



NEST DESCRIPTION AND NESTING BEHAVIOR OF THE RUFIOUS-CAPPED WARBLER (*BASILEUTERUS RUFIFRONS*)

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Abstract · The breeding biology of most tropical resident bird species is little-documented, particularly for sexually monomorphic species in which sex-specific contributions to nest-building and nestling provisioning are challenging to quantify. We describe nest structure and adult behavior throughout the nesting cycle for a color-banded population of Rufous-capped Warblers (*Basileuterus rufifrons*), a widespread sexually monomorphic tropical resident songbird. Using focal observations of 11 nests, combined with video monitoring during the incubation and nestling periods, we provide new information on this species' nesting behavior, particularly sex-specific parental contributions to nest-building, incubation, and nestling care. All nests were dome-shaped structures with a side entrance constructed of grasses, twigs, and leaves, as is typical for *Basileuterus* warblers. Females were the primary nest-builders, although we also observed male-assisted nest-building at one nest, which is a rare behavior in wood-warblers. Females were the sole incubators, and the incubation period in this population was 13–14 days. Video recordings confirmed that males and females made equivalent contributions to nestling feeding and nest sanitation. Our study provides detailed observations of both male and female Rufous-capped Warblers during all stages of the nesting cycle, and thus improves our understanding of nesting behavior in this common yet little-studied species.

Re resumen · Descripción del nido y comportamiento de anidación del Chipe gorrirrufo (*Basileuterus rufifrons*)

La biología reproductiva de la mayoría de las aves residentes tropicales es poco conocida, particularmente para especies monocromáticas en que las contribuciones de cada sexo a la construcción de nido y la alimentación de los pichones son difíciles de observar. Describimos la estructura del nido y el comportamiento de los adultos durante todo el ciclo de anidación para una población anillada del Chipe gorrirrufo (*Basileuterus rufifrons*), una especie común de Paseriforme residente tropical monocromática. Con base en observaciones de 11 nidos y monitoreo de video durante los períodos de incubación y presencia de pichones, proveemos nueva información sobre el comportamiento de anidación de esta especie, particularmente sobre las contribuciones de cada sexo a la construcción de nido, la incubación, y el cuidado de los pichones. Todos los nidos presentaron estructura en forma de domo con entrada lateral, contruidos con hierbas, palitos, y hojas, típicos de las especies de *Basileuterus*. Los nidos fueron contruidos principalmente por las hembras, aunque en un nido observamos que la construcción fue asistida por el macho, un comportamiento raro en la familia Parulidae. Solo las hembras incubaron los huevos, y el período de incubación en esta población fue de 13–14 días. Los videos confirmaron que los machos y las hembras contribuyeron igualmente a la alimentación de los pichones y la limpieza del nido. Nuestro estudio provee observaciones detalladas de ambos sexos del Chipe gorrirrufo durante todo el ciclo de anidación, mejorando nuestro entendimiento sobre el comportamiento de anidación en esta especie común pero poco estudiada.

Key words: *Basileuterus rufifrons* · Breeding biology · Costa Rica · Nest-building · Nest description · Parulidae · Rufous-capped Warbler

INTRODUCTION

The breeding biology and nesting behavior of tropical resident bird species have received little study compared to their temperate counterparts (Stutchbury & Morton 2001). Although nests are described for many tropical species, detailed observations on male and female behavior during different nesting stages are uncommon. This is especially true for sexually monomorphic species, where the contributions of males and females are more difficult to observe without a color-banded population (Cox & Martin 2009, Sandoval & Mennill 2012). This is the case for the family Parulidae (New World wood-warblers), in which life-history descriptions of species in the

Receipt 16 February 2018 · First decision 9 April 2018 · Acceptance 20 July 2018 · Online publication X 2018

Communicated by Kristina Cockle © The Neotropical Ornithological Society

monomorphic tropical resident genera *Basileuterus*, *Myioborus*, and *Myiothlypis* are scarce (reviewed in Cox & Martin 2009). All *Basileuterus* warblers studied to date have similar dome-shaped nests with a side entrance, built on or near the ground in a slope or under a shrub for concealment and protection from heavy rains (e.g., Rowley 1962, Skutch 1967, Greeney et al. 2005, Cox & Martin 2009). However, descriptions of nesting behavior, including nest-building, incubation, and parental provisioning of nestlings, are largely based on observations of unmarked individuals of unconfirmed sex.

