas horizontales de arboles en áreas disturbadas. El promedio de la altura de nidos sobre el suelo era 8,8 m y Alnus acuminata (Betulaceae) era la especie de árbol utilizado con mas frecuencia. El tamaño del puesto de huevos era dos en cuatro nidos y huevos eran blancos con manchas de color canela y morada. Solo un adulto, probablemente la hembra, construyó el nido y asentó sobre los huevos y pichones. Pocas observaciones durante incubación sugieren que los huevos están atendidos durante 67% del día. Ambos de los adultos atienden a los pichones, trayendo de una variedad de insectos volantes, generalmente 3–10 veces por hora. Un nido fue construido durante 14 días, el periodo de incubación era 16 días, y un pichón voló del nido 21 días después de eclosionar.

Abstract. – We studied the breeding behavior of the Smoke-colored Pewee (*Contopus fumigatus*), a common inhabitant of montane South America, in northeastern Ecuador from 2001–2008. We found nine nests which were all active from September to December, suggesting a reproductive peak during the drier months. Nests were shallow mossy cups, lined with lichen and/or pale fibers, and saddled over a horizontal branch in clearings or forest edges. Mean nest height was 8.8 m and *Alnus acuminata* (Betulaceae) was used as a substrate most frequently. Clutch size was two eggs at four nests and eggs were white with sparse cinnamon and lavender markings. Only one adult, presumably the female, built the nest, incubated, and brooded. Brief observations during incubation suggest that eggs are covered for c. 67% of daylight hours. Both adults, however, fed the nestlings, sharing the work almost evenly and feeding nestlings a variety of aerial invertebrates, generally at rates of 3–10 feedings/h. At one nest, construction lasted c. 14 days; incubation period was 16 days; and the single nestling left the nest after 21 days. *Accepted 5 September 2010*.

Key words: Nest construction behavior, *Contopus fumigatus*, cloud forest, Ecuador, egg, nest, nestling, parental care, Smoke-colored Pewee.

INTRODUCTION

The Smoke-colored Pewee (Contopus fumigatus) is a common and widespread Andean fly-

catcher (Tyrannidae), one of 14 species in the genus. It has a broad geographic range (c. 1,000,000 km² sensu BirdLife International 2004) ranging from Venezuela to northwest-

ern Argentina, and is predominantly found at elevations of 1000–2500 m a.s.l. (locally down to near sea level) (Hilty & Brown 1986, Ridgely & Greenfield 2001, Farnsworth & Lebbin 2004). It inhabits humid montane forest, forest borders, and clearings with scattered trees. In Ecuador, this species occurs on both slopes of the Andes and also on the coastal cordillera, with east Ecuadorian birds assigned to the subspecies *ardosiacus* (Ridgely & Greenfield 2001, Farnsworth & Lebbin 2004).

The biology of the Smoke-colored Pewee (Contopus fumigatus) is poorly studied. Understanding of its reproductive ecology is confined to a nest described only in passing by Skutch (1967) who reported a "shallow mossy cup built in the fork of a mossy branch" from eastern Ecuador near Baños. There remains no published information on incubation and nestling periods or for any aspect of parental care. Here we provide the first detailed description of the nest, as well as observations on nest building and nestling provisioning behavior from observations in northeastern Ecuador.

METHODS

We studied the nesting of the Smoky-colored Pewee from 2001-2008, at altitudes of 2050-2150 m a.s.l., in the vicinity of the Yanayacu Biological Station and Center for Creative Studies (00°36'S, 77°53'W), 5 km west of Cosanga (Napo Province, northeastern Ecuador). In January 2006, a single adult was captured and banded at the station. Based on observations of this adult at subsequent nests, we noted that it was the only adult to build nests or to incubate eggs, and thus infer that this banded adult was the female based on the parental division of labor in other tyrannid species (Fitzpatrick 2004). On 3 November 2007, we observed a nest (no. 1) with a single, mid-aged nestling, but ceased observations after 6 November when the nestling disappeared during the night. Subsequently, we made observations of the banded bird from this nest as it started to build a new nest (no. 2) on 9 November, c. 40 m from the old nest. We quantified observations on nest construction at nest no. 2 from 11-14 November 2007 and made observations of incubation behavior at the same nest in December 2007. At this nest we also gathered direct observational data during the nestling period by watching the nest from a distance of c. 25 m, using 10 x 40 binoculars. We observed this nest on 21 days, with observation periods ranging from 1-7 h and totaling 65 h of observation. We began observations some time after 05:45 h and finished prior to 16:00 h. Significance values were calculated using Spearman's Rank Correlation test (r_a).

