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REPRODUCTIVE SUCCESS OF THE CREAMY-BELLIED THRUSH IN A SOUTHERN TEMPERATE ZONE

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ABSTRACT.—We describe the breeding biology and reproductive success of a Creamy-bellied Thrush (*Turdus amaurochalinus*) population from a southern temperate zone in western Argentina. We found 236 Creamy-bellied Thrush nests of which most were predated (67%). The breeding season was from late October to late December and clutch size was three eggs. Egg survival, hatching success, and fledgling survival of non-depredated nests were quite high (0.67 ± 0.03, 0.74 ± 0.03, and 0.87 ± 0.04, respectively). The number of eggs in the nest did not affect egg survival or hatching success, but number of nestlings in the nest affected fledgling success. Daily nest mortality was higher during the early and late nestling period than during laying, and early and late incubation periods. Highest nest mortality coincided with periods when activity of parents at the nest was highest. The clutch size was similar to data reported for thrushes from the tropics and south temperate areas, and lower than reported for thrushes from north temperate areas. This latitudinal pattern is similar to the general pattern described for passerines in the tropics and southern temperate areas. *Received 8 February 2011. Accepted 14 September 2011.*

The study of avian breeding ecology in the Americas has mostly concerned tropical and northern temperate species. New data from the Southern Hemisphere suggest life history traits and behavior of southern temperate species are more similar to tropical than to northern temperate species (Martin 1996, Martin et al. 2000, Robinson et al. 2010). This conclusion is based on a limited number of southern temperate locations and species, and more information is needed on avian life history traits in southern temperate areas (Robinson et al. 2010).

The Turdidae (true thrushes, *Turdus* spp.) is a cosmopolitan group in the tropics, and northern and southern temperate areas around the world. Thus, they are an excellent model for study of life history evolution, breeding biology, and latitudinal variation among related species occupying different ecosystems. However, there are only a few comparative studies (Martin et al. 2000, Ferretti et al. 2005) and the available information is biased to north temperate species. Most information on breeding biology for species of *Turdus* in Argentina comes from studies in the Pampas and Yungas (e.g., Martin et al. 2000, Sackmann and Reboreda 2003, Ferretti et al. 2005). There are no studies available for populations from semi-arid areas of western Argentina (but see Mezquida and Marone 2001 for other passerine species).

The Creamy-bellied Thrush (*Turdus amaurochalinus*) is widespread in South America, but its breeding biology has only been recently studied (Astié and Reboreda 2005, 2006). The objectives of our study were to obtain information on breeding biology and reproductive success of a Creamy-bellied Thrush population from a southern temperate zone in western Argentina. Specifically, we examined if number of eggs and nestlings present in the nest affect reproductive success during different stages of the nestling cycle.

METHODS

Study Species.—The Creamy-bellied Thrush is a monomorphic and monotypic passerine of the genus *Turdus*. This species is widely distributed from southern Brazil to southern Argentina (Ridgely and Tudor 1989), but little is known about its breeding biology. Creamy-bellied Thrushes build open cup nests composed of grasses cemented with mud and lined with grasses and hairs. They lay three eggs with a pale greenish background and spots and blotches of reddish-brown concentrated at the larger pole (Astié and Reboreda 2005). The incubation period is 11.5 days and the nestling period is 12 days (Astié and Reboreda 2005, 2009a). Average adult mass is 55 g (Astié and Reboreda 2005). This species is heavily parasitized by the Shiny Cowbird (*Molothrus bonariensis*) in the study area (Astié and Reboreda 2005, 2006, 2009a, b).

Study Site.—The study was conducted at Guaymallén, Mendoza Province, Argentina (32° 51′ S, 68° 42′ W) during the 1999–2002 breeding seasons (October–December). Mendoza is in the Monte Desert region of Argentina. The Creamy-bellied

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Thrush only occupies areas irrigated for agriculture. The study area was a 1,000-ha cultivated field with vineyards, olives (*Olea europaea*), and poplar (*Populus nigra*) groves.

