

BREEDING BIOLOGY OF THE THORN-TAILED RAYADITO (FURNARIIDAE) IN SOUTH-TEMPERATE RAINFORESTS OF CHILE

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Abstract. We conducted a study of the breeding biology of the Thorn-tailed Rayadito (*Aphrastura spinicauda*) in secondary forests on the continental island of Chiloé (42° S), southern Chile. Rayaditos are small insectivorous furnariids inhabiting the south-temperate forests of Chile and Argentina. We followed the reproduction of rayadito pairs breeding in nest-boxes. Rayaditos build their nests mainly of rhizomes and stems of epiphytic vines, grasses, and hairs during periods of at least a week, and show a marked population asynchrony in laying dates of more than two months (October–December). Rayaditos lay clutches of 3–6 eggs with a mode of 4 and laying occurs on alternate days. Eggs are 50% larger and hatchlings are 30% larger than expected from allometric equations. Most broods hatch synchronously. Nestling growth curves adjust well to logistic functions and at 2 weeks nestlings attain masses similar to asymptotic values. Nestling growth, which occurs over 3 weeks, is 27% slower than expected from allometry. Fledglings attain adult size with respect to tarsus length, but have less developed plumage and higher body mass than adults. Rayaditos exhibit clutch and brood reduction, suggesting possible food limitation. The protracted breeding periods may preclude second breeding attempts for most pairs in Chiloé. There is evidence for declines in parental quality with season. The low seasonal fecundity, large eggs, and prolonged dependence periods of a truly south-temperate species like the Thorn-tailed Rayadito reflect a ‘slow’ life history similar to that of tropical passerines.

Key words: *breeding biology, Chiloé, fecundity, Furnariidae, life history, temperate rainforests, Thorn-tailed Rayadito.*

Biología Reproductiva de *Aphrastura spinicauda* (Furnariidae) en Bosques Lluviosos Templados Meridionales de Chile

Resumen. Realizamos un estudio de la biología reproductiva del Rayadito *Aphrastura spinicauda* en bosques secundarios de la isla continental de Chiloé (42° S), sur de Chile. Este pequeño furnarido insectívoro habita los bosques templados meridionales de Chile y Argentina. Seguimos las actividades reproductivas de parejas de rayaditos que utilizaron cajas artificiales para nidificar. Los rayaditos construyen sus nidos utilizando rizomas, hierbas y pelo durante períodos de al menos una semana, y muestran una marcada asincronía a nivel de población de más de dos meses (octubre a diciembre) en el inicio de la puesta. Las puestas incluyen de 3 a 6 huevos, con un tamaño modal de 4 huevos, los cuales son puestas en días alternos. Los huevos son 50% más grandes y los polluelos recién eclosionados 30% más grandes de lo esperado según ecuaciones alométricas. La mayoría de las nidadas eclosionan sincrónicamente. Las curvas de crecimiento se ajustan bien a funciones logísticas y el peso alcanza valores asintóticos a las dos semanas. El crecimiento de los polluelos, que ocurre durante un período de permanencia en el nido de tres semanas, es un 27% más lento de lo esperado por alometría. Los volantones alcanzan el tamaño adulto con respecto a la longitud de tarso, pero presentan un plumaje menos desarrollado y un mayor peso que los adultos. Esta especie presenta casos de reducción de la puesta o de la nidada, lo que sugiere posibles limitaciones en la disponibilidad de alimentos. Los prolongados períodos de reproducción pueden impedir el inicio de segundas puestas en Chiloé. Hay evidencia de disminuciones estacionales en la calidad parental. La baja fecundidad anual, el gran tamaño de los huevos y el prolongado período de crecimiento del Rayadito refleja una historia de vida ‘lenta’ similar a la de paseriformes tropicales.

