

## REPRODUCTIVE BIOLOGY OF THE GRAY-CROWNED YELLOWTHROAT (*GEOTHLYPIS POLIOCEPHALA PALPEBRALIS*) IN CENTRAL BELIZE

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**Resumen.** – **Biología reproductiva del Antifacito Coronigrís (*Geothlypis poliocephala palpebralis*) en Belice central.** – Estudiamos la biología reproductiva de *Geothlypis poliocephala palpebralis*, una raza del Antifacito Coronigrís que habita en la península de Yucatán. Aunque el nido y los huevos han sido descritos, se conoce muy poco de la biología reproductiva de esta especie. Nuestro estudio se llevó a cabo en hábitat de sabana de pino de tierras bajas en Belice central, desde el 6 de Abril al 3 de Agosto de los años 1999, 2000 y 2001. El estudio se llevó a cabo en dos sitios separados por aproximadamente 10 km, pero en hábitat similar. Veintisiete nidos fueron hallados y monitoreados. Basados en el número de huevos y/o polluelos presentes en el nido, determinamos que el tamaño de nidada fue dos o tres. La altura de nido varió de 2 a 50 cm y la altura de las plantas donde encontramos los nidos varió de 20 a 123 cm. La mayoría de nidos (20 o 74.1%) fueron hallados en hierbas. La construcción de nidos se inició a fines de Abril y la mayor cantidad de nidos fueron hallados durante el periodo de medianos de Mayo a fines de Junio, declinando considerablemente a principios de Agosto. El periodo de incubación varió de 12 a 14 días y el de anidación de los polluelos varió de 10 a 13 días. A lo largo del periodo de búsqueda de nidos, 23 individuos fueron capturados y anillados. De estos 23 individuos, cuatro (17.4%) tenían parche reproductivo, indicando condiciones reproductivas. La probabilidad diaria de sobrevivencia fue de 0.985 y la tasa de mortalidad diaria fue de 0.015. La probabilidad de éxito reproductivo desde el inicio del periodo de incubación al de anidación de los polluelos fue de 72.3%, lo que parece ser alto para una especie tropical.

**Abstract.** – We studied the breeding biology of *Geothlypis poliocephala palpebralis*, a race of the Gray-crowned Yellowthroat that occurs in the Yucatan peninsula. Although the nest and eggs have been described, little else is known about the breeding biology. Our research was conducted in lowland pine savanna habitats in central Belize from approximately 6 April to 3 August of 1999, 2000 and 2001. The study took place at two sites 10 km apart, but in similar habitats. Twenty-seven nests of the Gray-crowned Yellowthroat were found and monitored. Based on the number of eggs and/or nestlings present when the nests were found, the clutch size was two or three. Nest height ranged from 2 to 50 cm and substrate height ranged from 20 to 123 cm. The majority of nests (20 or 74.1%) were built in graminoid tussocks. Nest building was first recorded in late April, peaked from mid-May to late June, and declined significantly by early August. The incubation period ranged from 12 to 14 days and the nestling period ranged from 10 to 13 days. Throughout the nest searching period, 23 individuals were captured and banded. Of these 23 birds, four (17.4%) had a brood patch, indicating that they were in breeding condition at the time of banding. The daily probability of survival was 0.985 and the daily mortality rate was 0.015.

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The probability of nest success from the start of incubation to fledging was 72.3%, which appears to be high for a tropical species. *Accepted 30 March 2004.*

**Key words:** Gray-crowned Yellowthroat, *Geothlypis poliocephala palpebralis*, Belize, clutch size, incubation, nestling

## INTRODUCTION

The Birds Without Borders – *Aves Sin Fronteras*<sup>SM</sup> project has identified over 146 bird species in the lowland pine savanna and shrubland with pine (“broken ridge”) habitats of central Belize. Even though these habitats support a rich avifaunal diversity, very little ornithological research has been conducted to determine bird-habitat interactions. Residential development, citrus farming, gravel mining, forest fires, aquaculture and proposed sanitary landfills represent a few of the present threats to the rich biological diversity of pine savanna habitats.

