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NESTING BIOLOGY OF THE RED-CRESTED CARDINAL (*PAROARIA CORONATA*) IN SOUTH TEMPERATE FORESTS OF CENTRAL ARGENTINA

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ABSTRACT.—Studies on breeding biology in Neotropical birds are crucial for understanding different aspects of their life histories and also for their conservation. We describe the nesting biology of the Red-crested Cardinal (*Paroaria coronata*) in central Argentina, a common suboscine that inhabits south temperate forests. We monitored 367 nests from October to February 2005–2008. Nest initiation followed a unimodal distribution with a peak in November. Within the forest, no nests were built on exotic tree species. Mean clutch size was 3.05 ± 0.05 eggs and decreased with time within the breeding season; egg size did not vary across the breeding season. Nesting cycles lasted, on average, 25.8 ± 0.1 days (nest construction: 6.1 ± 0.4 days; incubation period: 11.9 ± 0.1 days; nestling period: 13.8 ± 0.1 days). At least one young fledged in 26% of nests, 62% were depredated, and 11% were abandoned. Egg survival rate was 0.95 ± 0.02, hatching success rate was 0.84 ± 0.02, and nestling survival rate was 0.81 ± 0.03. Partial nestling losses were detected in 45% of the nests, of which 52% were because of brood reduction. Each breeding pair had on average 4.4 ± 0.2 nesting attempts over the breeding season. Our results support the prediction that small clutch sizes are associated with extensive breeding seasons and several nesting attempts within a season. Except for the short incubation period, all other breeding features reported in this study differ from those of most north temperate birds and are consistent with the life history traits of Neotropical birds. *Received 23 June 2014. Accepted 17 November 2014.*

Key words: breeding success, Buenos Aires province, nesting habitat, reproductive biology, reproductive parameters, south temperate birds.

Studies on the breeding biology of birds are crucial for understanding different aspects of their life histories. During the last decades, many studies on avian breeding biology have focused on north temperate birds (Stutchbury and Morton 2001, Martin 2004, Lloyd et al. 2014), whereas Neotropical birds have been less well studied (Martin 1996, 2004). Likewise, among Neotropical birds, researchers have paid considerable more attention to tropical than south temperate birds (Martin 2004). As a consequence, available information on the breeding biology of south temperate birds is scarce and often not based on rigorous nest monitoring designs or adequate sample sizes (see Ricklefs 2000, Martin 2004).

Some authors have discussed the differences in life history traits between north temperate and tropical birds (see Martin 1996, Lloyd et al. 2014), arguing that the different breeding strategies used in each region could be mainly because of differences in breeding habitats and/or predation rates (Martin 1996). Compared to north temperate birds, tropical birds are characterized by longer breeding seasons with several nesting attempts per season, smaller clutch sizes, longer incubation and nestling periods, and greater fledging and adult survival (Martin 1996, Lloyd et al. 2014). Similarly, life histories might differ between tropical and south temperate birds, but data on the latter are limited (Auer et al. 2007; but see Yom-Tov 1987, Rowley and Russell 1991, Martin 1996). Cumulative information about breeding ecology of south temperate birds is crucial to understanding the diversity of life history strategies and reproductive traits across Neotropical and north temperate birds.

The Red-crested Cardinal (*Paroaria coronata*, Thraupidae; Burns et al. 2002) is a common suboscine inhabiting south temperate forests of South America (Ridgely and Tudor 2009). Despite being relatively ubiquitous in its range, specific information on the reproductive biology of this species was scarce until recent years, when some aspects of habitat use (Segura and Arturi 2009), brood parasitism (Segura and Reboreda 2012b), and nest survival (Segura and Berkunsky

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2012, Segura and Reboreda 2012a, Segura et al. 2012) were described. The Red-crested Cardinal is a sexually monomorphic species that inhabits semi-open areas with scattered trees and shrubs from east-central Argentina to southern Brazil, Paraguay, eastern Bolivia, and Uruguay (Ridgely and Tudor 2009).

