

## LIFE HISTORY TRAITS AND BREEDING SUCCESS OF THE SCARLET-HEADED BLACKBIRD (*AMBLYRAMPHUS HOLOSERICEUS*) IN THE ARGENTINEAN PAMPAS

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**Resumen.** – Rasgos de historias de vida y éxito reproductivo del Federal (*Amblyramphus holosericeus*) en las pampas argentinas. – En este trabajo presentamos datos acerca del éxito reproductivo y rasgos de historia de vida del Federal (*Amblyramphus holosericeus*) nidificando en las pampas argentinas. Durante las temporadas reproductivas de 1995–1997 y 2001–2002 (Septiembre–Diciembre), encontramos un total de 60 nidos de Federal. Alrededor del 40% de los nidos produjeron pichones volantes, y la tasa de mortalidad diaria no mostró diferencias entre los periodos de nidificación (puesta de huevos, incubación y cría de pichones). El tamaño de puesta fue de 3 huevos y el número medio de pichones volantes fue de  $1,33 \pm 0,78$ . La reducción de nidada fue una causa común de pérdida de pichones, ocurriendo en 39% de los nidos donde eclosionaron más de un pichón. Los resultados obtenidos de los nidos experimentales indicaron que la atención al nido incrementa la probabilidad de éxito de los nidos, dado que los nidos naturales tuvieron una menor tasa de depredación. Sugerimos en base a los resultados obtenidos que la mayor atención al nido detectada en esta especie puede ser responsable del mayor éxito de nidificación comparado con aquel encontrado en otras especies simpátricas. Sin embargo, la alta atención al nido puede implicar un costo adicional dado que ésta puede restringir el tiempo disponible de los padres para forrajeo, limitando entonces la cantidad de alimento entregada a los pichones.

**Abstract.** – In this paper we present data on the nesting success and life history traits of the Scarlet-headed Blackbird (*Amblyramphus holosericeus*) nesting in the Argentinean pampas. During the 1995–1997 and 2001–2002 breeding seasons (September–December), we found 60 Scarlet-headed Blackbird nests. About 40% of these nests produced fledglings, and daily nest mortality did not differ among nesting stages (laying, incubation, nestling). Clutch size was 3 eggs, and the mean number of fledglings was  $1.33 \pm 0.78$ . Brood reduction was a common cause of nestling loss as 39% of nest with more than 1 nestling lost the last hatched one. Results obtained from experimental nests indicate that parent nest attention increases the probability of nest success as natural nests showed a lower predation rate. We suggest that the high nest attention detected in this species could be responsible for the higher nesting success compared to other sympatric marsh nesting species. However, high nest attendance could also imply an additional cost as it may constrain the time available to parents for foraging, thus limiting the food delivered to nestlings. *Accepted 6 May 2007.*

**Key words:** *Amblyramphus holosericeus*, nesting behavior, nest predation, nesting success, territoriality, Scarlet-headed Blackbird.

## INTRODUCTION

Reproductive strategies of passerine birds have evolved under selection pressures generated mainly by food and predation (Lack 1968, Martin 1995). Predation is one of the most important factors of selection as it could affect nest site selection, parental investment, and nesting activity patterns (Ricklefs 1969, Martin 1995). Food availability also is likely to affect life history traits in passerines, in some cases interacting with nest predation rates to determine clutch and brood size (Martin 1995). In this paper, we analyze the breeding success and some life history traits of a population of Scarlet-headed Blackbirds (*Amblyramphus holoserisus*) in the pampas of Argentina, the southernmost area of its distribution. This region has suffered in the last 100 years from an intense transformation due to a rapid increase in land used for agriculture and cattle ranching, followed by a significant change in the animal communities (Vervoort 1967, León *et al.* 1984, Bucher & Nores 1988, Soriano 1991). Habitat alteration also usually involved the introduction of exotic predators like domestic cats (*Felis catus*) and rats (*Rattus* sp.), and the increase of native generalist predators (Evans 2004) which often reduce the breeding success of birds (Crooks & Soule 1999). Our study area, however, is mainly used for extensive cattle raising and is considered among the best preserved grasslands in the argentinian pampas (F. Rabuffetti & J. C. Reboresada unpubl.).

The Scarlet-headed Blackbird is an insectivorous passerine which inhabits temperate wetlands in southern Brazil, Paraguay, Uruguay and northeastern Argentina (Ridgely & Tudor 1989). Its social breeding system is monogamy, with both male and female involved in territory defense, nest building and feeding the nestlings but only females incubate and brood the nestling (Orians 1980,

Mermoz & Fernández 1999, Fernández & Mermoz 2000).