Data Collection.—We followed the fates of 236 thrush nests which were found by observing adult behavior and systematic search. Nests were visited every 1–2 days until nestlings fledged or the nest failed. We recorded the numbers of eggs and nestlings during visits. We considered a nest to have been predated when the complete clutch disappeared between two subsequent visits.

Data Analyses.—We divided the reproductive season into groups of 10 days starting with the first egg laid until the last nest in laying stage was found. We recorded the frequency of nests that started in each period and estimated the survival of nests (0–1) throughout the season with logistic regression including a subset of nests found during building and laying periods ($n = 98$ nests).

We calculated mean ± SE success of eggs and nestlings in nests in each nesting cycle period (egg laying, incubation, and nestling) that were not predated, deserted, or parasitized by the Shiny Cowbird. Egg survival was calculated as the proportion of eggs present in the nest at the end of incubation divided by the number of eggs in the nest at the start of incubation. We only considered nests found in building and laying stages that survived until the hatch of the first egg ($n = 48$ nests). We calculated hatching success as the proportion of eggs that hatched divided by the number of eggs in the nest at the end of incubation. We only considered nests found in building, laying, or incubation stages where at least one egg hatched ($n = 109$ nests). Fledgling survival was calculated as the proportion of fledglings divided by the number of eggs that hatched. We considered only nests found during building, laying, or incubation stages that fledged at least fledged one nestling ($n = 44$ nests). We used a Chi-square test to analyze if number of eggs in the nest affected egg survival (all eggs survived or at least 1 disappeared) or hatching success (all eggs hatched or at least 1 failed), and if fledgling survival was associated with number of nestlings (all nestlings survived or at least 1 died).

We evaluated if nest survival was associated with adult activity in the nest by subdividing the nesting cycle into five periods: laying (laying of the first and the second egg), early incubation (since the laying of the third egg until day 7), late incubation (day 8 until the first eggs hatched), early nestlings (from the day the first egg hatched until day 6), and late nestlings (from day 7 until the first fledgling left the nest).

Nest mortality risk (m) was calculated for each period following Mayfield (1975), and the standard error was calculated as suggested by Johnson (1979). We compared mortality rates with a Fisher test of contingence. We compared each nest mortality period versus every other period and applied a Bonferroni correction for multiple comparisons (Abdi 2007).

Adult activity in the nest was recorded by videotaping 20 nests with Hi8 Sony video cameras. Nests were recorded during 4 hrs beginning at 0700. Cameras were placed 2 m from the nest and camouflaged with leaves. We recorded two nests during the laying stage, six nests during early incubation, two during late incubation, four with early nestlings, and six with late nestlings. We obtained latencies (time elapsed since placement of the camera and the moment an adult returned to the nest), frequency of visits per hour (average number of times an adult entered the nest in 1 hr), and nest attentiveness (average proportion of time an adult stayed in the nest during 1 hr) for each video. All statistical tests were conducted with StatView 5.0 (SAS 1998).

RESULTS

We found 236 nests of Creamy-bellied Thrushes, 42% during the building and laying period, 51% during the incubation period, and 7% during the nestling period; 18 were found in 1999, 87 in 2000, 91 in 2001, and 40 in 2002. Sixty-seven percent of the nests were predated, 8% were deserted, and 2.5% were destroyed by strong winds or rain. Only 22.5% of the nests produced at least one fledgling. The majority of the nests (62%) were parasitized by the Shiny Cowbird and at least one egg in 68% of the nests was punctured.

Most of the nests (70%, $n = 236$) found were in vineyards and in olive trees, and the rest in poplar and fruit trees. Nest dimensions (mean ± SE) were: 10.5 ± 0.5 cm in external height, 6.1 ± 0.3 cm in depth, and 12.3 ± 0.2 cm in external width with an internal diameter of 7.9 ± 0.3 cm ($n = 20$ nests).