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INTRODUCTION

For the vast majority of species in the large passerine family Furnariidae, data on breeding biology are lacking (Remsen 2003). Furthermore, the species for which some information is available are clustered in Central America and eastern Argentina. Clearly, this leaves major gaps in our knowledge for most biomes where furnariids constitute an important part of the avifauna (Remsen 2003). What little information is available, points to important differences in life history between passerine suborders in South America, with furnariids (suborder deutero-oscines) laying smaller clutches than oscine passerines (Yom-Tov et al. 1994). The ecology of birds breeding in temperate regions is almost totally concerned with species of the Northern hemisphere and the contrast with the tropics is traditionally emphasized (Stutchbury and Morton 2001). However, there is increasing comparative evidence that the patterns of avian life history variation in south temperate regions are more similar to those of tropical birds than to north-temperate populations (Rowley and Russell 1991, Martin 1996, Martin et al. 2000, Russell et al. 2004). However, most information on south-temperate species concerns Australian and South African species breeding at latitudes not exceeding 40 degrees south. There is clearly a need to broaden the phylogenetic and geographic data base on the breeding traits of south-temperate birds including species that breed at similar latitudes to most populations studied in the Northern Hemisphere.

The Thorn-tailed Rayadito is a small, active, acrobatic furnariid (del Hoyo et al. 2003) with a distribution reaching the world's southernmost woodlands (Wallace 1991, Jaramillo et al. 2003), ranging from central Chile to Tierra del Fuego, and from the Andes to the Pacific coast. Rayaditos are characteristic of southern-temperate forests and adjacent second growth, although they may also inhabit conifer plantations and lowland scrub in the northern part of their range. Rayaditos are mainly insectivorous, gleaning prey items from foliage, mosses and lichens, and tree branches and trunks, from understory to canopy (Vuilleumier 1967). Johnson and Goodall (1967) described rayaditos as ecologically equivalent to the tits (Paridae) of the Northern hemisphere since both are cavity nesters with a

similar social structure. In winter, rayaditos are known to travel in mixed-species flocks, in which they are the nuclear species (Ippi and Trejo 2003).

Rayaditos offer a good opportunity to explore breeding adaptations of a truly temperate species that belongs to a family which is distributed almost entirely within the New World tropics. Rayaditos are cavity nesters which can be attracted to artificial nest boxes, thus increasing the possibility of attaining reasonable sample sizes and following the complete breeding cycle without excessive disturbance. To date, information on the breeding biology of this species is anecdotal (Johnson and Goodall 1967).

In two field seasons, we followed the breeding activities of rayaditos in temperate rainforests of Chiloé, a large continental island off the coast of Chile. Rayadito populations on Chiloé Island are considered to belong to the subspecies *fulva* due to the more extensive cinnamon color in breast and throat plumage, although we have evidence of continuous variation in this character with continental populations. Here we present extensive and detailed information about rayadito breeding biology.

METHODS

STUDY AREA

The study was conducted on Chiloé Island, Chile (41°52'S, 73°39'W), in the austral spring (October–December) of two years (2002–2003). Chiloé lies within 10 km of the mainland and supports similar forest bird communities (Johnson and Goodall 1967, Fjeldså and Krabbe 1990, Jaramillo et al. 2003). The continuous temperate rainforests experienced by Charles Darwin in 1834–1835 have been cleared in large areas of northern Chiloé, with remaining fragments embedded in an agricultural landscape (Willson and Armesto 1996). Nest boxes were placed in two large forest blocks, Senda Darwin Biological Station (300 nest boxes) and Fundo “Los Cisnes” (50 nest boxes), at the northern tip of the island and very close to mainland Chile. Both study sites include large fragments of regenerating evergreen forests of *Drimys winteri*, *Notofagus nitida*, *Weinmannia trichosperma*, several myrtaceous species, and the conifer *Podocarpus nubigena* (Veblen et al. 1996, Aravena et al. 2002). The understory included dense *Chusquea* spp. (bamboo) thickets and saplings.