The Rufous-capped Warbler (*Basileuterus rufifrons*) is a widely-distributed resident songbird found from southern Arizona to northern South America. This species lives in a variety of semi-open habitats and dry forest from 0–3000 m a.s.l. (Contreras-González et al. 2010, Curson 2010). Although pairs are territorial year-round, they breed seasonally during the rainy season (Stiles & Skutch 1989). There are two primary subspecies groups: the white-bellied *rufifrons* group of Mexico and western Guatemala, which inhabits arid scrub and semi-open montane habitats; and the yellow-bellied *delatirii* group of southeastern Mexico, Central and South America, which lives in dry forest and humid semi-open habitats (Howell & Webb 1995). There are previous nest descriptions of both subspecies groups. For the *rufifrons* group in Mexico, there are opportunistic observations of one nest in Jalisco (Zimmerman & Harry 1951), one nest in Oaxaca (Rowley 1966), and three nests in Morelos (Rowley 1962). For the *delatirii* group in Costa Rica, there is a description of one nest with eggs (Cherrie 1892), and detailed observations of five nests (two with eggs, three with nestlings), along with incubation and nestling watches on one nest each (Skutch 1967). Only the female incubates eggs and broods nestlings (Skutch 1967) but both parents feed nestlings (Zimmerman & Harry 1951, Skutch 1967).

In this study, we describe the nests, nestlings, and nesting behavior of Rufous-capped Warblers, based on data collected from *B. r. delatirii* in northwestern Costa Rica. In particular, we provide the first detailed record of sex-specific nesting behavior using a color-banded population. We observed nests during the nest-building, incubation, and nestling periods, and we also collected video recordings of selected nests during the incubation and nestling periods.

METHODS

We collected data from mid-May to early July 2013–2015 during the Rufous-capped Warbler breeding seasons at Sector Santa Rosa, Área de Conservación Guanacaste, northwestern Costa Rica (10°51'N, 85°36'30"W; 300 m a.s.l.). This site is a Neotropical dry forest with both second-growth and mature stands, where the warblers are common year-round residents in both habitat types. In this

population, birds breed only during the rainy season, which typically begins in May of each year. We captured and color-banded male and female warblers as part of a separate study on the territorial behavior of this species; either one or both adults was color-banded for each nesting pair included in this study. We sexed birds based on the presence of secondary sexual characteristics when captured (cloacal protuberance for males and brood patch for females) and behavior during focal observations (only males sing prolonged spontaneous song bouts).

Nest structure. We monitored 11 nests: one nest in 2013, four nests in 2014, and six nests in 2015. We located nests by following females carrying nesting material (N = 10) or adults carrying food to nestlings (N = 1). We monitored the number of eggs and nestlings weekly until fledging by conducting 20-min nest watches, after which time we approached the nest to check contents if the female was not on the nest. We did not flush females off nests to check nest contents, to minimize disturbance to incubating females. We color-banded and weighed nestlings (N = 14) from five nests (1–4 young per nest) in all cases where the young survived to 8–10 days old. We were not able to confirm fledging dates for these nests, because fledging occurred after our field expeditions had concluded. We estimate that the nestling period is approximately 12 days, since Skutch (1967) reported a 12-day nestling period for two nests in another Costa Rican population, and 10-day-old nestlings in our study population were highly mobile during and after banding (ADD pers. observ.).

We collected measurements of the nest and surrounding environment for 10 nests. One nest still contained small (i.e., 1–2-day old) nestlings at the end of our field expedition, so we did not remove the nestlings to measure the nest. We measured the inner height and width of the nest entrance (in mm), the horizontal depth of the nest from the entrance to the back wall (in mm), and the amount of tree canopy cover (estimated within 5%). We also described the overall nest structure and construction materials of all nests, and measured the length and width of two eggs from an abandoned nest and described their color pattern.