RESULTS

Nests. We found nine nests, all of which were situated in isolated pasture trees (n = 8) or at forest edges. Seven nests were built in alder trees (Alnus acuminata; Betulaceae), one in a Miconia tree (Melastomataceae), and one in Nectandra (Lauraceae). The nests in alders, however, were all built by a pair around the Yanayacu station, which is surrounded by predominantly this species of tree. Nevertheless, Alnus is likely the most commonly occurring tree in naturally disturbed areas (pers. observ.) and this may still be a typical substrate for Smoke-colored Pewee in the area. Mean (± SD) nest height was 8.8 ± 4.6 m (range = 3.5– 18 m), in substrate trees with a mean height of 17.3 \pm 4.7 m (range = 7–22 m). All nests were saddled over horizontal branches (mean diameter = 4.6 ± 1.1 cm; n = 4), and all were roughly centrally located between the main trunk and the end of the branch.

Nests were shallow cups built externally of moss and lichens with sparse amounts of spider web used to bind them. Internally they were sparsely lined with dark rootlets (n = 2) or with rootlets and *Usnea* lichens (n = 1), but this lining was not well differentiated from the external portion. Nests were saddled over horizontal branches and were externally slightly longer than wide (along the axis of the supporting branch). Internally, however, egg cups were nearly round. External measurements (cm) of three nests were: 12.8 ± 0.3 long by 10.0 ± 1.0 wide by 4.3 ± 1.4 tall. Internal measurements (cm) were: 6.2 ± 0.8 wide by 3.0 ± 0.9 deep.

Nest construction behavior. At the commencement of our observations of nest no. 2, the nest was only a simple, flat platform, lacking a well-defined cup. On 112 of 140 observed adult visits, we were able to see the legs well enough to determine whether or not it was the banded individual (hereafter female). The female usually arrived with lichens or rootlets, sat down on the nest, and incorporated the material into the nest. After incorporating the material, it generally rotated several times, alternating rotations with a movement whereby it pressed its breast into the cup and shuffled rapidly. Occasionally the female arrived without visible material, but still entered the nest and made wiping movements with its bill along the edge of the nest. During these visits she was likely wiping spider webs along the outer portion of the nest. Building visits lasted from 6 to 80 s (median = 20.0 s, Q_1 = 11.5 s, $Q_3 = 27.0$ s, n = 61; or mean = 23.4 s ± 15.56 , n = 61). On 12 November (4th day of nest construction), during 3 h of observations (12.00-15.00 h), the bird visited the nest with material 44 times (15 visits/h). The longest period of absence lasted 16 minutes. On 13 November, during 3.5 h of observations (08:30-12:00 h), we recorded 66 visits (19 visits/h). Within this period there were several bouts of higher visitation rates (up to 34 visits/h), and during this time the longest absence lasted 23 min. On 15 November, the

nest seemed complete, but the first egg was not laid until 7 days later (22 November). This was only 16 days after the loss of this pair's previous nest.

Eggs and incubation. Due to the precarious positioning of most nests, we were unable to remove any eggs for measuring. However, clutch size at four nests was two. Eggs were white with sparse brown, cinnamon, and lavender flecking. Markings were either heaviest around one end or formed an indistinct ring.

We watched a single nest (no. 2) during the incubation period during two hours (15:35–17:35 h) on 1 December 2007 (c. day 13 of incubation). During the observation period there were 12 periods of attendance and 12 absences. Incubation periods lasted from 1 to 11 min (total 80 min), and absences from 1 to 5 min, giving an incubation constancy of 67%. Both eggs at this nest were laid in the morning, roughly 48 h apart. At one nest incubation lasted 16 days, from clutch completion to hatching.