To learn more about how birds utilize pine savanna habitats, the Birds Without Borders project undertook comprehensive monitoring of bird populations within two pine savanna areas in central Belize. One component of this research was to study the breeding biology of bird species that are pine savanna obligates, since the ornithological literature regarding many of the Belize resident species occurring within these habitats is incomplete.

The Gray-crowned Yellowthroat (*Geothlypis poliocephala*), although common in central Belize (Jones & Vallely 2001), has not been studied in detail throughout its range. Paynter (1955) described the race *G. p. palpebralis* as occurring from Veracruz through eastern Mexico, including Campeche, Yucatan, and Quintana Roo, to eastern Guatemala and British Honduras. Russell (1964) studied the distribution of the Gray-crowned Yellowthroat in British Honduras (now Belize) and reported that it was not recorded south of the Yacos Lagoon. Six races of the Gray-crowned Yellowthroat occur along both

slopes of Middle America to western Panama. The race *G. p. palpebralis* “occurs on the Gulf and Caribbean slope from northern Veracruz, Mexico, southeast to northern Costa Rica, (including the Yucatan peninsula)” (Curson *et al.* 1994).

Paynter (1955) reported collecting reproductively active Gray-crowned Yellowthroat specimens in mid-May. Russell (1964) noted that he did not collect individuals with enlarged gonads before mid-April. He also described birds collected in late April and May as being in breeding condition. Howell & Webb (1995) and Stiles & Skutch (1989) described the nest and eggs, but provided no information on the incubation or nestling periods. To learn more about the breeding biology of the Gray-crowned Yellowthroat and other bird species breeding in pine savanna habitats, we conducted nest searching and monitoring, and bird banding during the breeding season, at two study sites in central Belize. In this paper, we describe several aspects of the breeding biology of the Gray-crowned Yellowthroat at these two sites.

## STUDY SITE AND METHODS

The research was conducted on privately owned lands at two study sites in central Belize. One site was located at the Tropical Education Center (TEC) of the Belize Zoo, and adjacent privately owned lands. This site is located in the Belize district (17°21'26.9"N, 88°32'26"W) at 46 m a.s.l., and encompassed an area of approximately 438 ha. The area used in this study consisted of 39.5 ha of lowland open pine savanna with areas of shrubland with pine. A 15–20 m strip of gallery forest traversed the northern section of the

study area. Caribbean pine (*Pinus caribaea*), palmetto (*Acoelorrhaphe wrightii*), savanna poisonwood (*Cameraria latifolia*), black poisonwood (*Metopium brownei*) and cutting grass (*Scleria bracteata*) were the dominant plant species. Graminoids and low shrubs dominated the low ground cover.

The second study site was located at the Runaway Creek Nature Preserve (RCNP), a 2500 ha preserve owned and managed by the Foundation for Wildlife Conservation, Inc. This site is located 10 km east (17°18'05.1"N, 88°27'31.8"W) of the TEC study site at 16 m a.s.l. The RCNP is dominated by two distinct vegetation types: tall semi-evergreen or evergreen forest and savanna (Meerman 1999). Of the approximately 500 ha of pine savanna habitat present at the RCNP, 40 ha were utilized for this study. This study area consisted of open pine savanna, shrubland with pine and pine-oak forest. Dominant plant species included Caribbean pine, live oak (*Quercus oleoides*), palmetto, schippea palm (*Schippaea concolor*), yaha (*Curatella americana*), craboo (*Byrsonima crassifolia*) and calabash (*Crescentia cujete*). Graminoids and herbaceous plants dominated the low ground cover. The savanna was dry during the dry season, but temporary ponds, wetlands and flowing water were prevalent during the rainy season.

Nest searching and monitoring were conducted from approximately 6 April to 3 August in 1999–2001. To facilitate the relocation of nests, a permanent nest searching plot was established using alphanumeric markers every 50 m. The TEC nest plot was 90,000 m<sup>2</sup> in 1999 and was enlarged to 395,000 m<sup>2</sup> in 2001. Research at the RCNP began in 2000. The nest plot at the RCNP was 320,000 m<sup>2</sup> in 2000 and was enlarged to 400,000 m<sup>2</sup> in 2001. Nest searching was conducted 5 days per week from just before sunrise to approximately 09:30 h CST, depending on weather conditions.