Breeding behavior. In 2014, we collected video recordings of two warbler nests. Each recording session was an approximately 4-hour continuous recording between 06:30–11:00 h CST; we placed video cameras on tripods 7–10 m away from the nest to avoid interference with normal parental behavior. We recorded Nest 3 during both the incubation and nestling periods, and Nest 4 during the nestling period only, for a total of 4 h 23 min during incubation and 8 h 4 min during the nestling period. We annotated the videos using VLC Media Player (v. 2.2.6). We identified adults by recording their color-bands whenever possible and noted the timing

Table 1. Nest structure and contents of 11 Rufous-capped Warbler (*Basileuterus rufifrons*) nests found during the 2013–2015 breeding seasons at Sector Santa Rosa, Guanacaste, Costa Rica. A blank space indicates measurement not collected; an asterisk (*) indicates unconfirmed clutch size or nestling number.

Nest	Primary material	Location	Nest entrance width (mm)	Nest entrance height (mm)	Nest depth (mm)	Cover (%)	Clutch size	No. of nestlings	Final status
1	small twigs	on flat ground; below shrub				25	3	3	nestlings
2	fine grasses, dead leaves	on slope; below leaf litter	65	45	90	70	1	0	abandoned
3	fine grasses	in side of bank; below rocks	60	45	75	90	4	4	nestlings
4	fine grasses, dead leaves	on slope; below leaf litter	80	50	95	90	4	4	nestlings
5	fine grasses, dead leaves	on flat ground; in hummock	70	60	95	90	2	0	abandoned
6	fine grasses	on slope; below shrub	43	30	84		unknown	0	depredated
7	small twigs	on slope; base of two rocks	66	38	85		3–4*	3	nestlings
8	fine grasses	on slope; below leaf litter	59	46	74	65	3	3	nestlings
9	fine grasses, dead leaves	on slope; below leaf litter	75	48	95	35	2–3*	2–3*	nestlings
10	large grasses	on slope; below leaf litter	46	32	75		unknown	0	depredated
11	fine grasses, dead leaves	on slope; below leaf litter	65	56	75		3	3	nestlings

and length of each adult visit to the nest. For both the incubation and nestling periods, we calculated nest attentiveness (i.e., percentage of total time spent by adults on or at the nest). For the nestling period only, we also observed adult behavior during nest visits (e.g., carrying food or fecal sacs). We found most nests during the nest-building stage, so we also described nest-building activity by both males and females during 30–60 min observation periods upon nest discovery.

RESULTS AND DISCUSSION

Nest structure and location. All of the Rufous-capped Warbler nests we studied were dome-shaped structures with a covered top and a side entrance, and were located on or near the ground (Table 1). The outer structure of the nests was constructed of fine grasses topped with dead leaves (N = 5; Figure 1A), fine grasses (N = 3; Figure 1B), small twigs (N = 2; Figure 1C), or large grasses (N = 1; Figure 1D), and all nests were lined with fine grasses. Nests measured on average 45 x 63 x 84 mm (height x width x depth), and canopy cover above nests was $66 \pm 27\%$ (mean \pm SD range: 25–90%; N = 10). Most nests were located on a slope, either below leaf litter and small shrubs (N = 7) or below large rocks (N = 2); two nests in areas

with flat terrain were located on the ground in a hummock (N = 1) or below a shrub (N = 1). The nest structure and placement of Rufous-capped Warbler nests at our study site were consistent with other accounts of *Basileuterus* nests (Cox & Martin 2009) and with previous reports of this species' nests (Cherrie 1892, Zimmerman & Harry 1951, Rowley 1962, Skutch 1967).

Clutch size and egg description. Clutch sizes were 3–4 eggs (N = 6 confirmed completed clutches; Table 1). Five nests were abandoned or depredated before clutch completion (N = 4) or were not observed during incubation (N = 1). We did not collect data on the frequency or timing of egg laying, although other accounts suggest that females of this species lay one egg per day (Skutch 1967). We measured two eggs: they measured 18.6 x 13.5 mm and 18.0 x 13.5 mm, and were pinkish-white with brown speckles concentrated at the wider end of the egg. Clutch size and egg descriptions are consistent with other published accounts for this species (Cherrie 1892, Rowley 1962, 1966, Skutch 1967) and other *Basileuterus* warblers (Cox & Martin 2009).