In this study we provide the first detailed report on the nesting biology of a south temperate thraupid, the Red-crested Cardinal, in a natural forest of central-east Argentina, and present morphometric data of eggs, nestlings, and nests, data on nesting seasonality and duration of breeding cycles, and estimates of breeding success. We also discuss the differences in life history traits between Red-crested Cardinals and tropical and north temperate birds.

METHODS

Study Site.—We conducted this study at 'Estancia La Matilde' (35° 20' S, 57° 11' W) in the Province of Buenos Aires, Argentina. The study site is a flat area of 400 ha within the Biosphere Reserve Parque Costero del Sur (MAB-UNESCO), composed of semi-open grasslands with several patches of low woodlands mainly dominated by native tree species including *Celtis ehrenbergiana*, *Scutia buxifolia*, and *Schinus longifolius*. These patches of woodlands represent the only native forest habitat available in the area. Potential terrestrial nest predators in our study area include white-eared opossums (*Didelphis albiventris*), lesser grisons (*Galictis cuja*), tree-climbing snakes (*Philodryas* spp.), and small rodents (*Akodon*, *Oligoryzomys*, and *Oxymycterus* spp). Potential avian nest predators include Chimango Caracara (*Milvago chimango*), Guira Cuckoo (*Guira guira*), Campo Flicker (*Colaptes campestris*), Green-barred Woodpecker (*Colaptes melanochloros*), and Narrow-billed Woodcreeper (*Lepidocolaptes angustirostris*). This region is characterized by warm and rainy summers (maximum temperature: 39.2°C) and cold winters (minimum temperature: -7.5°C), with most precipitation occurring between November–March. The National Meteorological Survey of Argentina from 2005–2007 reports mean annual rainfall as 891 mm and mean annual temperature as 16°C. Red-crested Cardinals are year-round residents in the area and breed from October–February (Segura and Arturi 2012).

Nest Monitoring.—We collected data during three consecutive breeding seasons (2005–2008) from September–February. We found nests by systematically searching potential nest sites and observing the behavior of territorial pairs (Martin and Geupel 1993). We monitored all nests until nestlings fledged or the nest failed. We visited nests daily during egg-laying and around the time of hatching, and every 2 days during the incubation and nestling stages. Eggs and nestlings within the nest were marked with waterproof ink for individual identification. Individual identification of nestlings after 8 days of age was made by a unique combination of colored plastic leg bands. Then, we inspected nests from a distance of 1–3 m to minimize the risk of premature fledging. Eggs were weighed to the nearest 0.1g with a 10 g Pesola spring balance, and width and length was measured to the nearest 0.05-mm using Vernier calipers within 3 days from clutch completion. Egg volumes were calculated using Hoyt's (1979) equation: volume = 0.51 x (length) x (width)^2. Before young fledged (nestling age = 12 days), we weighed nestlings to the nearest 0.6 g using Pesola spring balances of 60-g capacity, and measured tarsus, wing and bill length to the nearest 0.05 mm with a Vernier caliper. We considered a nest successful when at least one nestling left the nest. We considered a nest deserted if eggs were cold to the touch and no parental activity was observed near the nest during the visit (i.e., 15–20 mins), or when all chicks died mainly as a result of parasitism by botflies (*Philornis seguyi*; Segura and Reboreda 2011). We considered a nest depredated if nest contents disappeared between two consecutive visits, and no parental activity was detected near the nest. Nests abandoned before eggs were laid were not considered. Once we confirmed that the nestlings fledged or the nest failed, we took measurements of nest dimensions (i.e., internal and external diameter, internal, and external depth) with a tape measure. We defined brood reduction as the non-random loss of some nestlings relative to nestling size or hatching sequence (Lack 1954, 1968).