Nests were monitored when found, and

then every 3 to 5 days unless a hatch or fledging event was expected, in which case nests were monitored every 2 days. To minimize disturbance and the risk of predation, nests were monitored from a distance when possible, and as quickly as possible. Care was taken not to leave a dead-end trail to the nest, and to observe the general area for any sign of possible predators, particularly avian predators, prior to approaching the nest.

In an attempt to identify breeding territories at both the TEC and RCNP study sites, intensive point counts were conducted at selected points every 200 m, in the nest searching area, in April and May of 2001.

Incubation and nestling periods were calculated according to the method of Martin *et al.* (1997). Briefly, the incubation period started on the day the last egg was laid, and the nestling period started on the day the first egg hatched. The midpoint between nest visits was used to estimate when critical events in the nesting cycle occurred. The number of days the nest was under observation was calculated to the nearest half day. In some instances, the start of the nestling stage was estimated based on the description of the young at the time of monitoring.

The daily mortality rate was calculated according to the methods of Mayfield (1961, 1975). The daily probability of survival was calculated using methods described in Hensler & Nichols (1981). Variances were calculated utilizing the methods described in Johnson (1979) and Hensler & Nichols (1981). Nest success probability from incubation to fledging was calculated according to the methods of Mayfield (1961, 1975), and following the suggestions found in Manolis *et al.* (2000). Nests with uncertain fates were included in the calculations wherever possible.

Bird banding was conducted every 6–10 days during the nest searching period based on the methods of the Constant Effort Sites Scheme (Baillie 1990, Peach *et al.* 1996) and

TABLE 1. Nest substrate, number of nests, nest height and substrate height of the Gray-crowned Yellowthroat nests found from 1999 to 2001.

Nest substrate	Number of nests	Nest height (m) (Mean $\pm$ SD)	Substrate height (m) (Mean $\pm$ SD)
Graminoids	19 <sup>1</sup>	0.02-0.5 (0.22 $\pm$ 0.12)	0.2-1.23 (0.58 $\pm$ 0.24)
<i>Jacquinia</i> sp.	1	0.30	0.7
<i>Amyris</i> sp.	1	0.15	0.5
<i>Byrsonima crassifolia</i>	1	0.11	0.5
<i>Acoelorrhaphe wrightii</i>	1 <sup>1</sup>	0.43	0.62
<i>Myrica cerifera</i>	1	0.13	0.8
<i>Calea</i> sp.	1	0.20	1.2

<sup>1</sup>One additional nest in each of these substrates was destroyed before height measurements could be taken.

Monitoring Avian Productivity and Survivorship (MAPS) (Burton & DeSante 1998) protocols. Banding took place in the savanna and on the edge of the gallery forest (TEC site), or in the savanna and shrubland with pine (RCNP site). Ten nets were operated for 3 to 5 h each day depending on weather conditions. Birds were marked with numbered aluminum bands. Breeding condition was determined by the presence of a brood patch (BP) in females or cloacal protuberance (CP) in males. BP and CP were assessed using the criteria described in Burton & DeSante (1998).

## RESULTS

*Nesting period.* During the 1999–2001 field seasons, 27 nests were found, 26 of which reached at least the egg laying stage. Sixteen nests were found at the TEC study site, and 11 at the RCNP study site. Of the 27 nests, 11 (40.7%) were found during the building stage, 7 (25.9%) during the incubation stage, and 9 (33.3%) during the nestling stage. During the three field seasons of nest searching and monitoring, nest construction began in late April, and active nests (those containing eggs or nestlings) were found from May to early August. The time required for nest building

could not be determined, as daily observations were not conducted during this stage of the nesting cycle. During the early April to early August nest searching periods, 1 nest was found in April, 9 were found in May, 11 in June, 4 in July and 2 in August. Nesting activity appeared to peak in June as the majority of nests were found during this month.

*Clutch size, incubation and nestling period.* Of the 27 nests found, 16 (59.3%) contained three eggs, three (11.1%) were found with three nestlings, one (3.7%) with two eggs and one nestling, one (3.7%) with one egg and two nestlings, three (11.1%) with two nestlings, one (3.7%) with one egg and one nestling, one (3.7%) was abandoned with one egg, and one (3.7%) was destroyed before the egg laying stage. Based on the number of eggs or nestlings present when the nest was found, it appeared that the majority of nests had a clutch size of three ( $N = 21$ ), however, some nests contained only two eggs or nestlings ( $N = 4$ ). The mean clutch size was 2.7 ( $SD = 0.73$ ).