Nest-building behavior. We found 10 nests during the nest-building stage and one nest during the nest-



Figure 1. Rufous-capped Warbler (*Basileuterus rufifrons*) nests found at Sector Santa Rosa, Guanacaste, Costa Rica from April–June 2013–2015. Nests were dome-shaped with a side entrance and were constructed from different materials: (A) Nest 9 constructed of fine grasses topped with dead leaves; (B) Nest 8 constructed of fine grasses; (C) Nest 1 constructed of small twigs; and (D) Nest 10 constructed of large grasses. Photographs taken by A. Demko.

ling stage. We found the first nests of each breeding season ($N = 9$) within two days of the first major rain event of that year (22 May 2013, 10 May 2014, and 3 June 2015), whereas we located re-nests ($N = 2$) after depredation or nest abandonment up to 32 days after the first rain. Both re-nests were newly constructed; we did not observe warblers re-using a previous nest structure. Females were the primary nest builders, as is reported for other temperate and tropical wood-warbler species generally (Kendeigh 1945, Skutch 1954) and Rufous-capped Warblers specifically (Skutch 1967). During observation periods, females made many trips to the nest, bringing nest material (e.g., grasses, twigs, leaves). The females were largely silent while nest-building, but occasionally uttered soft *chip* calls when their male mates were nearby. While females were building the nest, males at 10 of 11 nests sang or produced *chip* calls 3–10 m away from the female, and three males accompanied the female while she collected nest materials.

We observed one male, whose sex we confirmed based on his color-bands, bringing twigs to the nest twice and entering the nest once. Nest-building by

males is rare in wood-warblers (Kendeigh 1945, Skutch 1954), and ours is the first report of this behavior in Rufous-capped Warblers (Zimmerman & Harry 1951, Rowley 1962, Skutch 1967). The temperate-breeding Louisiana Waterthrush (*Parkesia motacilla*; Mattsson et al. 2009) and the tropical resident Buff-rumped Warbler (*Myiothlypis fulvicauda*; Skutch 1954) are the only known wood-warbler species where males and females contribute equally to nest-building (Table 2). Occasional male-assisted nest-building, such as we observed, is reported for 12 other temperate-breeding and two tropical resident warbler species, in which some males carry material to the nest but contribute much less than females (Table 2). We suggest that careful observation of other tropical resident warblers may reveal that male nest-building is more prevalent in this family than previously reported.

Incubation and nestling provisioning behavior. Our observations during incubation and nestling periods are consistent with other reports in this species, in that only the female appears to incubate and brood nestlings, whereas both parents contribute equally to

Table 2. List of wood-warbler species (family Parulidae) with reported frequent (males contribute equally to females) or occasional (males contribute rarely) male-assisted nest-building.

Species	Breeding range	Reference
Frequent male nest-building		
Louisiana Waterthrush (<i>Parkesia motacilla</i>)	temperate	Mattsson et al. 2009
Buff-rumped Warbler (<i>Myiothlypis fulvicauda</i>)	tropical	Skutch 1954
Occasional male nest-building		
Blue-winged Warbler (<i>Vermivora cyanoptera</i>)	temperate	Gill et al. 2001
Prothonotary Warbler (<i>Protonotaria citrea</i>)	temperate	Petit 1999
Cerulean Warbler (<i>Setophaga cerulea</i>)	temperate	Boves & Buehler 2012
Northern Parula (<i>Setophaga americana</i>)	temperate	Moldenhauer & Regelski 2012
Magnolia Warbler (<i>Setophaga magnolia</i>)	temperate	Dunn & Hall 2010
Pine Warbler (<i>Setophaga pinus</i>)	temperate	Rodewald et al. 2013
Yellow-rumped Warbler (<i>Setophaga coronata</i>)	temperate	Hunt & Flaspohler 1998
Yellow-throated Warbler (<i>Setophaga dominica</i>)	temperate	McKay & Hall 2012
Golden-cheeked Warbler (<i>Setophaga chrysoparia</i>)	temperate	Ladd & Gass 1999
Black-throated Green Warbler (<i>Setophaga virens</i>)	temperate	Morse & Poole 2005
Black-throated Blue Warbler (<i>Setophaga caerulescens</i>)	temperate	Holmes et al. 2017
Canada Warbler (<i>Cardellina canadensis</i>)	temperate	Reitsma et al. 2009
Tropical Parula (<i>Setophaga pitiayumi</i>)	tropical	Regelski & Moldenhauer 2012
Slate-throated Redstart (<i>Myioborus miniatus</i>)	tropical	Skutch 1954
Rufous-capped Warbler (<i>Basileuterus rufifrons</i>)	tropical	this study