Nest boxes were made of wood and had a base of 18 cm × 16.5 cm (inner dimensions 16.5 × 14) and a height of 25 cm at the front and 30 cm at the back, with a sloping roof that overhung the front of the box by 3 cm. The entrance hole had a diameter of 3 cm and was located 19 cm from the bottom of the box. Nest boxes were fastened to tree trunks approximately 150 cm above the ground and placed near forest edges, with some up to 100 m within the forest.

NEST MONITORING

Nest boxes were checked for occupation beginning in October on a weekly basis. When occupied by rayaditos, nest-check frequency was increased to detect laying dates (date of first egg), hatching dates (first visit with chicks in the nest) and fledging dates (empty nest box). Two weeks after laying of the last egg, nests were checked on a daily basis to record the exact day of hatching. Three weeks after hatching, some nests were visited daily to record fledging date. Three late nesting attempts were considered as repeat attempts as they were initiated close to depredated nests in nest boxes, but pairs were not identified during the failed breeding attempt. Egg length and breadth were measured with a plastic digital calliper to the nearest 0.1 mm. Egg volume was obtained with Hoyt's (1979) formula: $\text{Volume} = 0.51 (\text{Length} \times \text{Breadth}^2)$. Eggs of one clutch were weighed on the day of laying of each egg. Some nests were removed after fledging to weigh them and determine composition of nest material.

Adults were captured with nest-box traps when chicks were 13 days (hatching day = day 0). They were banded with individual combinations of color bands and with metal bands (National Band and Tag, Co., Newport, KY, model 1242-3) under the authority of Servicio Agrícola y Ganadero, Chile. Following Svensson (1984), we measured tarsus length and bill length (using digital callipers, to the nearest 0.1 mm), flattened wing chord (nearest mm) and the two central rectrices on one side of the tail (nearest mm). The two central rectrices on each side of the tail are the longest and have a spine. We measured their entire length as well as the length of the spine. Adults could not be sexed using morphology since there is no marked sexual size or plumage dimorphism. In addition, all birds showed signs of a brood patch and there was no detectable variation in the size of cloacal

protuberances. Mass was recorded with a PE-SOLA (Baar, Switzerland) spring balance to the nearest 0.1 g. On the day of adult trapping, we also weighed nestlings and measured tarsus length, bill length (from tip to skull) and wing length using the same technique as for adults.

NESTLING GROWTH

Nestlings of eight broods were selected for a detailed study of growth. Nestlings were measured on days 2, 4, 6, 8, 10 and 14. Tarsus length, bill length, wing length and mass were recorded. Nestlings were recognized individually until day 6 (when they were banded) by cutting tufts of down on head or wings. Mass of nestlings of 2–8 days was recorded on a TANITATM (Japan) portable electronic balance to the nearest 0.1 g. Wing length before the appearance of feather shafts on day 8 was measured with digital callipers, and after day 8 with a ruler. In six nests, nestlings were measured on day 21 to obtain final measurements before fledging. In four nests, nestlings were weighed on the day of hatching.

STATISTICAL ANALYSES

Clutch and brood size at hatching showed distributions differing significantly from normality (Kolmogorov-Smirnov test, $P < 0.05$), thus data were logarithmically transformed before using parametric analyses. Measures of breeding success were arcsine transformed. Growth was adjusted to logistic regressions for all nestlings to obtain the asymptotes and growth constants characteristic of the population (Ricklefs 1968). For comparisons among broods, we used linear regressions for each nestling derived from the linear periods of growth for each trait. The within-brood average of linear growth rates was used for traits that showed significant within-brood repeatability. Data are presented as means ± SD. Tests were considered significant when $P \leq 0.05$.

RESULTS

NESTS

Time required for nest construction was estimated from a sample of nests for which we had records of the first appearance of nest material inside the nest-box. We considered nest construction to extend from the date of the first appearance of nest material to the laying of the first egg. Our estimate of 6.1 ± 4.8 days ($n = 15$) is a minimum because nest construction continued

during laying and the beginning of incubation. In several nests, the first egg was laid on a barely initiated nest.