Because nest site characteristics may vary between years and with time of breeding (i.e., date the first egg of each nest was laid; day 1 = 1 October), we recorded: (1) tree species on which a nest was built, (2) nest height above ground (m), (3) nest tree height above the ground (m), (4) nest-tree cover (m^2), and (5) tree canopies' cover in the nest surroundings (m^2). We measured height using a pole with marks every 10 cm. We used

QuickBird (5 m) images extracted from Google Earth (Digital Global Coverage, 10 January 2008) to calculate the cover of individual trees and proportion of canopy in the 100 m^2 nest surrounding area using the software IDRISI Kilimanjaro 14.01 (Eastman 2003).

Data Analysis.—Each nest was assigned a clutch initiation date (time of breeding), corresponding to the laying of the first egg. Clutch-initiation dates were determined directly for nests found during construction and egg-laying ($n = 177$ nests), or indirectly, through backdating from hatching dates for nests found during incubation ($n = 95$ nests), or by using nestling weights for nests found after hatching ($n = 40$ nests). In the latter, we used as a reference the day-by-day nestling weights found in Red-crested Cardinals (Segura 2011). For 55 nests that were found and that failed during incubation, we estimated clutch initiation dates (± 1–5 days) by assuming that the observed period was halfway between the end of egg laying (nest age = 3) and hatching (nest age = 13).

Red-crested Cardinals can breed more than once during a breeding season. We were able to establish the identity of breeders for 26 breeding attempts in which individuals were color-banded. When adults were unmarked, we assigned breeding attempts to breeding pairs based on observations of territorial limits. Breeding pairs are extremely territorial (mainly the male) and enabled us to easily delimit the territories (see Segura 2011). We cannot exclude the possibility that some nests were not independent among seasons (i.e., breeding attempts by the same pair). However, because adult survival rates for south-temperate shrub/canopy nesters between years is low (see Martin 1993, 1996), the proportion of nests that could have been nesting attempts by the same pair in different breeding seasons is relatively low (i.e., 30%, assuming that survival rates of males and females were independent and the divorce rate was 0%). The time elapsed between two nesting attempts of the same breeding pair was estimated as the number of days between the date of nest failure (or fledging date) and the initiation of the replacement nest (i.e., date of laying of the first egg).

We estimated clutch size using a subsample of 165 nests that we found during the nest construction phase and visited daily during the laying phase. These nests survived at least until egg laying finished (i.e., when we observed the same final number of eggs in the nest at least 2 days in a row). Incubation period was estimated as the number of days elapsed since laying of the last egg until hatching of the last chick (Nice 1954). Nestling period was estimated as the number of days elapsed since hatching of the last nestling until fledging. The date of fledging was established directly in a few cases where we observed the fledglings leave the nest. Chicks in most nests fledged between two successive visits, and we assumed that fledging was in the midpoint between those visits.

As eggs from the same clutch were not independent and measurements of individual eggs from the same nest were averaged; likewise, morphometric data of individual nestlings from the same nest were averaged. Morphometric data before fledging were obtained from 94 nests (22 broods with 1, 47 with 2, 24 with 3, and 1 with 4 nestlings).

We estimated overall nest survival as the proportion of nests that produced at least one fledgling. Reproductive success was estimated using three parameters: (1) egg survival, calculated as the proportion of eggs that survived until the end of the incubation in nests that survived until the nestling stage; (2) hatching success, calculated as the proportion of eggs that hatched out of the total number of eggs in the nest at hatching; and (3) chick survival, calculated as the proportion of chicks that fledged from those that hatched in nests that survived the entire nesting cycle.

We studied how seasonal effects impact nest characteristics and reproductive traits (''year'' was used as a categorical variable and ''time of breeding'' as the continuous variable). We analyzed the data using generalized linear mixed models (GLMM), where the breeding pair was included as a random variable. Based on banded breeding pairs and observational data, we assume that pairs remained together for the duration of the breeding season. We used binomial distribution when the dependent variable was binary (nest-tree species) and Poisson distribution for the rest of the dependent variables (physical characteristics of the nesting site, clutch size, egg size, incubation and nestling periods, egg and nestling survival, and hatching success). Reported values are means ± SE. Tests were two-tailed, and we considered differences to be significant at $P < 0.05$.