nestling provisioning (Skutch 1967). The incubation period, calculated as the time elapsed from the last egg laid to the first egg hatched, was 13 days for four nests, and 13–14 days for a fifth nest. We collected a video recording of Nest 3 on 27 June 2014 from 06:41–11:04 h, when the female was incubating four eggs. The female visited the nest twice for an average of 0.5 visits per hour and total nest attentiveness of 78.7%. The two incubation bouts were 70.4 min and ≥ 116.5 min; the total time of the second bout was unknown since the female was still on the nest at the end of the recording. The male was not detected at or near the nest during this video.

Our observations point to a slightly longer incubation bout length and a higher level of nest attentiveness than the observations of Skutch (1967). He reported average morning incubation bouts of 50.6 min, with the longest being 70 min, and nest attentiveness of 65.7%. These differences could be related to the time of the incubation period, although it was likely comparable between the two studies, since our nest was observed late in incubation (day 9 of 13–14) and Skutch's was "well advanced in incubation" (Skutch 1967). Since these differences could also be owing to low sample sizes, further observations at multiple intervals across the incubation stage with a large sample of nests would be useful to investigate patterns of within-species variability in incubation activity.

Nestling mass at 8–10 days old was 9.2 ± 1.1 g (range: 8–10.5 g; $N = 10$). Although we could not esti-

mate the exact age of the nestlings because eggs hatched over a 2-day period, the least-developed nestlings (estimated to be 8–9 days old) had open eyes, fully feathered heads, large pin feathers on the wings and tail, and narrow yellow feather tracts down the sides of the bare belly (Figure 2A–B). The most-developed nestlings (estimated to be 9–10 days old) had fully feathered wings with buffy wing bars, and wide yellow feather tracts covering most of the belly (Figure 2C–D).

We collected a video recording of Nest 4 on 3 June 2014 from 6:36–10:37 h, when it contained four nestlings that were 1–2 days old. Adults visited the nest 11 times for an average of 2.4 visits per hour, with average visit length of 7.4 ± 5.6 min (mean \pm SD; range: 0.4–19.7 min) and total nest attentiveness of 34.3%. Female visits ($N = 4$) were 7.4 ± 4.6 min (mean \pm SD; range: 2.9–12.7 min), and the female was also on the nest for the first 5.3 min of recording. The six remaining visits were made by unknown adults whose color-bands were not visible on the video. During 5 of 10 visits, an adult brought food items to the nestlings; because of the video quality, we could not identify any specific food items during these visits.

We collected a video recording of Nest 3 on 6 July 2014 from 06:39–10:42 h, when it contained four nestlings of 5–6 days old. Adults visited the nest 26 times for an average of 6.4 visits per hour. For the 21 visits of known length, the average length was 2.6 ± 5.2 min (mean \pm SD; range: 0.1–18.7 min). The total

