Breeding Biology of Spectacled Tyrant (*Hymenops perspicillatus*) In the Southeastern Pampas Region, Argentina

Author(s): Matías G. Pretelli and Juan P. Isacch
Source: The Wilson Journal of Ornithology, 125(2):275-279. 2013.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/12-143.1
URL: http://www.bioone.org/doi/full/10.1676/12-143.1

The Wilson Journal of Ornithology 125(2):275–279, 2013

BREEDING BIOLOGY OF SPECTACLED TYRANT (*HYMENOPS PERSPICILLATUS*) IN THE SOUTHEASTERN PAMPAS REGION, ARGENTINA

MATÍAS G. PRETELLI[1,2] AND JUAN P. ISACCH[1]

ABSTRACT.—The Spectacled Tyrant (*Hymenops perspicillatus*) is a flycatcher that inhabits open lands, grassy areas near water bodies, marshes, fields and pastures in southern South America. Our aim was to describe the breeding biology of Spectacled Tyrants in native tall grasslands, specifically by studying their reproductive phenology and breeding success. The study was developed in the southeastern Pampas region, Argentina. We conducted nest searching and monitoring during the 2010–2011 and 2011–2012 breeding seasons. We found 88 nests. The breeding season was from mid-October to late January. Clutch size was 2–3 eggs, mode = 2. Incubation and nestling periods were 15.8 ± 0.7 days and 14.7 ± 0.6 days, respectively. Nest predation was higher during the incubation period than during laying and nestling periods. The probability of nest success from egg-laying to fledging was 0.24. This species shows life-history traits in accordance with other South American temperate birds. *Received 29 August 2012. Accepted 10 November 2012.*

Key words: grasslands, *Hymenops perspicillatus*, incubation, nest predation, nesting success, nestling period, Spectacled Tyrant.

The Spectacled Tyrant (*Hymenops perspicillatus*) is a member of the family Tyrannidae that inhabits open lands, grassy areas near water bodies, marshes, and fields and pastures (Fitzpatrick 2004). The Spectacled Tyrant has two subspecies *H. p. perspicillatus* and *H. p. andinus*; the subspecies *perspicillatus* is distributed from southern Argentina to Paraguay, central Bolivia, Uruguay and southern Brazil (Fitzpatrick 2004). It is considered a partial migrant because part of the population in the south of Argentina moves northward during the post-reproductive period (Canevari et al. 1991). Although this tyrant is a common species along its distribution, and specifically in the Pampas region (Narosky and Di Giacomo 1993), limited information is available on its breeding biology. Most of this is descriptive information that comes from occasional observations about nest, nesting site, eggs, clutch size, and nesting season (Darrieu et al. 1988, de la Peña 1988, Canevari et al. 1991, Narosky and Salvador 1998, Cozzani and Zalba 2009).

Spectacled Tyrants inhabit mostly tall grasslands along the Pampas region, specifically during the breeding season (Comparatore et al. 1996, Martínez 2001, Cozzani and Zalba 2009). Because Spectacled Tyrants have an affinity for tall grasses, the species has declined in abundance and even disappeared in vast areas of the Pampas region following replacement of native tall grasslands by croplands and pasturelands (Codesido et al. 2011). The reproductive biology of birds that depend strongly on the native grasses of the Pampas region has been scarcely studied (Mermoz and Reboreda 1994, 1998; Cozzani et al. 2004; Llambías et al. 2009; Cardoni et al. 2012) even for common species. In this work, we present the first formal description of the breeding biology of Spectacled Tyrants, and we provide baseline data for egg-laying dates, nest and egg morphology, clutch size, incubation and nestling periods, and the estimated breeding success of a population inhabiting native tall grass in the southeastern Pampas region, Argentina.

METHODS

The study was conducted along a 135 km long coastal strip in the southeastern Pampas region (Cabrera 1976) in Buenos Aires Province, Argentina. The northernmost of our eight sampling sites, along this strip was located close to Villa Gesell (37° 13′ S, 57° 05′ W), and the southern end was located near Miramar (38° 14′ S, 57° 48′ W). The study area is characterized by grasslands of different sizes ranging from large undisturbed patches to areas with different degrees of fragmentation by urbanization, forestation, and agriculture. Tall grasslands along the coast are mostly dominated by *Cortaderia selloana* (Poaceae). *C.*

[1] Laboratorio de Vertebrados, Instituto de Investigaciones Marinas y Costeras (IIMyC), Consejo Nacional de Investigaciones Científicas y Técnicas, Universidad Nacional de Mar del Plata, Funes 3250, B7602AYJ Mar del Plata, Argentina.