The first nest was found on 21 October and the number of nests in the laying stage increased to a maximum between 23 and 25 November; the last nest in the laying stage was found on 25

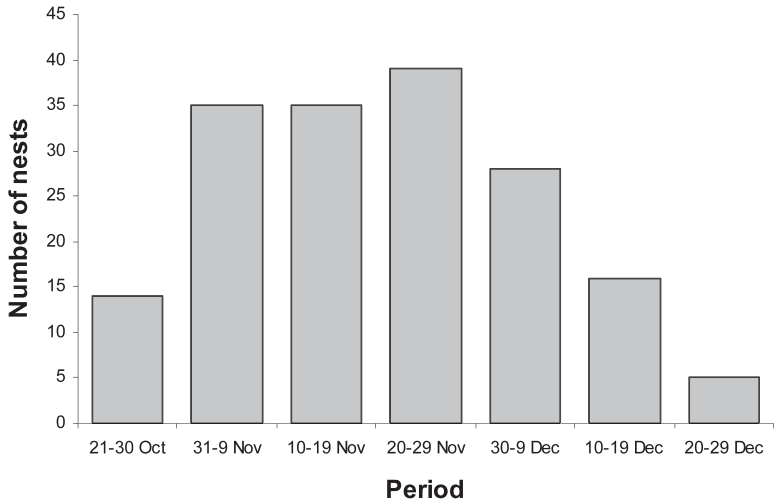

FIG. 1. Number of nests in the laying stage during the reproductive season of the Creamy-bellied Thrush. The reproductive season was divided into intervals of 10 days.

December (Fig. 1). Nest survival was not associated with time in the season when the nest was initiated; nests that failed or succeeded (0–1) were independent of the time when they were initiated (logistic regression: $X^2 = 1.03$, $P = 0.31$, $n = 98$ nests).

One egg was laid per day and incubation started with laying of the penultimate egg (for nests found during building and laying stages, $n = 98$). Egg survival was 0.67 ± 0.03 ($n = 48$ nests), hatching success was 0.74 ± 0.03 ($n = 109$ nests), and fledgling survival was 0.87 ± 0.04 ($n = 44$ nests). The number of eggs present in the nest did not affect egg survival or hatching success ($X^2 = 6.39$, $P = 0.09$, $n = 48$ and $X^2 = 0.12$, $P = 0.94$, $n = 109$, respectively), but the number of nestlings was negatively associated with fledgling success ($X^2 = 16.35$, $P = 0.001$, $n = 44$). At least one nestling died when there were three nestlings in 58% of the nests ($n = 12$ nests), at least one nestling died in 20% of the nests ($n = 15$ nests) when there were two nestlings, but only 4% died ($n = 17$ nests) when there was one nestling.

The Bonferroni correction for multiple comparisons set the significance level at $\alpha < 0.005$. Daily nest mortality was higher during laying (0.079 ± 0.006, $n = 39$) than during early incubation (0.013 ± 0.002, $n = 50$, $X^2_1 = 8.77$, $P = 0.003$), but there was no difference with late incubation (0.017 ± 0.002, $n = 53$, $X^2_1 = 4.62$, $P = 0.041$), early nestling (0.11 ± 0.006, $n = 50$, $X^2_1 = 2.13$, $P = 0.11$), and late nestling (0.10 ± 0.013, $n = 24$, $X^2_1 = 4.40$, $P = 0.022$) periods. We found no differences between early and late incubation ($X^2 = 1.09$, $P = 0.27$) nor between early and late nestling ($X^2_1 = 1.02$, $P = 0.28$) periods. Early incubation was significantly lower than early and late nestlings periods ($X^2_1 = 37.66$, $P < 0.001$ and $X^2_1 = 45.99$, $P < 0.001$, respectively) and late incubation was also significantly lower than early and late nestling periods ($X^2_1 = 37.54$, $P < 0.001$ and $X^2_1 = 45.14$, $P < 0.001$, respectively; Fig. 2)

We had small samples for parental care behavior and could not perform any statistical comparisons. We observed a trend of increased latency to return to the nest during the laying stage. Frequency of visits appeared to be highest during the nestling stage and time spent in the nest was highest during the incubation stage (Fig. 3).