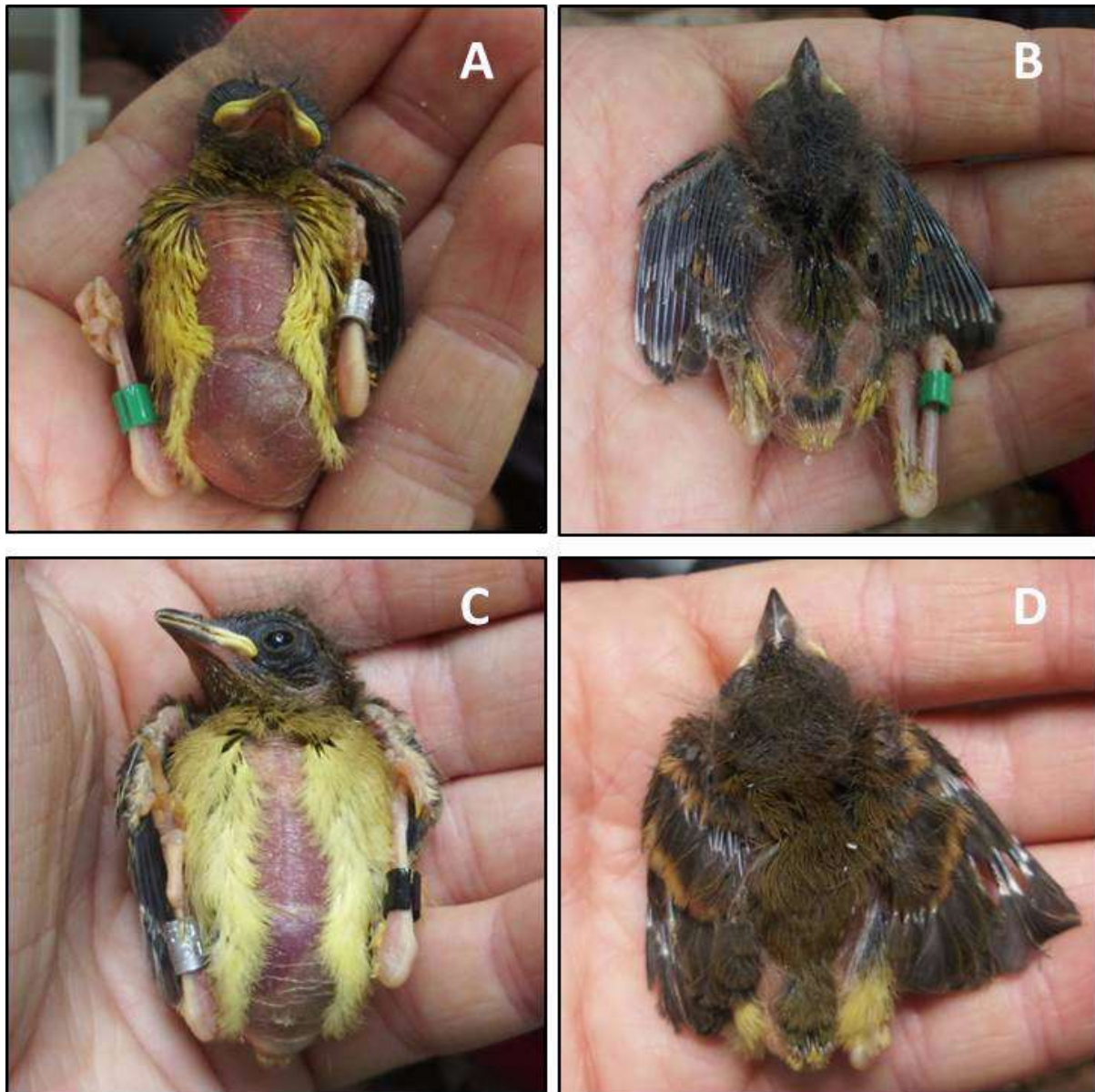


Figure 2. Rufous-capped Warbler (*Basileuterus rufifrons*) nestlings at Sector Santa Rosa, Guanacaste, Costa Rica: at age 8–9 days old on 6 July 2015 from Nest 11 (A: ventral view; B: dorsal view) and 9–10 days old on 2 July 2015 from Nest 7 (C: ventral view; D: dorsal view). Older nestlings had more extensive feathering on the wings, back, and belly than did younger nestlings. Photographs taken by A. Demko.

nest attentiveness was 39.9%; on seven occasions, the male and female were both present at the nest at the same time. We confirmed the bird's sex for 19 visits. Male visits ($N = 12$) were all short: 0.2 ± 0.2 min (mean \pm SD; range: 0.1–0.7 min). Female visits ($N = 7$) were more variable in length: 7.2 ± 7.2 min (mean \pm SD; range: 0.5–18.7 min). During five of these seven visits, the female entered the nest for > 5 min to brood the nestlings. During 23 of 26 visits, both adults made confirmed food deliveries to nestlings, including green caterpillars ($N = 3$ visits) and brown caterpillars ($N = 1$ visit; Figure 3). Both adults also contributed to nest sanitation by carrying fecal sacs away from the nest after feeding young ($N = 6$ visits: 4 female, 1 male, 1 unknown adult). Overall, these

video recordings suggest that males and females made a similar number of visits to feed nestlings, but female visits were longer because females often entered the nest for several minutes after feeding to brood nestlings rather than leaving immediately.