[2] Corresponding author; e-mail: matiaspretelli@gmail.com

selloana is a tall grass with average height of 120 cm, exceeding 2 m when spikes appear in late summer (MGP, unpubl. data). Spectacled Tyrants use mainly these tall grasslands as breeding habitat in the region (MGP and JPI, pers. obs.).

We systematically searched for nests in *C. selloana* grasslands from September to late January (austral spring-summer), during two breeding periods (2010–2011 and 2011–2012). We recorded nest locations with GPS and marked the nest area with plastic tape to facilitate subsequent monitoring. We visited nests every 5–7 days and took morphometric measurements of eggs and recorded their color. We weighed eggs and chicks and determined the lengths of the incubation and nestling periods. We used vernier calipers to measure width and height of eggs to the nearest 0.1 mm, and egg volume was calculated following Hoyt (1979). Weight of eggs and chicks were recorded with a portable electronic balance to the nearest 0.1 g. Since weight decreases during the course of incubation because of water loss (Ar and Rahn 1980), values were recorded at the beginning and end of this period. Chicks were weighed twice, at hatching (i.e., day 0), and in order to compare with the average weight of adults (20.1 g; Navas and Bó 2001), at the end of the nestling period (i.e., ~ day 12).

To avoid under-estimation of clutch size, we only consider nests found during building and egg-laying period. Laying duration was estimated as: (clutch size-1) × interval between eggs (days). We assume that the laying of eggs occurred every 48 hrs, since the rate of egg-laying in most species of Tyrannidae is every 2 days (Skutch 1960, Astheimer 1985), especially in the subfamily Fluvicolinae (Di Giacomo et al. 2011). The incubation period was defined as the interval from the day that the last egg was laid until the first egg hatched, and the nestling period included the day the first egg hatched to the day that the young fledged (Martin et al. 1997).

Four morphometric variables of nests (external and internal diameter, total height, and depth of the cup) were recorded with a metric ruler to the nearest 1 mm after the breeding season had finished. In addition, we noted the type of material with which the nests were lined.

We determined the fate of each nest and then calculated nesting success across the egg-laying, incubation, nestling and overall nesting period. Nests were checked until they were abandoned, depredated, or produced fledglings. At each visit, we recorded egg or chick loss and the presence of adults near the nest. The permanence of eggs following the estimated date of hatching and/or the absence of parents was the criteria used to consider a nest abandoned. We considered a nest to have been depredated when the complete clutch disappeared between two subsequent visits or when the chicks disappeared from their nests before they were old enough to fledge.

Nesting success was estimated using the Mayfield method (Mayfield 1975), which is based on all nest losses occurring over the entire period of field observation. Total exposure days were calculated as the interval from first egg-laying date or (when egg laying was already initiated) from the day when the nest was found until the day when the young fledged or half way between the two subsequent visits between which a nest failed. When the interval between nest visits was less than 2 days, it was assumed that nest loss occurred in the middle of the interval, but since nests were visited every 5–7 days, we assumed that nest loss occurred at 40% of the interval length to avoid the overestimation of nest survival (see Johnson 1979). Daily survival rate of nests was estimated for three periods: laying, incubation, and nestling. The total survival rate for each period was calculated by raising daily nest survival rate to a power equal to mean duration of each nesting stage. Finally, we calculated overall nest success by multiplying three probabilities together. Mean duration of these nesting stages was calculated using information from the population monitored in the area (see results).