RESULTS

We identified 51 breeding pairs in 2005–2006, 54 in 2006–2007, and 55 in 2007–2008. We found

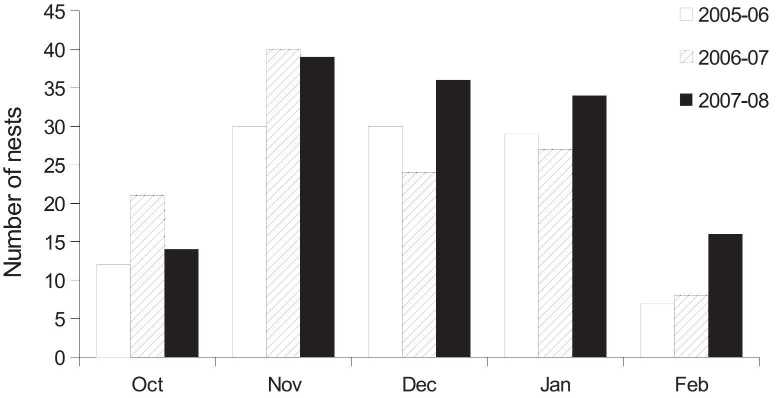

FIG. 1. Temporal distribution of nest initiation by Red-crested Cardinals for three breeding seasons (2005–2008) in a south temperate forest of central Argentina.

367 nests (108 in 2005–2006, 120 in 2006–2007, and 139 in 2007–2008). On average, each breeding pair had 4.4 ± 0.2 breeding attempts per season (range = 2–8). Eighty-six nests were found during construction, 91 during egg-laying, 150 during incubation, and 40 after hatching. Including all nests monitored, the earliest nest was initiated on October 5 and the latest on February 16. The earliest and latest fledging dates were November 5 and February 28, respectively. Clutch initiation showed a unimodal frequency distribution along the season, with a peak in November (Fig. 1).

Breeding pairs with at least one successful attempt had on average 3.2 ± 0.4 nesting attempts during the breeding season, while breeding pairs without successful attempts had on average 5.7 ± 0.5 nesting attempts (Table 1). The time elapsed since a nest failure and the initiation of the replacement nest was 8.2 ± 0.3 days, while the time elapsed since fledging date for a successful nest and the replacement nest was 28.3 ± 2.1 days (Table 1).

Nests were open cups built with twigs of native trees and lined with stems, roots, bristles, and hairs. External nest dimensions were: 13.5 ± 0.3 cm in diameter (range = 11.5–15.5 cm) and 8.5 ± 0.1 cm in depth (range = 8.0–9.5 cm). Inner nest cup dimensions were 7.6 ± 0.2 cm in diameter (range = 6.5–9.0 cm) and 3.9 ± 0.1 cm in depth (range = 3.5–4.5).

Nests were located mostly in tala *(Celtis ehrenbergiana*) and coronillo (*Scutia buxifolia*) trees (68 and 30%, respectively; $n = 367$ nests) and more rarely in molle (*Schinus longifolius*) trees (2%). The frequency of nests in each tree species did not differ among years (Chi-square: $\chi^2_2 = 7.4$, $P = 0.11$), but changed with time of breeding (Chi-square: $\chi^2_5 = 11.4$, $P = 0.02$). Cardinals used coronillo less frequently at the end of the season (Fig. 2). No significant differences were found in other physical nest site characteristics between years and only nest height and nest-tree cover increased with time of breeding (Table 2).