CONCLUSION

Our study provides new information on the nests and nesting behavior of Rufous-capped Warblers, particularly incubation times and sex-specific parental contributions to nest-building and nestling provisioning. Our work also advances our knowledge of breeding behavior in a little-studied genus of tropical resident wood-warblers. Published nest descriptions exist for

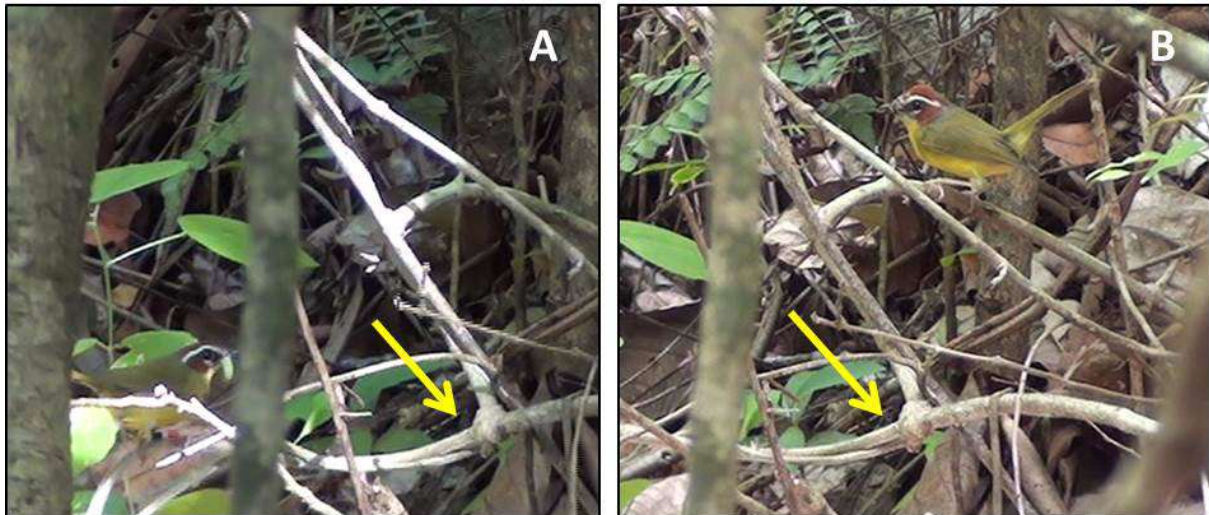


Figure 3. Photographic stills taken from a video recording of (A) a banded male and (B) an unbanded female Rufous-capped Warbler (*Basileuterus rufifrons*) delivering food items to 5–6 day old nestlings on 6 July 2014 at Sector Santa Rosa, Guanacaste, Costa Rica. Nest entrance is partially obscured by branches; yellow arrows indicate the nest location on the photographs.

only four of the nine *Basileuterus* species: Rufous-capped Warbler, Three-striped Warbler (*B. tristriatus*: Greeney et al. 2005, Cox & Martin 2009), Golden-crowned Warbler (*B. culicivorus*), and Black-cheeked Warbler (*B. melanogenys*: Skutch 1967). Natural history information on the remaining species, most of which have restricted distributions, will be useful not only to compare temperate and tropical wood-warbler breeding biology, but also to focus conservation efforts for rare species using further data on their habitat and nest site requirements.

ACKNOWLEDGMENTS

We thank A. Demarse for field assistance, and the staff of Sector Santa Rosa, especially R. Blanco, for logistical support. Funding for this research was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC) and the University of Windsor. The University of Windsor (Animal Care Permit # AUPP-13-15) and the Government of Costa Rica (MINAE permit) provided necessary permits authorizing our research. We thank K. Cockle, H. Greeney, and one anonymous reviewer for feedback that improved the manuscript.

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