The incubation period ranged from 12 to 14 days ( $N = 3$  nests) with a mean of 12.8 days ( $SD = 1.04$ ). The nestling period ranged from 10 to 13 days ( $N = 10$  nests) with a mean of 11 days ( $SD = 0.94$ ).

TABLE 2. Number of Gray-crowned Yellowthroats banded, breeding condition and date banded during 1999–2001.

Date	Number banded	Breeding condition	
		Cloacal protuberance	Brood patch
14 April 1999	1	Absent	Absent
30 April 1999	1	Absent	Absent
26 April 2000	1	Absent	Absent
26 April 2000	1	Absent	Absent
26 April 2000	1	Absent	Absent
24 May 2000	1	Absent	Absent
1 May 2001	1	Present	Absent
1 May 2001	1	Absent	Absent
23 May 2001	1	Present	Absent
31 May 2001	1	Present	Absent
3 June 1999	1	Present	Absent
12 June 1999	1	Absent	Present
21 June 1999	1	Absent	Absent
1 June 2000	1	Present	Absent
1 June 2001	1	Absent	Present
1 June 2001	1	Present	Absent
1 June 2001	1	Absent	Present
16 June 2000	1	Absent	Present
16 June 2000	1	Present	Absent
5 July 2001	1	Absent	Absent
5 July 2001	1	Absent	Absent
5 July 2001	1	Absent	Absent
12 July 2000	1	Absent	Absent
Total	23	7	4

*Nest substrate.* Of the 27 nests studied, 20 (74.1%) were built in open pine savanna and were constructed in graminoids (Table 1). Six additional species of plants were utilized as a nest substrate (Table 1). Two nests were constructed in palmettos (7.4%). One nest (3.7%) was constructed in each of the following substrates: *Myrica cerifera*, *Jacquinia* sp., *Amyris* sp., craboo and *Calea* sp.

Of the 25 nests for which measurements could be taken, nest height ranged from 2 to 50 cm (Table 1) with a mean of 21.8 cm (SD = 11.8 cm). The substrate height ranged from 20 to 123 cm (N = 25) (Table 1) with a mean of 61.5 cm (SD = 24.4 cm). Vegetation measurements were not conducted on two nests

due to human disturbance. A bulldozer entered the study plot and destroyed the nests before the vegetation measurements could be completed.

*Nest outcomes.* Of the 27 nests found and monitored, 19 (70.4%) were considered to be successful, meaning they fledged at least one young. Five nests (18.5%) failed due to predation, two nests (7.4%) were destroyed by the human disturbance described above, and one nest (3.7%) was deserted for unknown reasons.

Twenty-four of the 27 nests reached the incubation stage and could be included in the daily probability of survival, mortality rate,

and nest success probability calculations. The daily probability of survival was 0.985 (N = 24 nests, total exposure days = 337.15, total nests lost = 5, variance = 0.0000438, 95% confidence interval = 0.972 to 0.998). The daily mortality rate was 0.015. The probability of nest success was 72.3% (N = 24 nests, total days that the nests were under observation ranged from 2 to 26, mean number of observation days = 14.1, total exposure days = 337.15, variance = 0.0083, 95% confidence interval = 0.54 to 0.90. For these calculations, the mean incubation period = 12.83 days and the mean nestling period = 11 days.).

*Breeding season bird banding.* During bird banding that took place during the 1999–2001 nest searching periods, 23 Gray-crowned Yellowthroats were captured and banded (Table 2). Of these, four had a brood patch indicating that they were breeding in the area (Brewer *et al.* 1991). Seven birds had a cloacal protuberance at the time of banding, indicating that these male birds were approaching readiness to breed or in breeding condition (Pyle 1997).

## DISCUSSION

Nests of Gray-crowned Yellowthroats were located in areas of open pine savanna lacking a closed tree canopy. The species appeared to be a nest site specialist (Aguilar *et al.* 2000), requiring areas containing dense graminoids since the majority of nests (20 or 74.1%) were found concealed in graminoid tussocks. Only seven (25.9%) nests were found built on substrates consisting of both shrubs and graminoids and were located in areas of pine savanna dominated by shrubs.