Nest structure was made of small twigs, rhizomes and fine stems of rain forest epiphytes, primarily filmy ferns (Hymenophyllaceae). Nests were covered around the rim by fine grasses (including understory bamboo) and animal hairs. Nests have a dry weight of 33.7 ± 5.1 g (range 27.0–43.9 g, $n = 12$). Neither hatching date nor clutch size showed any significant association with dry nest weight ($P > 0.30$). No measure of reproductive success was correlated with nest weight ($P > 0.50$).

BREEDING PHENOLOGY

Laying was significantly earlier in 2003 than in 2002 ($F_{1,27} = 4.5$, $P = 0.04$), although the sample of nests followed in 2002 was small ($n = 5$). For the following analyses, data from both years were pooled. First clutches were laid between 5 October and 29 November with a median laying date of 30 October ($n = 29$). Hatching of first clutches occurred between 26 October and 16 December, with a median hatch date of 18 November ($n = 23$). Fledging of first broods occurred between 18 November and 4 January (median = 4 December, $n = 18$). Only one pair laid a second clutch, 15 days after their first brood fledged. This nest was depredated before eggs hatched, but had the nest been successful, chicks would have fledged at the end of January. Three repeat clutches, where the pair was not identified during the presumed first nesting attempt (see Methods), were initiated between 23 November and 12 December. These nests hatched on 15 December and 28 December, respectively; the remaining repeat clutch did not hatch. One repeat brood fledged young in the second half of January.

CLUTCH SIZE AND BROOD SIZE

In two late nests that were visited daily during laying, one egg was laid every other day for all eggs in both nests (three and four eggs, respectively). Clutch size ranged from three to six eggs (4.1 ± 0.8 , $n = 30$) and modal clutch size was four eggs. There was no difference in clutch size between years ($F_{1,28} = 2.8$, $P = 0.11$), and there was no seasonal trend in clutch size within years (year: $F_{1,18} = 1.28$, $P = 0.27$; laying date: $F_{1,18} = 0.23$, $P = 0.64$). Brood size at hatching ranged from three to six chicks (4.2 ± 0.7 , $n =$

22) and modal brood size was four chicks. Brood size on day 13 (hatching day = day 0) ranged from two to five nestlings (3.7 ± 0.9 , $n = 23$) and modal brood size was three chicks.

EGG SIZE

Rayadito females laid eggs 18.6 ± 0.5 mm long and 14.7 ± 0.7 mm wide ($n = 57$). Egg length, width and volume measurements had high repeatability within clutches (length: $r = 0.75$, $P < 0.001$; width: $r = 0.90$, $P < 0.001$; volume: $r = 0.90$, $P < 0.001$). Mean egg volume was 2010 ± 200 mm³ ($n = 57$). There was no association between mean egg volume and clutch size ($F_{1,12} = 2.48$, $P = 0.14$) or between mean egg volume and laying date ($F_{1,12} = 0.13$, $P = 0.72$). The egg mass predicted from dimensions using Hoyt's (1979) formula was 2.2 g, a value similar to our findings of rayadito egg mass (2.1 ± 0.1 g, $n = 5$ eggs from 2 clutches). With an adult body mass of 11 g, the allometric equation for passerines (Rahn et al. 1985) predicts that eggs should weigh 1.5 g. Thus, rayadito eggs are almost 50% larger than expected from body size.