RESULTS

Clutch Size, Incubation, and Nestling Period.— We found 88 nests of Spectacled Tyrants, 11 during the building and egg-laying period, 67 during incubation, and 10 with nestlings; 31 were found in October, 33 in November, 18 in December, and six in January. From the eight nesting sites sampled, two were within 0–100 m of wetlands, where 22 nests were found; five sites were within 400–700 m of wetlands with 52 nests, and one site was within 3–4 km of wetlands with 14 nests. First males arrived to breeding patches of *C. selloana* in early September, and first females at the end of the same month. First evidence of nest building was on 12 October 2011, and the latest evidence of nest activity was a

nest in the laying stage on 27 January 2012. Mean clutch size was 2.2 ± 0.4 eggs (range = 2–3 eggs, mode = 2, n = 9 nests). One nest contained an egg from a Shiny Cowbird (*Molothrus bonariensis*). Mean egg-laying period was 2.36 ± 0.8 days (range = 2–4 days, mode = 2, n = 11). The mean incubation period was 15.8 ± 0.7 days (range = 15–17 days, n = 8) and weight of chicks at hatching was 2.4 ± 0.3 g (range = 1.9–2.8 g, n = 8). The mean nestling period was 14.7 ± 0.6 days (range = 14–16 days, n = 8). In nests with one chick, young left the nest at a mean weight of 21.9 ± 1.7 g (range = 20.1–23.4 g, n = 4). When two chicks were reared together, they left the nest at a mean weight of 20.4 ± 1.4 g (range = 18.7–23.5 g, n = 8), with a mean weight difference between them of 1.5 ± 1.2 g (range = 0.5–0.64 g, n = 4).

Nest and Egg Descriptions.—Nests were built in a period of 5–11 days (n = 4). The nest consisted of an open cup, interwoven mainly with remains of *C. selloana* spikes. The mean external diameter of 20 nests was 9.7 ± 0.9 cm (range = 8.8–10.7 cm) and the internal 6.2 ± 0.4 cm (range = 5.2–6.9 cm). Total height of the nests was 7.3 ± 0.9 cm (range = 5.5–8.9 cm), and the depth of the cup was 4.9 ± 0.7 cm (range = 4–6.3 cm). From these 20 nests, 14 (70%) contained feathers, eight (40%) cow hair, while three (15%) had no extra elements. Egg color was predominantly white with brown and reddish spots generally on the wider end of the egg, with only three eggs (4.2%) of an immaculate white. Measurements of eggs were as follows: mean width was 16.2 mm (SD = 0.6, range = 14.3–17.4 mm), mean length 21.1 mm (SD = 0.9, range = 19.3–23.5 mm), and mean volume 282.1 mm^3 (SD = 29.3, range = 201.8–362.2 mm^3, n = 113). The differences in egg width, length, and volume within two-egg clutches were as follows: 0.3 ± 1.3 mm, 0.5 ± 3.2 mm, and 14.4 ± 11.4 mm^3 (n = 43), respectively. Mean weight in early stages of the incubation period of seven eggs was 2.9 g (SD = 0.3, range = 2.6–3.2 g), while in later stages it was 2.7 g (SD = 0.3, range = 2.3–2.8 g), losing about 10% of their weight during the incubation process.

Breeding Success.—Of the 54 nesting attempts used to calculate nesting success, 35 were depredated (two of 11 nests during egg-laying, 25 of 51 nests during incubation, and eight of 23 nests with nestlings), and the other 15 produced fledglings. Only two nests were abandoned, and two nests reused, one of them successfully (i.e., raised two chicks). The average number of fledglings per successful nest was 1.7 (SD = 0.5, range = 1–2 fledglings). Daily survival rate based on 24 nest days during egg-laying was 0.92 with a total survival rate for this period of 0.81. Daily survival rate based on 492 nest days during incubation was 0.95 with a total survival rate for this period of 0.47. Daily survival rate based on 230 nest days during the nestling period was 0.97 with a survival rate for the nestling period of 0.63. The probability of nest success from laying to fledgling was 0.24.

DISCUSSION

Spectacled Tyrants use tall grasslands of *C. selloana* of the Pampas region to nest from mid-October to late January. There is a lack of information on the breeding biology of this species. In this work, we provide new data (see Fitzpatrick 2004) of nesting success, predation rate, and length of the incubation and nestling period.

The Spectacled Tyrant has been described as a species strongly associated with wetlands and surrounding areas (Partridge 1953, de la Peña 1988, Canevari et al. 1991, Fitzpatrick 2004) that nests near streams (Narosky and Salvador 1998). In our study, while Spectacled Tyrants showed some habitat preferences for wetlands, proximity to water was not always a basic requirement for nesting, since they made use of upland grasslands without immediate presence of water on the ground.