In this study we describe the breeding biology of the Scarlet-headed Blackbird and analyze the factors affecting its breeding success using experimental nests. Further, we present life history traits of this species and discuss their potential influence on nesting success. We also compare our data with those from other species of sympatric icterids nesting in similar habitats.

## MATERIALS AND METHODS

We conducted the study mainly along primary and secondary roads near the town of General Lavalle, Buenos Aires Province (36°26'S, 56°25'W), Argentina, during the 1995–1997 and 2001–2002 breeding seasons (September–December). The climate of the region is sub-humid with an average monthly temperature of 23°C in January (summer) and 13°C in July (winter), and a total annual precipitation of 1500 mm (Soriano 1991). The study site was located in the “flooding pampas”, an open grassland characterized by abundant marshes and lagoons, which cover 60% of the region. Higher elevations (about 510 m a.s.l.) were covered by woods patches dominated by *Celtis tala* and *Scutia buxifolia*, while the vegetation at lower elevations included cattails (*Typha* sp.), bulrush (*Scirpus* sp.) and stands of *Solanum glaucophyllum*.

Although we worked in the same area for 5 years, our effort was higher during 1995–1997. In these breeding seasons, we searched for nests every 2–3 days whereas, during 2001–2002 breeding season, nest searching was performed weekly and restricted to two main roads. We searched for nests in the marshes close to the roads using both behavioral clues and systematic searching techniques. We recorded the location of each nest with GPS (Garmin 12 XL; Garmin International Inc.) and identified the plant species,

substrate and date of the first laid egg (initiation date) for each nest. We estimated the initiation date based on the number of laid eggs for nests found during egg-laying. For nests found during incubation, we estimated the initiation date by the degree of egg development (Hays & LeCroy 1971). During the nestling period, we estimated the laying date by considering the degree of physical development of the nestlings.

We checked nests every 1 or 2 days until the nest was depredated, deserted or the nestlings fledged. During each visit we recorded the number of eggs and nestlings, and the presence of adults close to the nest.

We numbered the eggs with "water proof" ink according to the laying order and checked the eggs in order to detect punctures or cracks. We marked young nestlings with water proof ink on the legs, and banded nestlings with plastic-color bands after they were 7-day old. We weighed each nestling using a Pesola scale (50–100 g; error: 0.1 g). During the breeding season of 2001, we also measured tarsus length, wing chord and bill length, and determined the degree of development of both primaries and retrices. In August 2001, one adult male was captured and marked with plastic-color bands when we were capturing Brown-and-yellow Marshbirds (*Pseudoleistes virescens*). No other adults were systematically captured due to their low density and to avoid disturbing nesting birds.

Clutch size was determined from nests that were found during building and survived throughout the laying period. We estimated the hatching success by dividing the number of nestlings by the number of eggs present at the end of the incubation period (Koenig 1982). Fledgling success was calculated by dividing the number of fledglings by the number of hatchlings. To avoid biases when estimating this variable, we excluded from the analysis those nests found after the eggs had hatched.

We estimated nestling development by using the curve of nestling mass growth following Ricklefs (1967). The adjusted weight for a nestling at  $t$  age is represented as:  $\text{Mass} = A / (1 + e^{-K(t-t_0)})$ , where  $A$  is the asymptote of the growth curve,  $e$  refers to base of the natural logarithm,  $K$  the mean growth rate,  $t_0$  the point of inflexion or age of maximum growth using the mean day mass of the nestlings from all the nests. We used non linear models and minimum squares, minimized with the option Quasi-Newton, with the program SYSTAT (Wilkinson *et al.* 1992). Because the asymptote could be sensitive to the number of measurements taken during the last part of the nestling period, we re-estimated  $K$  and  $t_0$ , fixing the asymptote at 46.7 g, based on the weight estimated from growth curves of solitary nestlings (nestlings without nest companions). We used this value because we considered it as the maximum growth that a nestling can reach within in a nest without competition. We estimated the development of the nestlings using tarsus length and analyzed it in a similar way to mass as described above. We also estimated  $K$  and  $t_0$ , fixing the asymptote value to that corresponding to the first nestling hatched (no data of tarsus length of solitary nestlings were available).

Since brood reduction was frequent (see Results), we estimated the survivorship of the nestlings using the method of Kaplan-Meier (McCallum 2000) according to the order of hatching. We compared the survival rate of different nestlings using Log Rank and analyzed how it was affected by hatching order with Cox regression (McCallum 2000).