During the three field seasons that nest searching and monitoring were conducted, nesting activities were documented as early as 29 April (nest building), and as late as 17 August (nestling present) (data not shown).

This differs somewhat from the May to July nesting and breeding period in Costa Rica described by Stiles & Skutch (1989). One reason why the breeding periods may differ could be due to differential timing of breeding between the races of the Gray-crowned Yellowthroat. It may also be due to variation in the environmental conditions, such as the length of the rainy and dry seasons in each geographical region. In Belize, Gray-crowned Yellowthroat reproduction took place during the rainy season, which extends from May to November and peaks in July, with a short dry period occurring in August. Additional breeding studies in each region and their correlation with rainy and dry seasons may help to determine if weather affects the timing of breeding in each race of the Gray-crowned Yellowthroat.

The nest height (2 to 50 cm) and substrate (dense graminoid tussocks) of the 25 Gray-crowned Yellowthroat nests for which vegetation could be measured are similar to those described by other authors. Stiles & Skutch (1989) described nests in Costa Rica as being built in large grass tussocks at heights of 15 to 50 cm. Howell & Webb (1995) described the nests as built near the ground in grass tussock or tangle.

Our study found that the clutch size of the Gray-crowned Yellowthroat breeding in central Belize was two to three eggs. This agrees with the clutch size of two to three eggs reported by Howell & Webb (1995) and Stiles & Skutch (1989). In contrast, Baicich & Harrison (1997) reported Gray-crowned Yellowthroats which formerly bred in the lower Rio Grande Valley of Texas, U.S.A., as having a clutch size of usually four, and sometimes three eggs. The mean clutch size in our study was 2.7, consistent with the pattern of tropical bird species having smaller clutch sizes than their temperate relatives (Kulesza 1990).

Paynter (1955) described Gray-crowned Yellowthroats collected in mid-May as being

reproductively active. Russell (1964) described birds collected after mid-April and during May as being in breeding condition. Paynter (1955) did not define his criteria for being reproductively active, but Russell (1964) defined breeding condition as enlarged gonads. In our study, of the 23 Gray-crowned Yellowthroats banded from April–August, birds with a cloacal protuberance were captured in both May and June, while birds with a brood patch were captured only during the month of June (Table 2). We found the highest number of nests (11) during June. From our nest and brood patch data, it appears that June is the month in which reproduction peaks in Gray-crowned Yellowthroats breeding in pine savanna habitats of central Belize. Conducting nest searching and banding before April and after early August may assist in determining the complete breeding season of this race.

We determined that the incubation period of the Gray-crowned Yellowthroat ranged from 12 to 14 days ( $N = 3$  nests). To obtain a better estimate of the incubation period, data on additional nests would be beneficial. We determined that the nestling period ranged from 10 to 13 days ( $N = 10$  nests). This information was not previously provided in the ornithological literature (Stiles & Skutch 1989, Howell & Webb 1995, and Baicich & Harrison 1997).

Tropical birds are often reported to suffer higher rates of nest loss than temperate species (Skutch 1985, Robinson *et al.* 2000). In our study, the Gray-crowned Yellowthroat in central Belize had a nest success of 70.4%, which correlated well with the Mayfield (1961, 1975) nest survival probability from incubation to fledging of 72.3%. The daily probability of survival was 0.985 and the daily mortality rate was 0.015. Reproductive success at each site could not be calculated and compared as only 16 nests were found at the TEC study site, and 11 at the RCNP study

site. Predation was the cause of failure in only five (18.5%) of the nests studied. For the depredated nests, the predator(s) were not determined. For one depredated nest, one nestling was missing and the remaining egg and intact nest were covered with black ants. Three of the other depredated nests were intact, but the contents were missing. Unexpected human disturbance (destruction by a bulldozer) was the cause of failure in two (7.4%) of the nests.