Spectacled Tyrants in the Pampas region have several characteristics typical of tropical and southern temperate birds: low nest survival, high predation rates, and small clutch size (e.g., Skutch 1949, Ricklefs 1969, Yom-Tov et al. 1994, reviewed in Martin 1996). In addition, a long breeding period and developmental periods for Spectacled Tyrants coincides with the life-history traits of southern temperate birds, which were relatively longer than in northern temperate birds (see review by Martin 1996), supporting the slow breeding strategy for southern hemisphere birds (Russell et al. 2004).

The nesting season lasted from mid-October to late January (~105 days), consistent with previous studies (Fitzpatrick 2004). A similar length period (120 days) was reported by Di Giacomo et al. (2011) for the Strange-tailed Tyrant (*Alectrurus risora*), another member of the subfamily Fluvico-

linae nesting in tall grasslands of northeastern Argentina.

The clutch size of Spectacled Tyrants was relatively small (mean = 2.2 eggs) and similar to the mean value of 2.7 eggs reported by Yom-Tov et al. (1994) for the family Tyrannidae in southern South America. Our mean was especially similar to the average clutch size of nine Tyrannidae species of comparable size from the same region (2.35 eggs, range = 2–2.9 eggs) (Mason 1985, Mezquida 2002, Auer et al. 2007).

The Spectacled Tyrant is the only species in the genus *Hymenops* (Fitzpatrick 2004), but compared to other tyrant flycatchers, its incubation period was within the range of most species of Tyrannidae studied in detail from the south temperate region (range = 12.8–17 days, n = 15 species) (Mason 1985, Mezquida and Marone 2000, Mezquida 2002, Auer et al. 2007, Di Giacomo et al. 2011). The same applies for the nestling period (range = 13–14 days, n = 13 species) (Mason 1985, Mezquida and Marone 2000, Mezquida 2002, Di Giacomo et al. 2011). Incubation and nesting periods are somewhat longer in our study area than in North America (13.1 ± 1.4 and 12.6 ± 2.9 days, respectively n = 31 genera; Geffen and Yom-Tov 2000).

Nest predation was the primary cause of nestling mortality at our site, which is consistent with studies for most birds (Ricklefs 1969, Martin 1995). Nest predation varied during the nesting cycle and was highest during the incubation period. In general, predation rate is higher during the nestling stage because of the increase in parental activity and nestling calling (Martin et al. 2000, Haff and Magrath 2011). However, some studies have found higher rates of predation during incubation, probably because parents increase defensive behavior when nestlings are present (Roper and Goldstein 1997, Farnsworth and Simons 1999).

The probability of a nest of a Spectacled Tyrant surviving the entire nesting cycle was relatively low (24%) when compared to nest survival of three grassland-breeding bird species within the Pampas region: 33% for Brown-and-yellow Marshbird (*Pseudoleistes virescens*) nesting also in *C. selloana* (Mermoz and Reboreda 1998), 50% for Pampas Meadowlark (*Sturnella defilippii*) nesting in *Stipa* and *Piptochaetium* grasslands (Cozzani et al. 2004), and 51% for Bay-capped Wren-Spinetail (*Spartonoica maluroides*) nesting in *Juncus* and *Spartina* grasslands (Llambías et al. 2009). Spectacled Tryants exhibited a nesting success lower to the average (36%) for six species of Tyrannidae in the Reserve of Ñacuñán at Mendoza Province, Argentina (Mezquida and Marone 2001). In addition, nesting success was low when compared with the mean nesting successes reported for Nearctic open-nesting species in shrublands and grasslands (50–60%, Martin 1993). Despite unknown breeding success of Spectacled Tyrants before anthropogenic habitat change in the Pampas, the relatively low breeding success in the southeast of the Pampas region could be evidence of habitat degradation that has led to greater exposure to predation.