Mean clutch size was 3.09 ± 0.05 eggs ($n = 165$ nests). Most nests (70%) had three eggs, and more rarely two (11%), four (18%), or five (1%). There were no differences in clutch size among years ($F_{2,165} = 0.27$, $P = 0.78$), but there was a decreasing trend in clutch size with time of breeding ($F_{1,165} = -1.99$, $P = 0.04$, $n = 46$ breeding pairs with three or more breeding attempts during the same season, Fig. 3). Eggs weighed 3.80 ± 0.04 g (range = 3.0–5.2 g) and were 25.2 ± 0.12 mm in length (range = 22–28.7 mm) and 17.2 ± 0.08 mm in width (range = 14.9–19.5 mm; $n = 105$ nests). Mean egg volume was 3.82 ± 0.03 cm^3 (range = 2.61–5.57 cm^3; $n = 105$ nests). Egg dimensions did not vary among years (weight: $F_{2,105} = 0.6$, $P = 0.55$; length: $F_{2,105} = -0.28$, $P = 0.77$; width: $F_{2,105} = 0.11$, $P = 0.91$; volume: $F_{2,105} = 0.23$, $P = 0.75$) or with time of breeding (weight, $F_{1,105} = -0.06$, $P = 0.95$; length, $F_{1,105} = -0.01$, $P = 0.99$; width, $F_{1,105} = -0.08$, $P = 0.94$; volume, $F_{1,105} = -0.14$, $P = 0.88$, $n = 28$ breeding pairs with three or more breeding attempts during the same season).

Incubation started after laying of the second egg and hatching was asynchronous (1 day of asynchrony between the first two and the third nestling and 2 days of asynchrony with the fourth

TABLE 1. Mean number ± SE (min–max) of Red-crested Cardinals' nesting attempts during the breeding season and time elapsed until the following nesting attempt for three consecutive breeding seasons (2005–2008) in central Argentina.

	2005–2006	2006–2007	2007–2008
Nesting attempts [a]	3.9 ± 0.3 (3–5)	4.4 ± 0.5 (2–7)	4.8 ± 0.4 (2–8)
Time between failed nest and new nesting attempt (days) [b]	8.9 ± 0.5 (5–13)	7.6 ± 0.6 (5–13)	8.1 ± 0.3 (5–11)
Time between successful nest and new nesting attempt (days) [c]	31.8 ± 3.1 (20–41)	22.8 ± 2.5 (15–35)	28.7 ± 2.6 (17–43)

[a] Calculated from 9, 11, and 15 breeding pairs, respectively, where we could observe all nesting attempts over the breeding season.
[b] Calculated from 15, 17, and 24 breeding pairs, respectively, where we could observe a failed nest and the following nesting attempt.
[c] Calculated from 6, 7, and 9 breeding pairs, respectively, where we could observe a successful nest and the following nesting attempt.

nestling). Incubation period was 11.9 ± 0.1 days (range = 11–13, mode = 12 days, n = 84 nests) and did not vary among years ($F_{2,84} = 0.06$, P = 0.95) or with time of breeding ($F_{1,84} = 0.12$, P = 0.91). Partial egg loss during incubation was detected at 13% of nests (11 of 84 nests where we could observe the entire incubation period). Egg losses in three of these nests (27%) resulted from egg-puncturing by female Shiny Cowbirds (*Molothrus bonariensis*), while in the remaining nests (82%) the causes were unknown.

Mean number of hatchlings per nest was 2.5 ± 0.1 (range = 1–4, n = 149 nests). Nestlings remained in the nest, on average, 13.9 ± 0.1 days (range = 12-18, n = 67 nests). Year and time of breeding had no significant effects on nestling weight and tarsus, wing, or bill length at 12 days of age. Morphometric data before fledging (nestling age = 12 days) are summarized in Table 3. Partial brood losses were detected in 45% of 74 nests that survived the entire nestling period. In 17 of these nests (52%) brood losses were because of brood reduction, whereas in five nests (15%) some nestlings failed because of ectoparasitic larvae of the genus *Philornis*, and 11 nests (33%) because of unknown causes. Brood reduction occurred at 3.8 ± 0.5 days (range = 2–8 days, n = 17 nests). Proportion of nests with brood reduction increased with the number of hatchlings present in the nest (Chi-square: χ^2_3 = 8.8, P = 0.01): two (1 of 21 nests), three (10 of 39 nests) and four (6 of 7 nests).