Our study revealed that the Gray-crowned Yellowthroat nests in open pine savanna without a closed tree canopy and that nest success and daily probability of survival were high for a tropical species. This species has also been described as being found in a number of habitats including grassy cattle lands and pastures, brushy, grassy and damp fields, grassy areas with low bushes, thickets of pine ridges, low second growth, hedgerows, sugar cane fields and other open habitats (Paynter 1955, Russell 1964, Slud 1964, Stiles & Skutch 1989, Curson *et al.* 1994). Stiles & Skutch (1989) and Curson *et al.* (1994) suggest that the Gray-crowned Yellowthroat has increased in areas where forests were cleared for pasture. However, the reproductive success of birds utilizing these cleared habitats remains to be studied. In central Belize, high reproductive success was found in Gray-crowned Yellowthroats breeding in pine savanna areas, therefore conservation of this habitat type should be emphasized in management plans.

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## REFERENCES

- Aguilar M. T., M. M. Coelho, & M. A. Marini. 2000. Nesting biology of the Gray-hooded Flycatcher (*Mionectes rufiventris*). *Ornitol. Neotrop.* 11: 223–230.
- Baichich, P. J., & C. J. O. Harrison. 1997. A guide to the nests, eggs & nestlings of North American birds. 2 ed. Academic Press, San Diego, California.
- Baillie, S. R. 1990. Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis* 132: 151–166.
- Brewer, R., G. A. McPeck, & R. N. Adams, Jr. 1991. The atlas of breeding birds of Michigan. Michigan State Univ. Press, East Lansing, Michigan.
- Burton, K. M., & D. F. DeSante. 1998. MAPS manual. Instructions for the establishment and operation of stations as part of the Monitoring Avian Productivity and Survivorship Program. Institute for Bird Populations, Point Reyes Station, California.
- Curson J., D. Quinn, & D. Beadle. 1994. Warblers of the Americas: an identification guide. Houghton Mifflin, Boston, Massachusetts.
- Hensler, G. L., & J. D. Nichols. 1981. The Mayfield method of estimating nesting success: A model, estimators and simulation results. *Wilson Bull.* 93: 42–53.
- Howell, S. N. G., & S. Webb. 1995. A guide to the birds of Mexico & northern Central America. Oxford Univ. Press, Oxford, UK.
- Johnson, D. H. 1979. Estimating nest success: The Mayfield method and an alternative. *Auk* 96: 651–661.
- Jones H. L., & A. C. Valley. 2001. Annotated checklist of the birds of Belize. Lynx Edicions, Barcelona, Spain.
- Kulesza, G. 1990. An analysis of clutch-size in New World passerine birds. *Ibis* 132: 407–422.
- Manolis, J. C., D. E. Andersen, & F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117: 615–626.
- Martin, T. E., C. Paine, J. C. Conway, W. M. Hochachka, A. Paul, & W. Jenkins. 1997. BBIRD field protocol. Biological Resources Division, Montana Cooperative Wildlife Research Unit, Univ. of Montana, Missoula, Montana.
- Mayfield, H. 1961. Nesting success calculated from exposure. *Wilson Bull.* 73: 255–261.
- Mayfield, H. 1975. Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- Meerman, J. C. 1999. Rapid ecological assessment, Runaway Creek, Belize. Belize Environmental Consultancies Ltd. Report to the Foundation for Wildlife Conservation, Inc., Belize District, Belize.
- Paynter, R. A. 1955. The ornithogeography of the Yucatan Peninsula. *Peabody Mus. Nat. Hist. Yale Univ. Bull.* 9: 1–347.
- Peach, W. J., S. T. Buckland, & S. R. Baillie. 1996. The use of constant effort mist-netting to measure between-year changes in the abundance and productivity of common passerines. *Bird Study* 43: 142–156.
- Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California.
- Robinson, W. D., T. R. Robinson, S. K. Robinson, & J. D. Brawn. 2000. Nesting success of understory forest birds in central Panama. *J. Avian Biol.* 31: 151–164.
- Russell, S. M. 1964. A distributional study of the birds of British Honduras. *Ornithol. Monogr.* 1: 1–195.
- Skutch, A. F. 1985. Clutch size, nesting success and predation on nests of Neotropical birds, reviewed. *Ornithol. Monogr.* 36: 575–594.
- Slud, P. 1964. The birds of Costa Rica: distribution and ecology. *Bull. Amer. Mus. Nat. Hist.* 128: 1–430.
- Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York.