ACKNOWLEDGMENTS

We would like to thank G. Martínez and D. A. Cardoni for help with fieldwork. We also want to thank I. J. Pretelli for her contributions to the literature search. We appreciate the improvements in English usage made by Bruce Peterson through the Association of Field Ornithologists' program of editorial assistance. We are grateful to two anonymous reviewers for comments and suggestions on the manuscript. The research received financial support from Neotropical Grassland Conservancy (NGC), Beca ''Conservar la Argentina'' (Aves Argentinas), Universidad Nacional de Mar del Plata and Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina). MGP was supported by a doctoral scholarship from CONICET.

LITERATURE CITED

AR, A. AND H. RAHN. 1980. Water in the avian egg: overall budget of incubation. American Zoologist 20:373–384.

ASTHEIMER, L. B. 1985. Long laying intervals: a possible mechanism and its implications. Auk 102:401–409.

AUER, S. K., R. D. BASSAR, J. J. FONTAINE, AND T. E. MARTIN. 2007. Breeding biology of passerines in a subtropical montane forest in northwestern Argentina. Condor 109:321–333.

CABRERA, A. L. 1976. Regiones Fitogeográficas Argentinas. Pages 1–85 *in* Enciclopedia Argentina de agricultura y jardinería (W. F. Kugler, Editor). Editorial ACME S.A.C.I., Buenos Aires, Argentina.

CANEVARI, M., P. CANEVARI, G. CARRIZO, G. HARRIS, J. RODRÍGUEZ MATA, AND R. STRANECK. 1991. Nueva guía de las aves Argentinas. Tomo II. Fundación Acindar, Buenos Aires, Argentina.

CARDONI, D. A., J. P. ISACCH, AND O. O. IRIBARNE. 2012. Effects of cattle grazing and fire on the abundance, habitat selection, and nesting success of the Bay-Capped Wren-Spinetail (*Spartonoica maluroides*) in coastal saltmarshes of the Pampas region. Condor 114:803–811.

CODESIDO, M., C. GONZÁLEZ-FISCHER, AND D. BILENCA. 2011. Distributional changes of landbird species in agroecosystems of central Argentina. Condor 113: 266–273.

COMPARATORE, V. M., M. M. MARTÍNEZ, A. I. VASSALLO, M. BARG, AND J. P. ISACCH. 1996. Abundancia y

relaciones con el hábitat de aves y mamíferos en pastizales de *Paspalum quadrifarium* (Paja Colorada) manejados con fuego (Prov. Buenos Aires, Argentina). Interciencia 21:228–237.

COZZANI, N., R. SÁNCHEZ, AND S. M. ZALBA. 2004. Nidificación de la Loica Pampeana (*Sturnella defilippii*) en la provincia de Buenos Aires, Argentina. Hornero 19:47–52.

COZZANI, N. AND S. M. ZALBA. 2009. Estructura de la vegetación y selección de hábitats reproductivos en aves del pastizal pampeano. Ecología Austral 19:35–44.

DARRIEU, C. A., G. SOAVE, AND E. SOAVE. 1988. Nidificación de passeriformes en la reserva integral de Punta Lara y sus alrededores, Buenos Aires, Argentina. Hornero 13:53–58.

DE LA PEÑA, M. 1988. Guía de aves Argentinas. Tomo V. Passeriformes. Dendrocolaptidae - Furnariidae - Formicariidae - Tyrannidae. Literature of Latin America, Buenos Aires, Argentina.

DI GIACOMO, A. S., A. G. DI GIACOMO, AND J. C. REBOREDA. 2011. Male and female reproductive success in a threatened polygynous species: the Strange-tailed Tyrant, *Alectrurus risora*. Condor 113: 619–628.

FARNSWORTH, G. L. AND T. R. SIMONS. 1999. Factors affecting nesting success of wood thrushes in Great Smoky Mountains National Park. Auk 116:1075–1082.

FITZPATRICK, J. W. 2004. Family Tyrannidae. Pages 170–462 *in* Handbook of the Birds of the World. Volume 9: Cotingas to pipits and wagtails (J. del Hoyo, A. Elliott, and D. A. Christie, Editors). Lynx Edicions, Barcelona, Spain.

GEFFEN, E. AND Y. YOM-TOV. 2000. Are incubation and fledging periods longer in the tropics? Journal of Animal Ecology 69:59–73.