*Breeding success.* We considered that a breeding attempt was successful when the nest produced at least one fledgling and nests were considered deserted if between two consecutive visits nestlings or eggs were unattended. In most cases, desertion was caused by egg damage or removal. Nests were considered

depredated if between two consecutive visits eggs or nestlings disappeared. Potential common predators in the study area were: Chimango Caracara (*Milvago chimango*), Long-winged Harrier (*Circus buffoni*), lutrine opossum (*Lutreolina crassicaudata*), and Barn Owl (*Tyto alba*) (Svigelj *et al.* 2003). Shiny Cowbirds (*Molothrus bonariensis*) also generated egg losses and caused nest desertion in host nests. Cowbirds frequently parasitized icterids in our study area causing egg loss by egg pecking (Mermoz & Reboresda 1994, 1999; Lyon 1997, Massoni & Reboresda 1998).

We estimated the probability of nest survival ( $\hat{S}$ ) at different stages using Mayfield methodology (Mayfield 1975). When the time between two consecutive visits to the nest was less than 3 days and the nest was depredated, we calculated the number of days the nest was active by assuming that the predation event occurred in the middle of the interval (Mayfield 1975). In those cases where the time between visits was more than 3 days, we estimated the time the nest survived by considering 40% of the length of the period (Johnson 1979). We estimated the variance of  $\hat{S}$  using Johnson's (1979) equation  $V = [(DN - P) \cdot P] / DN^3$ , where  $V$  is the variance,  $DN$  is the number of nest-days exposed, and  $P$  is the number of nests that failed.

The survival rate of the nest was estimated for the three stages: egg laying (interval between laying of the first egg and the laying of the last egg), incubation (time elapsed from 1 day after the laying of the last egg until the first egg hatched), nestling rearing (interval from the hatching of the first nestling until the first nestling fledged). We compared the daily survival rates between different stages using the program CONTRAST (Hines & Sauer 1989).

*Nest attendance.* To estimate the time the female spent incubating the eggs, we video-

recorded five nests from egg laying or the beginning of incubation using a Hi8 Sony video camera (Sony Corporation). The video-recorder was placed at least 5 m away from the nest and recordings were taken in the morning (06:00–13:00 h) for approximately 30 min (mean:  $31.6 \pm 0.4$  min). We also recorded the presence of adults close to the nest throughout the nesting stages when we checked the nests (total number of visits: 140).

We also evaluated parental behavior during the nestling stage, by filming 14 nests with Hi8 Sony videocameras. We camouflaged the cameras and placed them 10 m from the nests. Every nest was filmed once, in the morning (07:00–09:30 h) or in the afternoon (16:00–19:00 h) for 40–140 min. (average:  $45.45 \pm 5.98$  min). We excluded from the analysis two nests to which the adults did not return after the cameras were set up. In both cases, we removed the camera to avoid further disturbance. We estimated the parents feeding rate from video recordings analyzed in the laboratory. Scarlet-headed Blackbirds typically carry one food item by trip, and so we expressed the feeding rate as number of visits/nestling/h.

We evaluated the effect of parents nest attendance using experimental nests. Old Brown-and-yellow Marshbird nests were placed in marshes. We used Brown-and-yellow Marshbirds nests because they are similar in shape and size to Scarlet-headed Blackbird nests, and because artificial nests could attract predators other than the ones that predate on natural nests (Willebrand & Marcström 1988). We used these nests because Brown-and-yellow Marshbird nests are more common in the study area than Scarlet-headed Blackbirds ones, and could be removed from plant substrate without structural damage. Brown-and-yellow Marshbird nests were

TABLE 1. Growth parameters of Scarlet-headed Blackbird nestlings according to the hatching order, using the Ricklefs method (Ricklefs 1967). Solitary nestling refers to nests with only one nestling present; complete brood refers to broods where all three nestling hatched. A: asymptotic weight; K: mean growth rate;  $t_0$ : age at which nestling reached the maximum growth rate. \* Estimated values assuming variable asymptotic weight at the end of the nestling period; \*\* Estimated values assuming a constant asymptotic weight/tarsus length.

Morphological traits	Parameters	Solitary nestlings	Complete broods		
			Nestling 1	Nestling 2	Nestling 3
Weight (g)	A*	46.74	49.24	46.73	42.65
	K*	0.37	0.41	0.41	0.45
	$t_0$ *	5.85	6.25	6.25	6.14
	K**	—	0.46	0.41	0.39
	$t_0$ **	—	5.91	6.25	6.68
Tarsos (mm)	A*	—	35.86	32.37	32.49
	K*	—	0.38	0.443	0.33
	$t_0$ *	—	6.37	5.98	6.28
	K**	—	0.38	0.35	0.28
	$t_0$ **	—	6.37	6.64	7.07

cleaned and stored up to 15 days before being used.