From all nests monitored (n = 367), 26% were successful, 62% were depredated, 11% were abandoned, and 1% failed after heavy storms. Proportion of successful nests did not differ among years (Chi-square: χ^2_2 = 0.1, P = 0.94). Egg survival rate was 0.95 ± 0.02 (range = 0.5–1, n = 93 nests), hatching survival rate was 0.84 ± 0.02 (range = 0.33–1, n = 109 nests), and nestling survival rate was 0.81 ± 0.03 (range = 0.25–1, n = 74 nests). None of these breeding

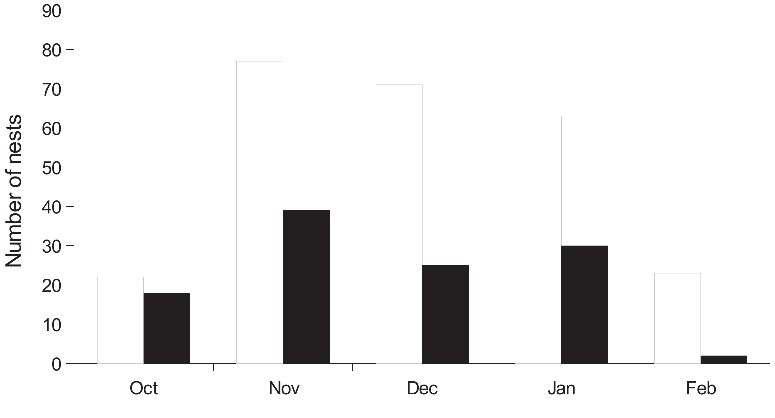

FIG. 2. Frequency distribution of the number of nests of Red-crested Cardinals built in tala (*Celtis ehrenbergiana*) trees (white) and coronillo (*Scutia buxifolia*) trees (black) throughout the breeding season in a south temperate forest of central Argentina.

TABLE 2. Mean values ± SE, minimum and maximum values, differences among years and time of breeding of nest placement characteristics for 367 nests of Red-crested Cardinals in central Argentina. Results of generalized linear mixed models (GLMM) analysis are shown.

			Year		Time of breeding	
	Mean ± SE	Range	*F*	*P*	*F*	*P*
Nest height (m)	3.7 ± 0.06	1.5–7.7	1.12	0.26	2.28	0.02
Nest-tree height (m)	6.2 ± 0.07	3.2–10.5	1.27	0.21	1.42	0.16
Nest-tree cover (m^2)	42.2 ± 1.4	2.4–148.5	1.11	0.26	4.35	<0.001
Surrounding tree cover (%)	39.8 ± 0.9	5.2–89.2	0.21	0.83	−0.98	0.33

parameters varied significantly with year (egg survival: $F_{2,93}$ = -0.42, P = 0.67; hatching success: $F_{2,109}$ = 0.77, P = 0.44; nestling survival: $F_{2,74}$ = 0.64, P = 0.52); or time of breeding ($F_{1,93}$ = 0.43, P = 0.67; $F_{1,109}$ = 0.30, P = 0.76; $F_{1,74}$ = 0.38, P = 0.70).

DISCUSSION

Red-crested Cardinals showed: (1) an extended breeding season (Oct–Feb) where nest initiation followed a unimodal distribution over the breeding season, (2) several nesting attempts during the breeding season, (3) nesting only occurred on native tree species, (4) small clutch size (modal clutch size of 3 eggs), (5) an incubation period of only 12 days and a nestling period of 14 days, and (6) high rates of nest failure because of predation.

Other members of the genus *Paroaria* that were reported to nest during the austral summer in Brazil, show, in most cases, shorter breeding periods (i.e., Nov–Jan; Buzzetti and Silva 2005, Vasconcelos et al. 2006, Dornas 2008). However, in *Neothraupis fasciata* (the sister species of the genus *Paroaria*; Dávalos and Porzecanski 2009) there has also been reported breeding periods of almost 5 months, from August to December (Alves 1990, Alves and Cavalcanti 1990, Duca Soares 2007). Our results are consistent with Martin's (1996) suggestions about the extended breeding seasons of Neotropical birds.