HAFF, T. M. AND R. D. MAGRATH. 2011. Calling at a cost: elevated nestling calling attracts predators to active nests. Biology Letters 7:493–495.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

JOHNSON, D. H. 1979. Estimating nest success: the Mayfield method and an alternative. Auk 96:651–661.

LLAMBÍAS, P. E., V. FERRETTI, D. A. CARDONI, AND J. E. MALDONADO. 2009. Breeding success and social mating system of the Bay-capped Wren-Spinetail (*Spartonoica maluroides*). Wilson Journal of Ornithology 121:803–807.

MARTIN, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. American Naturalist 141:897–913.

MARTIN, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101–127.

MARTIN, T. E. 1996. Life history evolution in tropical and south temperate birds: What do we really know? Journal of Avian Biology 27:263–272.

MARTIN, T. E., C. R. PAINE, C. J. CONWAY, W. M. HOCHACHKA, P. ALLEN, AND W. JENKINS.1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, USA.

MARTIN, T. E., J. SCOTT, AND C. MENGE. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. Proceedings of the Royal Society of London B 267:2287–2293.

MARTÍNEZ, M. M. 2001. Avifauna de Mar Chiquita. Pages 227–250 *in* Reserva de Biosfera Mar Chiquita: Características físicas, biológicas y ecológicas (O. Iribarne, Editor). Editorial Martín, Mar del Plata, Argentina.

MASON, P. 1985. The nesting biology of some passerines of Buenos Aires, Argentina. Ornithological Monographs 36:954–972.

MAYFIELD, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456–466.

MERMOZ, M. E. AND J. C. REBOREDA. 1994. Brood parasitism of the Shiny Cowbird, *Molothrus bonariensis*, on the Brown-and-yellow Marshbird, *Pseudoleistes virescens*. Condor 96:716–721.

MERMOZ, M. E. AND J. C. REBOREDA. 1998. Nesting success in Brown-and-yellow Marshbirds: effects of timing, nest site, and brood parasitism. Auk 115:871–878.

MEZQUIDA, E. T. AND L. MARONE. 2000. Breeding biology of Gray-crowned Tyrannulet in the Monte Desert, Argentina. Condor 102:205–210.

MEZQUIDA, E. T. AND L. MARONE. 2001. Factors affecting nesting success of a bird assembly in the central Monte Desert, Argentina. Journal of Avian Biology 32:287–296.

MEZQUIDA, E. T. 2002. Nidificación de ocho especies de Tyrannidae en la reserva de Ñacuñán, Mendoza, Argentina. Hornero 17:31–40.

NAROSKY, T. AND A. DI GIACOMO. 1993. Las aves de la Provincia de Buenos Aires: Distribución y estatus. Asociación Ornitológica del Plata, Vázquez Mazzini Editores, Buenos Aires, Argentina.

NAROSKY, T. AND S. SALVADOR. 1998. Nidificación de las aves Argentinas. Tyrannidae. Asociación Ornitológica del Plata, Buenos Aires, Argentina.

NAVAS, J. R. AND N. A. BÓ. 2001. Aportes al conocimiento de la distribución, la cría y el peso de aves de las provincias de Mendoza y San Juan, República Argentina. Segunda parte (Aves: Falconidae, Scolopacidae, Thinocoridae, Columbidae, Psittacidae, Strigidae, Caprimulgidae, Apodidae, Furnariidae, Rhinocryptidae y Tyrannidae). Hornero 16:31–37.

PARTRIDGE, W. H. 1953. Observaciones sobre aves de las provincias de Córdoba y San Luis. Hornero 10:23–73.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1–48.

ROPER, R. J. AND R. R. GOLDSTEIN. 1997. A test of the Skutch hypothesis: Does activity at nest increase nest predation risk? Journal of Avian Biology 28:111–116.

RUSSELL, E. M., Y. YOM-TOV, AND E. GEFFEN. 2004. Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared. Behavioral Ecology 15:831–838.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SKUTCH, A. F. 1960. Life histories of Central American birds. Volume 1. Pacific Coast Avifauna 34. Cooper Ornithological Society, Berkeley, CA, USA.

YOM-TOV, Y., M. I. CHRISTIE, AND G. J. IGLESIAS. 1994. Clutch size in passerines of southern South America. Condor 96:170–177.