INCUBATION PERIOD

In two nests where the initiation of incubation was recorded through daily visits during laying, incubation started with the last egg laid. The predicted incubation period based on egg mass was 13.8 days (Rahn and Ar 1974). Incubation period, assuming eggs were laid on alternate days and incubation started with the last egg, ranged from 9–16 days (12.8 ± 1.9 , $n = 16$) with a mode of 14 days. In one nest where incubation was accurately determined by checking egg temperature, incubation lasted 15 days. Incubation period was not significantly correlated with laying date (ANCOVA: date $F_{1,13} = 3.1$, $P = 0.10$; year $F_{1,13} = 4.3$, $P = 0.06$). After controlling for differences between years, the period between laying of the first egg and hatching of the brood was negatively related to laying date (Fig. 1, ANCOVA: date: $F_{1,14} = 11.3$, $P = 0.005$, year: $F_{1,14} = 6.8$, $P = 0.02$). This indicates that either laying intervals were shortened or embryonic developmental rate increased over the course of the season.

NESTLING PERIOD

All nestlings in the brood hatched within one day in 6 of the 9 broods visited daily during hatching. In the remaining nests, one had an egg

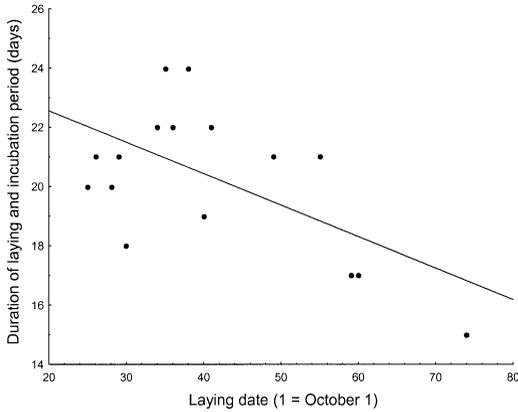


FIGURE 1. Linear regression of the duration of the laying and incubation period on laying date for Thorn-tailed Rayaditos (*Aphrastura spinicauda*) breeding in south-temperate rainforests on Chiloé Island, Chile ($r = -0.60$, $F_{1,15} = 8.4$, $P = 0.01$).

that did not hatch, and the other two nests had one nestling that hatched before the following visit. The nestling period ranged from 16 to 23 days (21.8 ± 1.7 , $n = 15$). There was a negative association of nestling period duration with hatching date after controlling for year (AN-

COVA: date: $F_{1,12} = 6.7$, $P = 0.02$; year: $F_{1,12} = 10.1$, $P < 0.001$).

NESTLING GROWTH

According to the allometric equation for hatchling mass (Blueweiss et al. 1978), we should expect a hatchling mass of 1.6 g. On average, nestlings weighed 2.1 ± 0.3 g ($n = 15$) on the day of hatching, thus hatchlings are 30% larger than predicted. Given the egg masses recorded, these chicks had likely received some food prior to weighing. Growth in mass, tarsus, bill, and wing can be described with logistic functions that explained more than 95% of variation in growth of all traits (Fig. 2). Following Ricklefs (1968), we estimated that it required 10.2 days for nestlings to grow between 10 and 90% (t_{10-90}) of asymptotic mass, which is 27% longer than the time predicted by allometry (Ricklefs 1968) and the observed asymptotic mass.

The periods with linear growth differed among morphological traits. For mass, tarsus, and bill length, growth was linear between days 2–8, while linear growth was observed between days 8–14 for wing length (Fig. 2). We calculated linear growth rates for each nestling in 8