We placed eight experimental nests near to the main road in *Solanum malacoxylon* patches, a common substrate for Scarlet-headed Blackbird nests (Orians 1980), at heights and in vegetation cover typical for the species nests. Nests were at least 1km apart. Each experimental nest was baited with two Quail (*Coturnix coturnix*) eggs. We checked experimental nests every other day for 9 days. This time was arbitrarily decided assuming that most of nest predation and egg losses occurred in the first days (see Svagelj *et al.* 2003). For each experimental nest, we calculated the survival time and the time the eggs remained in the nest before they were depredated or the observation period was completed. We considered the nests as depredated when at least one egg disappeared or was found broken (Zanette & Jenkins 2000). We assessed the effect of adult nest attendance on nest survival by comparing survival time of experimental nests with active natural Scarlet-headed Blackbird

nests found before laying of the first egg ( $n = 19$ ).

## RESULTS

*Breeding biology.* During the 5 years of the study, we found 60 Scarlet-headed Blackbird nests. The breeding season started in early September and lasted until the end of December but the breeding activity reached a peak by 15 November (Fig. 1). However, blackbirds established territories by the end of the southern winter or early spring (August–September) and we saw blackbirds defending them against both predators and conspecifics. We recorded the earliest nest of the season on 15 September and the latest starting on 20 December. These findings confirm the breeding pattern we described in a previous study (Fernández & Mermoz 2000).

Scarlet-headed Blackbirds built their nests on shallow marshes either on cattails or *Solanum glaucophyllum*. In 6 cases, when the first breeding attempt failed, blackbirds re-nested on the same territories, between 2 and 20 m

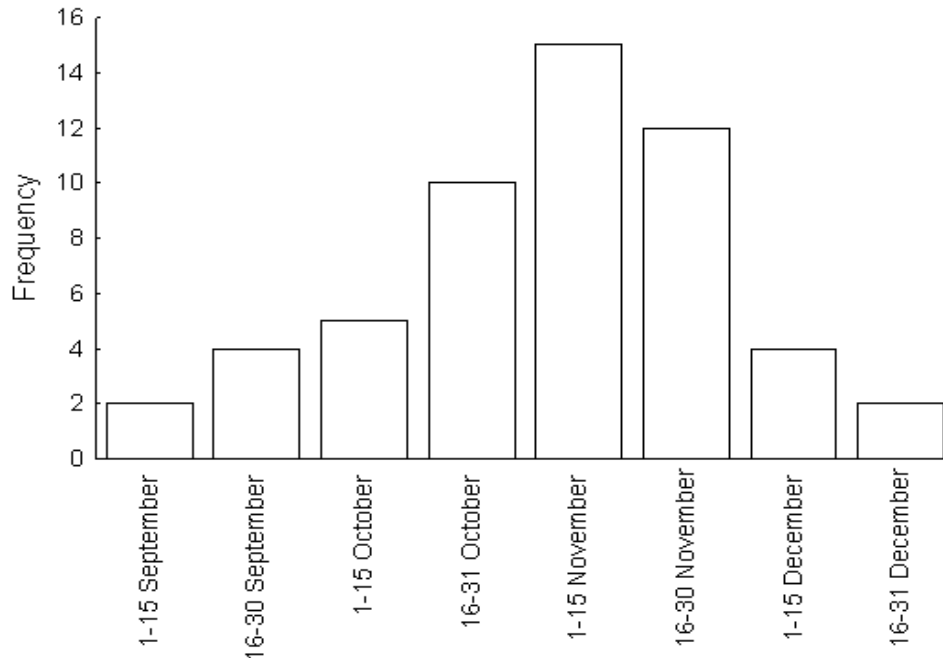


FIG. 1. Seasonal variation of nesting activity of the Scarlet-headed Blackbird in Buenos Aires, Argentine, during the 1995–1997 and 2001–2002 breeding seasons ( $n = 60$ ). Bars correspond to the number of nests that started egg laying within each 15-day interval.

from the original site, and 6–12 days after failure. One of these breeding pairs started a third nest when its second attempt failed on the same territory.

Blackbirds built their nest close to the site used the previous year and the spatial nest distribution was similar between years. The index of relative abundance of nests registered over the roads varied among years between 0.11 and 0.38 nests/km (Fig. 2). The adult male banded during 2001 bred in the same territory during 3 consecutive years (2001–2003). The first and last years he paired with a female with adult plumage, while the second year the female had juvenile plumage. During 2004–2005, we did not resight the male and the territory remained vacant. We observed 3 other instances of individuals breeding in juvenile plumage, and parental

behavior of these individuals was similar to that of adults.

Females laid an egg daily until clutch size was completed. The mean clutch size was  $3.12 \pm 0.33$  eggs ( $n = 19$  nests; mode = 3). Clutch size was three eggs in 17 nests while only two nests belonging to the same pair had four eggs.