Long breeding seasons of south temperate birds (in relation to north temperate ones) have been associated with a reduced clutch size and the possibility of greater re-nesting attempts (Martin 1996, but see Auer et al. 2007 that reported mean breeding periods only ~50 days in northwestern Argentina). Cardinals clearly show these two conditions (long breeding seasons and small clutch sizes) and effectively performed several nesting attempts during the breeding season (some pairs were able to carry out up to eight nesting attempts per season). Cardinals are able to build a replacement nest after a predation event (~8 days), sometimes leading to up to four unsuccessful attempts during the same month (LNS, pers. obs.). Our results clearly support the perception that small clutch sizes relate to extensive breeding seasons and several nesting attempts within a season.

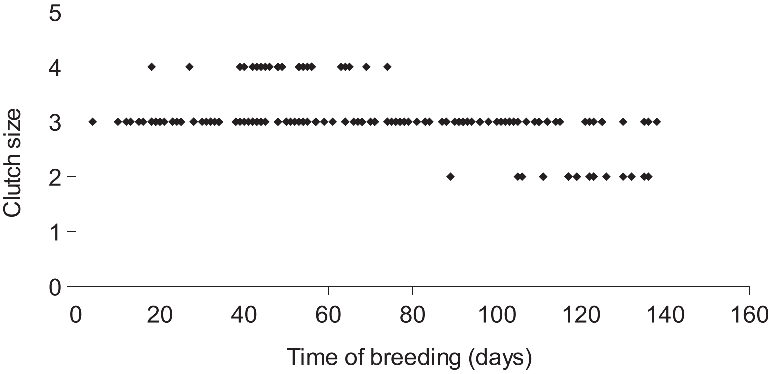

FIG. 3. Red-crested Cardinals' clutch size related to time of breeding season in a south temperate forest of central Argentina.

TABLE 3. Mean values ± SE, minimum and maximum values, differences among years and time of breeding of Red-crested Cardinals' nestling growth parameters before fledging (nestling age = 12 days) in central Argentina. Results of generalized linear mixed models (GLMM) analysis are shown.

			Year		Time of breeding	
	Mean ± SE	Range	*F*	*P*	*F*	*P*
Weight (g)	29.41 ± 0.32	22.2–34.2	0.26	0.79	−0.76	0.44
Wing (mm)	54.16 ± 1.3	30–67	0.15	0.88	−1.6	0.11
Tarsus (mm)	25.69 ± 0.18	22–28	0.32	0.74	0.05	0.95
Bill (mm)	10.43 ± 0.08	9.3–11.6	0.55	0.58	0.03	0.97

Red-crested Cardinals are able to nest in sites with different physical characteristics (Segura and Arturi 2009). Although at our study site even though it is possible to find a variety of exotic trees, Red-crested Cardinals used only native trees to build their nests. The frequency of use of talas and coronillos trees varied throughout the breeding season, with proportionately less use of coronillo trees at the end (Jan–Feb) than the beginning of the season (Oct–Nov). This could be because of differences in the canopy foliage among the two tree species throughout the breeding season. Tala trees are deciduous species whose canopy foliage is not completely out until November–December, while coronillo trees are evergreen species whose canopy foliage is complete at the beginning of the season. The need to protect nests from adverse weather conditions and conceal them from predators (Martin 1993) may have led Red-crested Cardinals to use coronillo trees only at the beginning of the season. Towards the end of the season, Red-crested Cardinals used nest-trees with greater canopy coverage and built their nests higher. Following Martin's (1993) suggestions, higher nests in larger trees could reduce the rates of nest predation.