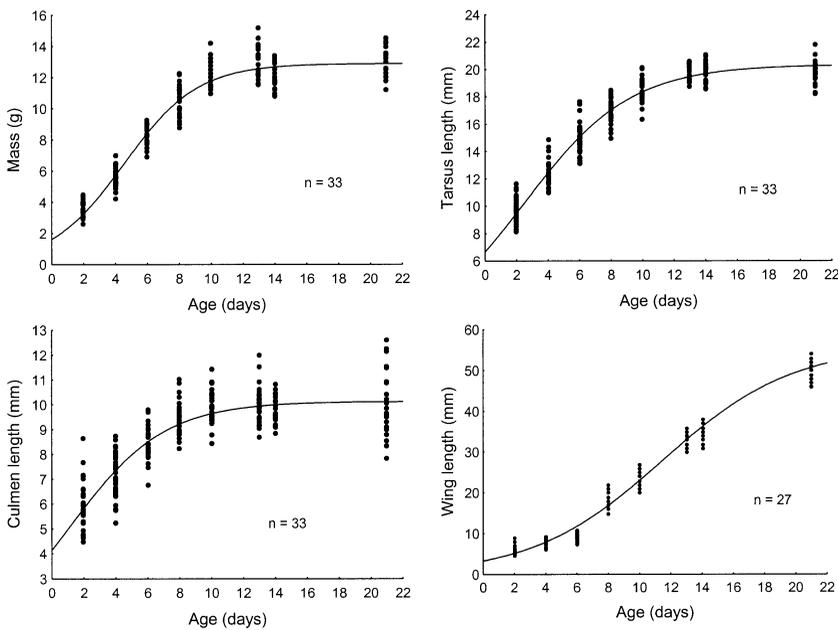


FIGURE 2. Logistic regressions of mass, tarsus length, bill length, and wing length on nestling age of Thorn-tailed Rayaditos (*Aphrastura spinicauda*) using the equation: $y = A(1 + e^{-K(\text{age}-t)})^{-1}$. Parameters are: Mass, $A = 12.9$, $K = 0.43$, $t = 4.5$; Tarsus length, $A = 20.3$, $K = 0.29$, $t = 2.5$; Bill length, $A = 10.1$, $K = 0.34$, $t = 1.1$; Wing length, $A = 55.8$, $K = 0.24$, $t = 11.5$; all parameters are highly significant, $P < 0.001$.

TABLE 1. Comparison of morphological measurements and mass of nestlings, on the day before fledging (day 21), and adult Thorn-tailed Rayaditos (*Aphrastura spinicauda*) in south-temperate rainforests of Chiloé Island, Chile. Data are presented as mean \pm SD (*n*).

Morphological trait	Nestlings 21 days	Adults	<i>t</i>	<i>P</i>
Tarsus length (mm)	19.9 \pm 0.8 (26)	19.7 \pm 0.7 (42)	0.7	0.50
Bill length (mm)	10.0 \pm 1.4 (26)	13.9 \pm 0.6 (42)	16.0	<0.001
Wing length (mm)	50.9 \pm 2.0 (26)	56.3 \pm 2.3 (42)	10.0	<0.001
Total length of central rectrix (mm)	32.8 \pm 2.3 (19)	70.1 \pm 4.1 (42)	36.7	<0.001
Length of central rectrix without spine (mm)	19.8 \pm 3.2 (11)	51.0 \pm 4.1 (42)	23.3	<0.001
Total length of 2nd innermost rectrix (mm)	30.7 \pm 1.0 (14)	56.7 \pm 2.5 (32)	36.8	<0.001
Length of 2nd innermost rectrix without spine (mm)	22.0 \pm 1.2 (14)	47.8 \pm 2.3 (32)	39.2	<0.001
Mass (g)	13.0 \pm 1.0 (25)	10.8 \pm 0.8 (41)	9.4	<0.001

broods and found that growth rate explains a large proportion of variation in tarsus length, mass, and wing length (all $\beta > 0.90$), while it explains less variation in bill length (all $\beta > 0.80$). Nestlings within broods were similar in linear rates of growth with respect to tarsus length ($r = 0.39$), mass ($r = 0.40$), and wing length ($r = 0.41$, all repeatabilities $P < 0.01$), but not with respect to bill length ($r = 0.21$, $P = 0.09$). Hatching date showed a significant negative association with average wing growth rate of each brood ($r = -0.80$, $P = 0.03$), but not with mass growth rate ($r = -0.04$, $P = 0.93$) or tarsus growth rate ($r = -0.36$, $P = 0.39$). There were no relationships between average growth rate and brood size (wing: $r = 0.20$, $P = 0.66$; mass: $r = 0.31$, $P = 0.46$; tarsus length: $r = 0.12$, $P = 0.77$) or mean egg volume (wing: $r = 0.67$, $P = 0.15$; mass: $r = -0.15$, $P = 0.77$; tarsus length: $r = -0.33$, $P = 0.52$).