Nestlings. Nestlings were able to lift their heads above the rim of the nest for the first time at the age of 10 days. At 13 days, nestlings were visible above the rim even with their heads lowered. By this age the dorsal areas were covered with white-grayish down. Frequently we observed the nestlings panting and hanging their heads over the edge of the nest while it was in direct sunlight. At the age of 16 days, we first observed nestlings preening their plumage and exercising their wings. Nestlings at this age were well feathered, with only a few remnant tufts of pale down. On the 17th day, wing flapping became more common and, for the first time, observed nestlings ejecting fecal material over the rim of the nest (previously fecal sacs were removed by parents). We first observed nestlings to be able to hover briefly, low above the nest, on day 19. At this age few

down tufts remained, confined mostly to the sides of their heads, and nestlings produced all fecal sacs in the absence of adults, ejecting them from the nest. By the afternoon of day 20, nestlings began to leave the nest, occasionally up to 1 m, walking cautiously out on the supporting branch. That day the female arrived twice without food, sitting on the empty nest until the young returned down the branch. At a nest at which only one egg hatched, the single nestling left the nest at 08:00 h at 21 days of age. At this time it was sitting c. 0.5 m from the nest and spontaneously flew from the tree and disappeared into the nearby forest.

Nestling provisioning and behavior. Except where noted, the following observations were gathered at a nest no. 2, containing a single nestling and at which only the adult female was banded. Across the entire observation period (33.5 h), feeding rates ranged from 3.7 to 9.3 visits/h (Table 1), and showed no change correlated with nestling age ($r_s = 0.006$, P =0.976). Visits were randomly (not regularly or clumped) distributed during the day (Index of Dispersion; Fowler et al. 1998, pp. 62-66). Fourteen days after hatching, however, one bout of very intense provisioning was recorded (not included in Table 1), at which time the nestling was fed 29 times/h (from 16:23-17:23 h). A typical example of daily patterns of provisioning is provided by our 7 h of observation on day 10 of the nestling period. Absences (n = 36) ranged from 1 to 37 min (mean = 9.14 ± 9.04 min.). Across the entire observation period we recorded 258 provisioning visits, 115 (56%) by the banded female, 91 (44%) by the male, and an additional 52 visits where we could not distinguish the sex of the adult. As it was easier to observe when the adults were banded than it was to confirm they were not, we suspect that the male's contribution is underrepresented by these numbers and it is likely that parental contributions to nestling provisioning were nearly equal. Our unquantified impression was that the foraging areas of the two adults did not overlapped much, with the female foraging closer to the nest than male. On 14 occasions, both parents landed on the nest nearly simultaneously, and fed the nestling in quick succession. On two occasions, when arriving simultaneously, the male passed the prey to female, and left before she fed it to the nestling. Once the brooding female left the nest and flew c. 20 m to where the male was perched and took a prev item from his bill, returning immediately to feed the nestling. On 12 instances, prey items were very large (compared to nestling size) and, after several attempts to feed nestling, the prey item was consumed by the female. Once, however, the female attempted to force the large prey into the nestling's gape, and after 6 min succeeded. At this nest, we were only able to identify six prey items: adult Lepidoptera (5) and a dragonfly (Anisoptera) (1). At a nest containing two nestlings in late October 2003, we identified 27 prey items: a dragonfly (1), damselflies (Zygoptera) (3), cicadas (Cicadidae) (15), and adult Lepidoptera (9) which included five in the tribe Pronophilina including two Pronophila orcus, one Lymanopoda albocincta, and one Corades ulema. At this nest, when adults captured a cicada they usually thrashed it several times against their perch, often knocking off the abdomen, and feeding only the head and thorax to the nestlings. On several occasions, the movements of the thrashing adult attracted the second adult, and the falling portion of the cicada was caught and consumed or carried to the nest by the second adult.

At the other nest found in October 2006, we noted that there was a great deal of interaction between the two siblings. When adults arrived there was a good deal of seemingly aggressive contact between the nestlings, often nearly resulting in the pushing of one

TABLE 1. Pattern of provisioning rates in the nest no.2 of the Smoky-colored Pewee.