The mean egg size was  $26.18 \pm 0.98 \times 19.03 \pm 0.78$  mm ( $n = 33$  nests). Incubation started after the laying of the penultimate egg and was performed exclusively by the female. The first nestling hatched after 13–14 days of incubation. Twenty-four percent (6/25) of the nests suffered from egg losses during incubation and the mean number of eggs lost was  $1.33 \pm 0.08$ .

The hatching of the eggs was asynchronous and the mean number of nestlings that

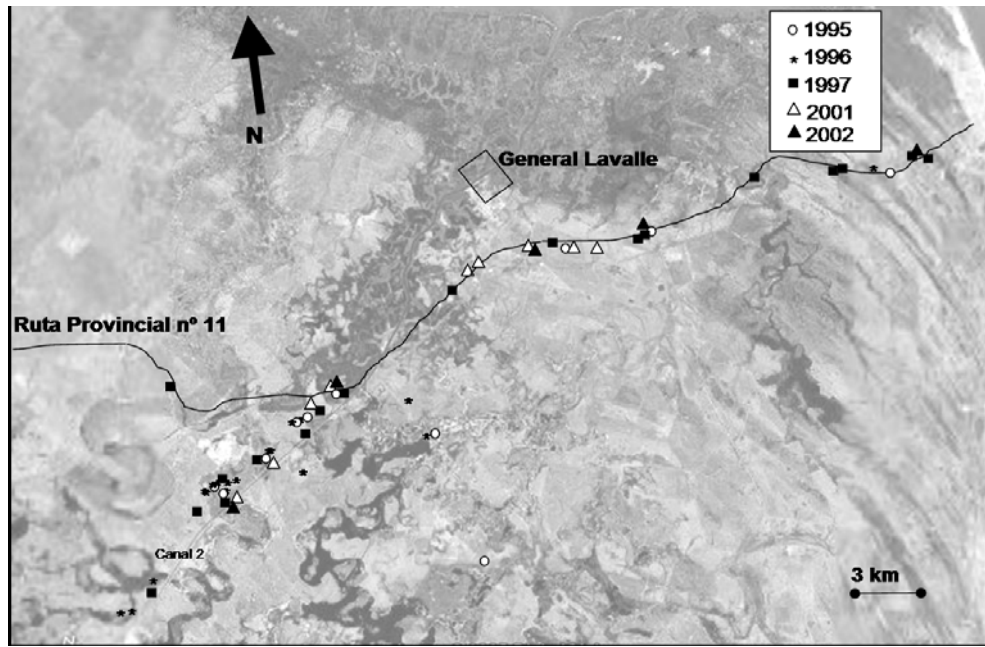


FIG. 2. Study area and location of nest found during the 1995–1997 and 2001–2002 breeding seasons.

hatched was  $2.79 \pm 0.78$  ( $n = 17$ , mode = 3). In nests with three eggs, the third nestling usually hatched a day after the two siblings. The first two nestlings were almost synchronic in their hatching. The hatching success of nests not parasitized by cowbirds was  $98.04\% \pm 8.08$  ( $n = 17$ ). Only 15.4% of nests that completed clutches were parasitized by cowbirds ( $n = 39$ ), and only one nest produced a cowbird fledgling (see Mermoz & Fernández 1999).

The nestlings remained in the nest for 12–13 days before fledging. Fledging success (fledglings/nestlings) was  $78.27 \pm 23.89\%$  ( $n = 17$ ), and the number of nestlings that fledged per nest was  $1.94 \pm 0.77$  ( $n = 17$ , mode = 2). None of the marked fledglings ( $n = 11$ ) were resighted in the study area in subsequent years.

Brood reduction was common and always involved the mortality of the youngest nestling. At least one nestling died in 38.89% (7/

18) of the nests where three nestlings hatched. The survival analysis suggests that hatching order was the best predictor of the probability of survival of the nestlings (Cox regression,  $\chi^2_1 = 3.81$ ,  $P = 0.05$ ). The last nestling to hatch gained mass at a slower rate and had a lower asymptotic mass ( $A$ ) when compared with the other two siblings (Fig. 3a and Table 1). Tarsus length before fledging did not show such a strong difference as mass, but still the asymptote was lower (Fig. 3b and Table 1). The last nestling to hatch tended to have a lower probability of survival when compared to the first and second nestlings, although differences were statistically marginal (Log Rank = 1.91,  $P = 0.06$ ; and Log Rank = 1.56,  $P = 0.12$ , respectively,  $n = 16$  nests; Fig. 4).