Nestlings on day 13 had attained asymptotic size with respect to tarsus and bill length, and mass, but not with respect to wing length (Fig. 2). Within-brood similarity in morphology was significant for bill and wing length (bill: $r = 0.61$, $P < 0.001$; wing: $r = 0.84$, $P < 0.001$) but not for tarsus ($r = 0.17$, $P = 0.07$) or mass ($r = 0.14$, $P = 0.10$). Neither mean bill length nor mean wing length per brood was associated with brood size or hatching date (all $P > 0.05$).

Tarsus length was the only morphological trait to attain full adult size by fledging (Table 1). At fledging, rayaditos were 28% smaller than adults with respect to bill length, 10% smaller with respect to wing length, and 53–61% smaller with respect to rectrix length, and were 20% heavier than adults at the end of the nestling stage. Due to energetic constraints of parental care, adults probably reach their lowest body mass level at

this stage of the nesting cycle (Moreno 1989). The relationship between the asymptote of fledging mass to adult mass (ratio = 1.19) indicates that nestlings fledged with a higher mass than expected from a 22-day nestling period (expected ratio = 1.03, after Ricklefs 1976). From our observation of color-banded family flocks, post-fledging care duration is at least one month.

REPRODUCTIVE SUCCESS

Of 34 clutches, 8 (24% failure) were depredated during the egg stage. Of the remaining 26 broods that hatched, two were depredated and one was deserted at an early stage, giving an overall failure rate of 32%. We calculated daily survival rates using the Mayfield (1975) method for all nests (excluding the one case of nest desertion) during each stage of the nesting cycle. Daily survival rates were 0.43, 0.71 and 0.91 during the laying, incubation, and nestling stages, respectively.

Hatching (% eggs hatched), fledging (% hatched chicks fledging) and breeding success (% eggs fledged) for all nests that hatched young ($n = 26$) were 95.2 ± 10.2 , 83.4 ± 32.6 and 76.7 ± 31.0 , respectively. Including nests depredated at the egg stage ($n = 34$), hatching, fledging, and breeding success were 72.8 ± 42.0 , 63.8 ± 45.8 and 58.7 ± 42.7 , respectively. Clutch size and laying date were not related to hatching success in ANCOVA controlling for year ($P > 0.10$). For all nests that hatched young, the number of young fledged was 3.2 ± 1.4 (range = 2–5 young). When including nests depredated during the egg stage, the average number of fledged young was 2.5 ± 1.9 ($n = 34$). Controlling for year effects, neither brood size nor hatching date showed any association

with fledging or breeding success (ANCOVA, all $P > 0.10$).

We also found evidence of apparent clutch and brood reduction by parents. At least one egg was removed without signs of predation prior to hatching; all remaining eggs hatched and fledged. An unhatched egg also disappeared from one nest after the remaining eggs hatched, showing that parents are able to eject eggs from the nest. In three cases, chicks (two at 7–8 days and one newly hatched) were found starved outside of the nest cup. Three starved chicks older than one week were found dead among their siblings in three other broods.

AGE OF FIRST BREEDING

A pair of nestlings raised in the same nest in 2002 bred together as a pair in 2003. Thus, age of first breeding can be as low as one year.

DISCUSSION

The need to widen the geographic scope of study of avian life histories has been stressed recently (Martin 1996, Stutchbury and Morton 2001). Furnariids constitute a large group of understudied passerine species (Remsen 2003). Most attention has focussed on nest-building behaviour (Zyskowski and Prum 1999), while life-history information is obtained mostly from museum data or from handbooks and guides based on studies with very small samples (Yom-Tov et al. 1994). Thorn-tailed Rayadito breeding biology has not been the subject of a detailed study, despite it being one of the most southern-breeding passerines worldwide.