Nesting age (days)	No. of observation hours	Visits/hour
9	2	5.5
10	7	5.7
11	2	4.0
14	2	3.7
16	5	4.2
17	2	9.0
18	3	4.0
19	5	5.6
20	3	5.0
21	2.5	5.2

from the nest. Even in the absence of adults, nestlings continued to jostle and push against each other. Older nestlings would often stand and flap their wings vigorously, often dislodging themselves from the nest and onto the adjacent branch where they would continue exercising their wings for several additional minutes. On one occasion, a c. 20 day-old nestling stood in the nest, leaned into the cup, and rapidly probed its bill into the nest lining in a sewing-machine-like fashion.

Brooding behavior. The sex of the adult which performed brooding of the young was identified 42 times, always as the female. Two nestlings (2 and 3 days old) were brooded during > 50% of the observation period. After 9 days of age, brooding diminished sharply (Table 2). There was a significant negative correlation between nestling age and time devoted to brooding ($r_s = -0.898$, n = 8, P = 0.018) (Table 2). However, during heavy rain, the female with a c. 11 day-old nestling brooded it without interruption for 49 min, resulting in a brooding rate of 45.6% during a 3 h observation period. By day 17-21, nestlings were rarely brooded and then usually only in short bouts of a few minutes. At this time, the nestlings were so large that the

TABLE 2. Time devoted to brooding and nestling age in nest no. 2 of the Smoky-colored Pewee.

Nestling age (days)	Observation time (h)	Brooding time
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4	1	51.7
9	2	35.8
10	7	12.1
11	2	13.3
14	2	3.3
17	2	7.5 (rain)
19	5	0.7
21	2.5	3.3

brooding female was able to cover only the rear portion of the nestlings. Twice, on sunny days around midday, the female perched on the edge of nest, apparently trying to shade the nestlings.

Nesting seasonality. Of the nine nests we found, the earliest was a nest with incubation under way on 6 September. We found three nests under construction in mid-November, another incubating on 23 December, and nests with nestlings on 16 October, 2 November, and 2 December. The last active nest we found contained two nestlings on 26 December. In addition to these observations, on two separate occasions we observed adults actively feeding fledglings on 19 and 22 January. In combination, these records suggest that Smoke-colored Pewee exhibits fairly marked breeding seasonality, confining most activity to the drier months in our area.

DISCUSSION

There are 14 species of *Contopus* worldwide (Fitzpatrick 2004), including 3 species in North America and 11 species in the Neotropical region (Farnsworth & Lebbin 2004). Little is known about breeding biology of the Neotropical species, with the exception of the wide-ranging the Tropical Pewee (*C. cinereus*)

and the Hispaniolan Pewee (C. hispaniolensis). Most of the temperate species are better studied. Clutch size of the Smoke-colored Pewee was two eggs while in six other species of Contopus (including 3 North American species) clutch size ranges from two to four eggs. At one nest, nestling period was 21 days. This suggests that the Smoke-colored Pewee may have a longer fledgling period than temperate Contopus spp. (14-18 days; Farnsworth & Lebbin 2004). Other aspects of breeding biology seem to be very similar across the genus. For example, in the Tropical and Hispaniolan Pewee only females build nests and incubate while nestlings are fed by both parents (Bemis & Rising 1999, Bent 1963, Farnsworth & Lebbin 2004, McCarty 1996, Skutch 1997). Habitat and nest placement of the Smokecolored Pewee, on horizontal branches distant from the centre of the substrate, is also similar to other congeners (see previous citations).

In both nests we observed from hatching, two eggs hatched but after several days only one nestling remained. Partial brood losses from predation are rare (e.g., Halupka 1998), and we suggest that nestling competition explains this phenomenon in the Smoke-colored Pewee. This supposition is supported by our observations of frequent physical interactions between nest mates in this species. We hope this contribution encourages others to document the breeding biology of this and other Neotropical birds, as many of even the most common and wide-spread species are in need of further study.

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