DISCUSSION

The Creamy-bellied Thrush in the southern temperate Monte Desert has several characteristics typical of tropical birds: low nest survival, high predation rates, and small clutch size. Nests at our study site had a low survival rate, as only 22.5% of the nests produced at least one fledgling; predation was the major cause of nest failure (67%). Nest predation was constant throughout the season and was not related to the time a nest was initiated. Nest mortality varied during the nestling cycle and was highest during the late nestling period (Fig. 2). Parental activity

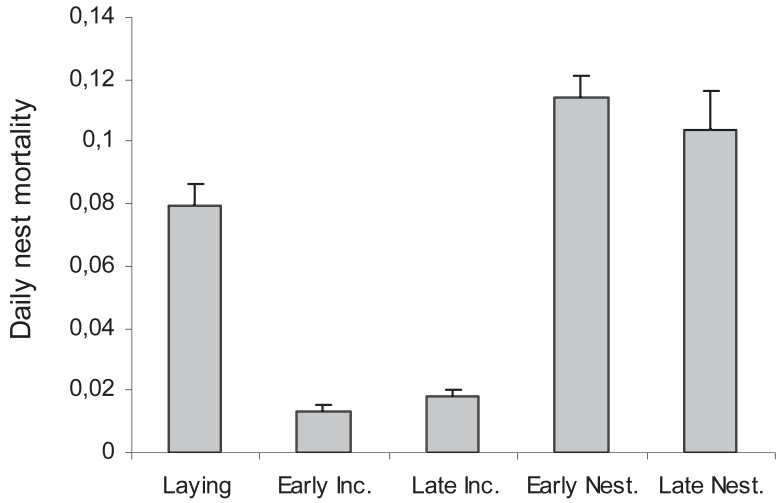

FIG. 2. Daily nest mortality (mean ± SE) during laying, early incubation, late incubation, early nestling and late nestling periods of the Creamy-bellied Thrush. The number of nests included was 39 in laying, 50 in early incubation, 53 in late incubation, 50 in early nestling, and 24 in late nestling periods.

during this stage was highest around the nest (Fig. 3) and suggests that visual predators were involved. This could be related to attraction of visual predators when parental activity increased around the nest (Skutch 1949, Martin et al. 2000, Martin et al. 2011). An experimental approach would be needed to rule out other alternative hypothesis (e.g., older nestlings/nests may produce stronger odors that may attract the attention of predators). We observed that 33% of the eggs disappeared during the incubation stage. This could be caused by partial predation or by brood parasitism, as Shiny Cowbirds puncture eggs in parasitized and in unparasitized nests (Astié and Reboreda 2006).

Hatching success, and egg and fledgling survival in successful nests (nests that were not predated or deserted) was high (74, 67, and 87%. respectively). Hatching success and egg survival were not related to number of eggs present in the nest. There was a proportion of eggs that did not hatch (0.26) and this may be caused by infertility or by death of the embryo caused by insufficient incubation (Davies and Brooke 1988, Svensson et al. 2007). We found that number of eggs present in the nest had no effect on hatching success and it is unlikely that insufficient incubation was the main cause. Nestlings died from starvation more often when they shared the nest with more than one sibling, suggesting that food competition between nestlings was strong. Most of the nestlings survived when only one or two eggs hatched due to previous egg loss or hatching failure. However, when all eggs hatched, at least one nestling died. The brood reduction hypothesis (Lack 1947, Ricklefs 1965) suggests that some species lay more eggs than they can rear nestlings because food supply may vary unpredictably. Thus, parents may lay a large clutch appropriate for a food-rich year and, in food-poor years, nestling survival would be mediated by sibling competition. The brood reduction hypothesis could be a possible explanation for Creamy-bellied Thrush nestling mortality. However, future studies should evaluate if nests with three nestlings improve nestling survival in food-good years.