*Nesting success.* Data obtained in this study confirm and extend our previously reported data (Fernández & Mermoz 2000). Nineteen out of 49 nests produced fledglings and no differ-

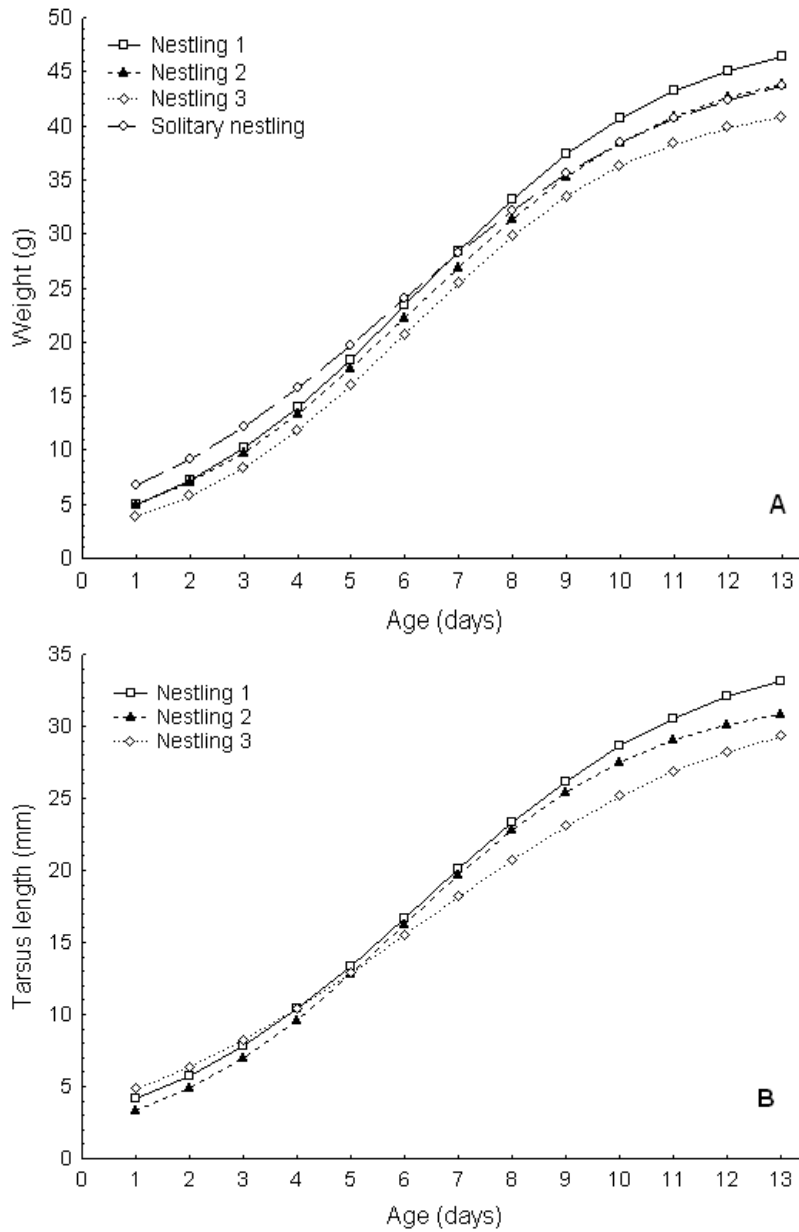


FIG. 3. Weight (A) and tarsi (B) growth of Scarlet-headed Blackbird nestlings throughout the nestling period according to their hatching order. Data estimated from nests with 3 nestlings and nests with solitary nestlings (i.e., nests where only one nestling hatched).

ences among years were detected (mean: 39%; range: 33–53%,  $\chi^2_3 = 1.29$ ,  $P = 0.73$ ). Four nests were deserted after building, and one after the eggs were pecked by cowbirds