The mean clutch size of three eggs found in this study is similar to that reported for other open-nesting passerines in south temperate forests (Mason 1985, Skutch 1985, Yom-Tov et al. 1994, Auer et al. 2007, Jetz et al. 2008, Lloyd et al. 2014) and smaller than that for north temperate birds (see Martin et al. 2000). In particular for the family Thraupidae, Yom-Tov et al. (1994) reported clutch sizes of 2.7 eggs for tropical birds (northern South America) and 3.3 eggs for south temperate birds (southern South America). Similar clutch sizes have been reported for other members of the genus *Paroaria* (Thomas 1979, Cruz and Andrews 1989, Alves and Cavalcanti 1990, Buzzetti and Silva 2005, de la Peña 2005, Di Giacomo 2005, Greeney and Merino M. 2006), and for *Neothraupis fasciata* (Duca Soares 2007). The relatively small clutch size of Red-crested Cardinals may reflect an adaptation in response to high rates of nest predation (Martin 1996). Since each egg represents an additional nest day, the overall nesting period can be reduced by producing small clutches, thereby creating opportunities for repeat-and replacement-breeding attempts during the breeding season. Alternatively, small clutches may also reduce parental investment on any one particular brood, allowing females to save reproductive effort in the case that the nest is depredated.

Clutch size was not constant throughout the breeding season. Early in the season, nests with 3–4 eggs were more frequent, while throughout the end of the season nests contained 2–3 eggs. Egg size did not vary with time of breeding, supporting the hypothesis that there is little individual variation in egg size between clutches (Christians 2002). The temporal adjustment in egg number (and not in egg size) has been subject of intense debate in recent decades (see Ricklefs 2000). One hypothesis predicts that energetic costs to the female after repeated nesting attempts could cause smaller clutch sizes throughout the end of the breeding season (Verhulst et al. 1995, Winkler and Allen 1996, Monaghan and Nager 1997, Hansson et al. 2000). Some of our breeding pairs made as many as eight unsuccessful nesting attempts within the same season, laying a total of 24 eggs (LNS, unpubl. data) that represent ~90 g for a bird who weighs on average 45 g.

The incubation period found in this study is similar to those reported by Di Giacomo (2005) for Red-crested Cardinals in northern Argentina, but lower than de la Peña (2005) reports in central

Argentina (14–15 days) or Duca Soares (2007) for *N. fasciata* in central Brazil (13–14 days). An incubation period of 12 days is similar to the range reported for the family Thraupidae (12–14 days; Isler and Isler 1999), and more similar to the incubation periods of north temperate birds than tropical or south temperate birds (14–18 days; Auer et al. 2007, Martin and Schwabl 2008). The reduction in the incubation periods has been intensively discussed (see Martin 2002) and is mainly attributed to shorter nest exposure to potential predators (Martin 2002, Remeš and Martin 2002, Martin et al. 2007).

Nestling stages of ~14 days are similar to those reported for Red-crested Cardinals in central (de la Peña 2005) and northern Argentina (Di Giacomo 2005), and for other passerines in northern Argentina (Auer et al. 2007). However, nestling stages in *N. fasciata* in central Brazil were shorter (9–12 days; Alves and Cavalcanti 1990, Duca Soares 2007). Our results are more consistent with nestling stages of tropical than north temperate birds (~10 days; Russell et al. 2004). More time that parents spend feeding and protecting the nestlings could be related to higher fledging (Martin 1996) and post-fledging survival rates (Skutch 1976, Rowley et al. 1991, Franklin et al. 1995).

Another typical characteristic of Neotropical birds is the high rate of nest predation compared with north temperate birds (Martin 1996). Our results are consistent with these findings, as >70% of the nests failed mainly because of predation. In addition, it has been reported that populations of Red-crested Cardinals in central-eastern Argentina show high rates of nest failure (Segura and Berkunsky 2012, Segura and Reboreda 2012a, Segura et al. 2012), with nest predation rates exceeding 80%. High rates of nest predation of Neotropical birds may reflect some differences in predator communities of these types of habitats compared with north temperate habitats.

Except for the short incubation period reported in this study, all other breeding features are consistent with Martin's (1996) suggestions for Neotropical birds (i.e., long breeding seasons with several nesting attempts per season, small clutch sizes, long nestling periods, and high nest failure rates). In turn, these features show more similarity with tropical birds of South America than north temperate birds.

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