The clutch size of Creamy-bellied Thrushes at our study site was small (mean = 3 eggs) and typical of tropical and southern temperate birds. There is a lack of information of the breeding biology of most thrushes, but the available data suggests this group has the same pattern as other passerines. The clutch size reported for thrushes from north temperate areas is 4–5 eggs (Arheimer and Svensson 1991, Schnack 1991, Morton and Pereyra 2010), and is 2–3 eggs for thrushes in tropic and south temperate areas (Lichtenstein 1998, Sackmann and Reboreda 2003, Akinpelu 2005, Astié and Reboreda 2005, Halupka and Greeney 2009). Ours is the first study presenting data from a *Turdus* species that inhabits an arid temperate area as far as we know. We did not

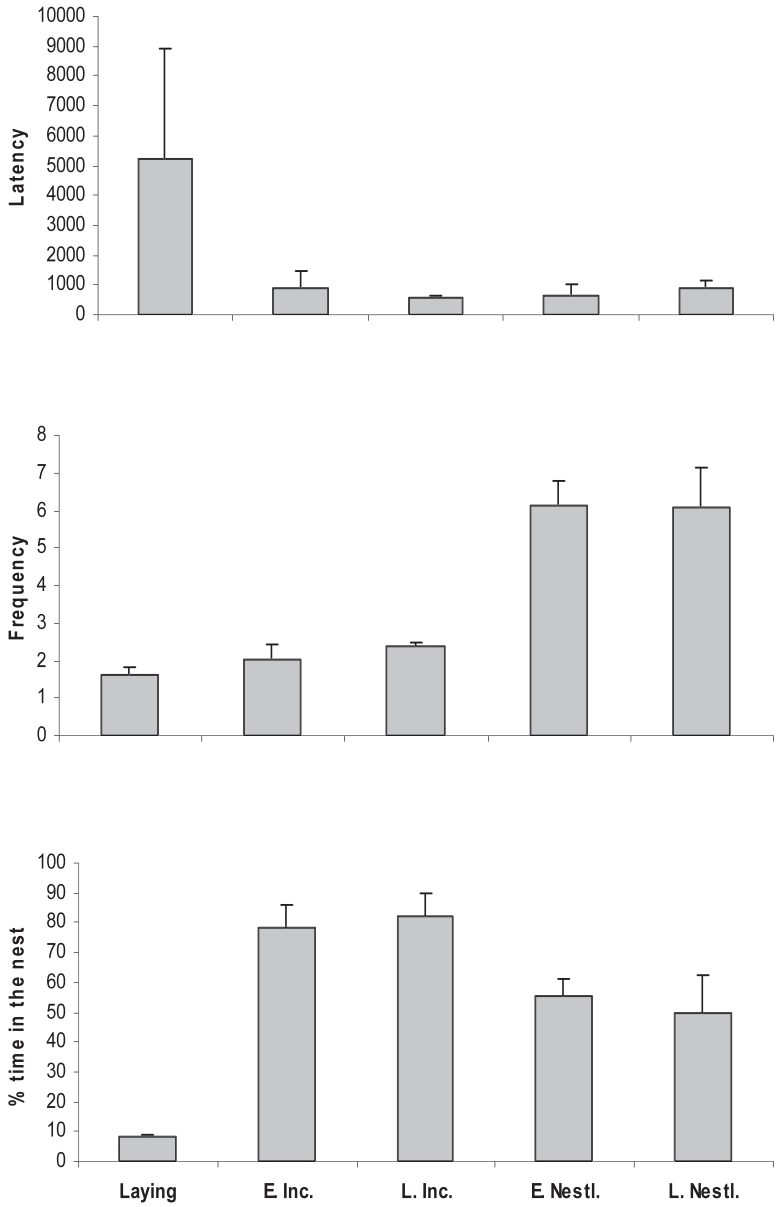

FIG. 3. Latency (time in seconds an adult spent in returning to the nest after we placed the camera), frequency (number of visits/hr), and nest attentiveness (percentage of time in the nest during each nestling period). All data are presented as mean ± SE.

conduct our study in a tropical environment, but life-history traits of the Creamy-bellied Thrush are similar to tropical birds. Future research on the breeding biology of southern temperate thrushes may offer new understanding of the evolution of life-history traits.

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