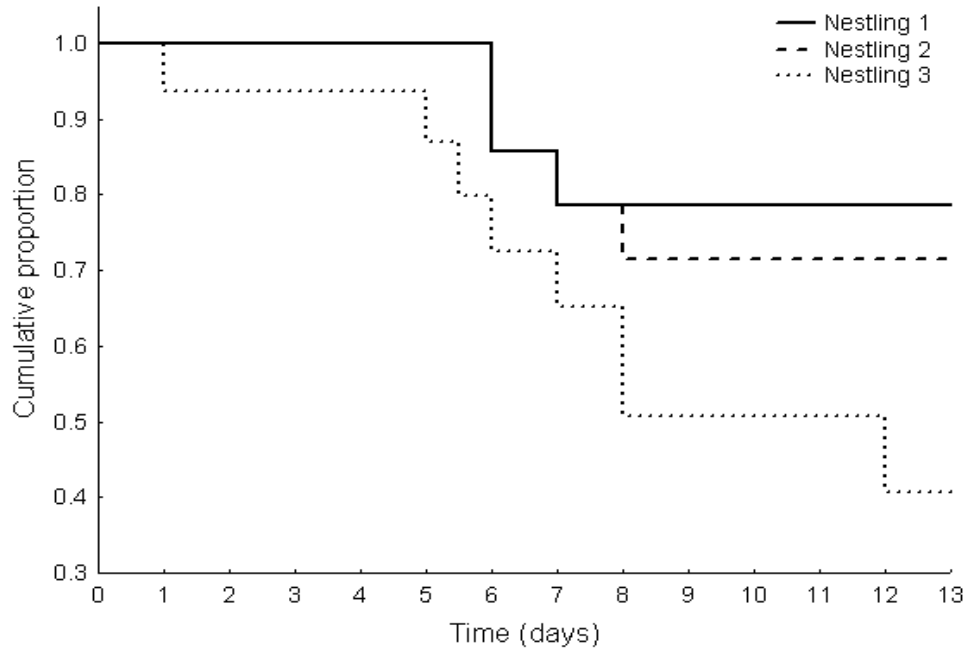


FIG. 4. Kaplan-Meier survival function of Scarlet-headed Blackbird nestlings according to their hatching order. Data included only nests where hatched all three nestlings.

during laying. Six nests were depredated during egg laying, 11 during incubation and 9 during the nestling period. There were no significant differences in the daily mortality rate (DMR) between the laying, incubation or nestling period ( $\chi^2 = 2.81$ ,  $P = 0.25$ ; DMR:  $0.10 \pm 0.04$ ,  $0.03 \pm 0.01$ ,  $0.3 \pm 0.01$  nest losses/nest/day, for laying, incubation and nestling rearing stages, respectively). The probability of a given pair completing a clutch of three eggs was 0.72, while the probability of completing the incubation period of 12 days was 0.45, and the probability of rearing a fledgling was 0.29.

*Nest attendance.* Nest attendance of the breeding pair did not vary between the different nesting stages (Homogeneity test,  $G = 0.04$ ,  $df = 2$ ,  $P = 0.98$ ). At least one parent was close to the nest (< 20 m) in 93.2% of the vis-

its to the nest during egg laying and incubation ( $n = 74$ ), and in 92.4% of our visits during the nestling period ( $n = 66$ ).

Female attendance at the nest increased from about 8% of time during the laying of the first eggs, to 47.3% at the laying of the last egg, and about 83% at the end of incubation period. Low sample size ( $n = 5$ ) preclude us to compare statistically nest attendance among egg stages.

*Feeding rate.* Both adults fed the young on the nest and carried only one prey item by visit. The feeding rate per nestling increased as nestlings grew older, but variation among nests was high. During the first days after hatching (1–3 days old), the feeding rate was of 2–2.92 items/nestling/h (mean: 2.15;  $n = 2$ ) while, when nestlings were 5–7 days old, the feeding rate was 1.47–4.67 items/nest-

ling/h (mean: 3.97;  $n = 4$ ). By the end of the nestling period, feeding rate ranged from 2.87 to 9.22 items/nestling/h (mean: 5.08;  $n = 6$ ).

*Effect of nest attendance on nest survival.* Experimental nests located in marshes had a lower probability of survival than natural nests (Mann Whitney test,  $n_1 = 8$ ,  $n_2 = 19$ ,  $Z = 2.92$ ,  $P = 0.003$ ). The mean number of days an experimental nest survived was  $3.37 \pm 0.29$ , while for natural nests the mean was  $16.16 \pm 0.55$  days.

## DISCUSSION

During our 5-year study we confirmed that Scarlet-headed Blackbird was territorial during the breeding season. Blackbirds established territories by the end of the southern winter or early spring (August–September) and defended them against both predators and conspecifics. In Argentina, Orians (1980) observed that territorial defense in blackbirds was carried out by both sexes and in many cases, simultaneously.

During three consecutive years we observed a color-banded male occupying the same breeding territory suggesting that blackbirds might keep their breeding territories for consecutive years. Territories were large enough and, therefore, neighbor nests were located between 0.5 and 5 km from each other. Also, 42% of the nests were built close to the site where a nest was located the previous year. Since marshes constitute more than 60% of the study area, we do not think that nest site philopatry was a consequence of low availability of appropriate breeding sites.