Rayadito breeding biology presents features that differentiate them from equivalent north-temperate cavity nesters such as asynchronous breeding, laying of eggs on alternate days, small clutches, large eggs and extended periods of parental dependence. The large population asynchrony in breeding onset of more than 2 months suggests large parental quality differences based presumably on age and experience (the pair of one-year old breeders were among the latest pairs). Compared to their north-temperate counterparts, south-temperate passerines appear to exhibit low annual fecundities (Yom-Tov 1987, Rowley and Russell 1991, Yom-Tov et al. 1994, Martin 1996, Stutchbury and Morton 2001). As South American cavity nesters have similar clutch sizes as open nesters (Yom-Tov et al. 1994), nest type cannot explain these differenc-

es. However, suboscine passerines like rayaditos seem to have low annual fecundities as a group (Yom-Tov et al. 1994), which suggests a phylogenetic aspect to life history variation that an intraspecific study cannot resolve.

Rayadito eggs are 50% larger than expected from body size (Rahn et al. 1985), which probably explains the long laying intervals for such a small passerine. The few furnariids studied also lay eggs on alternate days, possibly due to the high cost of producing such large eggs (Remsen 2003). However, Geffen and Yom-Tov (2000) found no difference in egg size between temperate and tropical regions when correcting for phylogeny, so the large egg volumes of rayaditos may be just a characteristic of furnariids. Alternatively, populations maintained near carrying capacity may favor high investment in offspring, as expressed as large egg volumes and prolonged dependence periods (Ashmole 1963, Yom-Tov and Geffen 2002). South-temperate rainforests may not exhibit large fluctuations in food availability due to the reduced range of climatic variation compared with northern equivalent areas, and the high proportions of residents in avian communities suggests that populations are, in fact, maintained at carrying capacity.

We also observed seasonal declines in the combined laying and incubation periods and also in the nestling period. The former may have resulted from more efficient incubation with increased temperature, whereas the latter was possibly a consequence of seasonally increased food availability or of parents forcing earlier fledging to reduce costs. Also, high annual adult survival rates in the south (Martin 1996, 2002, Peach et al. 2001, Stutchbury and Morton 2001) may favour prudent reproduction. Rayaditos showed some evidence of reproductive constraint as expressed through clutch and brood reduction.

One of the most striking aspects of rayadito breeding biology is undoubtedly the long period of parental dependence, a pattern also found in coexisting tapaculos (de Santo et al. 2002). Nestlings hatch synchronously and are 30% larger than expected from adult body size (Blueweiss et al. 1978). Hatchlings have exceptionally well-developed down (JM, pers. obs.) but take more than 3 weeks to fledge, and gain mass 27% slower than predicted from body size. They attain adult skeletal size before fledging, as indicated by tarsus length, but have less developed plumage, especially with respect to their char-

acteristic thorn-tail. Fledglings weigh more than adults and more than expected based on the duration of the nestling period (Ricklefs 1976), although water content in relation with maturity of tissues at this stage could explain the difference (Ricklefs 1979). Generally, offspring remain with their parents prolonged periods after fledging in southern hemisphere and tropical-nesting passerines (Russell et al. 2004). Rayaditos follow a similar pattern; we observed color-banded family flocks, consisting of adults and fledged young, together one month after the completion of nesting.

To conclude, in common with other cavity nesters in the area (de Santo et al. 2002), rayaditos invest annually in few offspring from large eggs with fledglings exhibiting prolonged periods of parental dependence. This pattern, uncommon in north-temperate passerine cavity nesters, may be explained both by phylogeny and adaptation to their environment (Yom-Tov et al. 1994, Martin 1996, Ricklefs 2002). To fully understand life history variation at a large geographic scale, information on age-specific mortality of Thorn-tailed Rayaditos and other south-temperate species is required.

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