Scarlet-headed Blackbirds in our study site had low clutch size variability. Seventeen out of 19 nests that we found during the building period had a clutch size of three eggs. Orians (1980) observed a similar pattern, although his sample size was small (9 nests). Small clutch size is common among South Ameri-

can icterids (Jaramillo & Burke 1999), but such a low variation in this trait has not been previously reported for the southern temperate members of the family. Although most of the nests contained three eggs, usually two nestlings fledged since the younger one died from starvation.

The breeding success of the Scarlet-headed Blackbirds was slightly higher when compared with two other sympatric marsh-nesting icterids. In our study area, Mermoz & Reboreda (1998) and Fernández & Mermoz (2000) estimated that the nesting success of the Brown-and-yellow Marshbirds was 10–30%, while Massoni (2001) reported that, in the Yellow-winged Blackbird (*Chrysomus thilinus*), the breeding success was 17.4%. We found that 39% (27% using the Mayfield method) of Scarlet-headed Blackbird nests produced fledglings. Higher breeding success in this blackbird could be the consequence of high nest attendance and territory defense against predators. In contrast to the Scarlet-headed Blackbird, in both Brown-and-yellow Marshbird and the Yellow-winged Blackbird, males usually follow the females at a close distance during most of the nesting stage (Orians 1980), leaving the nest without protection. On the other hand, in the Scarlet-headed Blackbird, 90% of the time at least one adult was observed close to the nest.

Results from experimental nests gave additional support to the benefits of high nest attendance in the Scarlet-headed Blackbird. Active natural blackbird nests had higher probability of survival than experimental nests, suggesting that nest attendance in the Scarlet-headed Blackbird might be a strategy to reduce nest predation. Nests with quail eggs would underestimate predation rates on passerine eggs (Haskell 1995, DeGraaf & Maier 1996, Bayne & Hobson 1999, Svagelj *et al.* 2003), and then, real predation rates on unattended nests of Scarlet-headed Blackbirds would be higher than those registered by us.

Also, natural Scarlet-headed Blackbird nests suffered similar or slightly less predation than Brown-and-yellow Marshbird nests built on thistles (nest survival probability: 0.25 and 0.14, respectively; Fernández & Mermoz 2000). This result reinforces the idea that parental attendance in Scarlet-headed Blackbirds could be a main strategy to reduce the nest predation risk.

Another benefit of high nest attendance is a reduction in Shiny Cowbird parasitism. Both Brown-and-yellow Marshbird and Yellow-winged Blackbird had higher cowbird parasitism (62–74% and 36.6% of the nests parasitized, respectively; Mermoz & Reboreda 1994, 1999; Massoni & Reboreda 1998). Mermoz & Fernández (1999) suggested that the low rate of brood parasitism in Scarlet-headed Blackbirds is the consequence of non specific responses, namely territorial defense and nest attendance, instead of a specific strategy to reduce brood parasitism.

High nest attendance can have high costs in terms of breeding success. The high percentage of time a blackbird spends close to the nest could constrain time spent searching for food for nestlings. This constraint could limit the food delivered to the nest and would be responsible for the high brood reduction we observed (39%). Orians (1980) also proposed that the high frequency of brood reduction in the Scarlet-headed Blackbird could be the consequence of a highly specialized feeding behavior and food quality delivered by the parents. However, preliminary data available do not support his hypothesis, as the mean feeding rate in Scarlet-headed Blackbirds is similar to that in other icterid species nesting in the area. In the Yellow-winged Blackbird, adults performed 4 visits/nestling/h (Massoni *et al.* 2005), whereas adults of the Brown-and-yellow Marshbird make 2.5 visits/nestling/hour (M. Mermoz & G. Fernández unpubl.). Moreover, in these two species brood reduction is rather rare. In the Yellow-

winged Blackbird, brood reduction was not recorded (Massoni 2001), while in the Brown-and-yellow Marshbird only 17.8% of the nests without cowbird parasitism suffered from brood reduction (N. Duré Ruiz, M. Mermoz & G. Fernández in prep.). Further data on foraging behavior and diet of Scarlet-headed Blackbirds are necessary to test Orians hypothesis.

In summary, we found that breeding success of Scarlet-headed Blackbirds is mainly affected by predation and, probably, by food quality and availability. Future work should focus on the interaction of these three factors to shed new light on their effects on breeding success of this species and could contribute to elucidate the evolution of its life history strategies.

#### ACKNOWLEDGMENTS

We thank M. Beade for his logistical support in the field, A. Vilá and A. Serret from Fundación Vida Silvestre Argentina for their support of this project. We also thank V. Massoni, R. Fraga and an anonymous reviewer for their comments and suggestions for an earlier version of this manuscript. This study was supported by a grant of the Univ. of Buenos Aires to GJF (UBACYT-X007), and a grant of the Consejo de Investigaciones Científicas y Técnicas to MEM (CONICET-PIP5223).

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