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EFFECT OF PREDATION AND COWBIRD PARASITISM ON THE NESTING SUCCESS OF TWO SYMPATRIC NEOTROPICAL MARSHBIRDS

GUSTAVO J. FERNÁNDEZ[1,2] AND MYRIAM E. MERMOZ[1,3]

ABSTRACT.—We compared the effect of nest predation and cowbird parasitism on the breeding success of two simultaneously nesting ecologically similar blackbird species that differ in their breeding strategies. The Scarlet-headed Blackbird (*Amblyramphus holosericeus*) is a monogamous species that performs territorial defense. In contrast, the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) is a non-territorial monogamous breeder that performs mate guarding and has helpers at the nest. Both species suffered similar nest predation rates throughout their nesting cycle. However, the Brown-and-yellow Marshbird suffered higher parasitism from Shiny (*Molothrus bonariensis*) and Screaming cowbirds (*M. rufoaxillaris*) than the Scarlet-headed Blackbird (62.6% vs 15.4%). Brood parasitism accounted for most of the egg losses and hatching failures in Brown-and-yellow Marshbird. Parasitized nests had lower egg survival and hatching success than non-parasitized ones. Mean clutch size was 1.5 eggs larger in Brown-and-yellow Marshbird than in Scarlet-headed Blackbird. However, Scarlet-headed Blackbird had higher hatching success than Brown-and-yellow Marshbird and similar fledging success. Consequently, both species produced similar numbers of fledglings. We did not detect any relationship between the reproductive success of these species and their breeding strategies. The presence of helpers at Brown-and-yellow Marshbird nests did not affect nest defense or chick survival, but helpers might account for reduced parental effort by supplementing food delivery to chicks/fledglings. *Received 10 Nov. 1999, accepted 15 May 2000.*

Avian reproductive strategies can result from the influences of ecological factors including the temporal and spatial patterns of food distribution, the form and intensity of predation on both adults and nests (Lack 1968, Ricklefs 1969, Emlen and Oring 1977, Picman 1988), and their evolutionary history (Brooks and McLennan 1991). Typically, studies of comparative nesting success focused on how reproductive traits such as clutch size, brood size, and nestling stage length may be affected by selective forces such as food availability, territory quality, and predation risk (e.g., Lack 1968; Ricklefs 1969; Slagsvold 1982; Martin 1987, 1992, 1995). Less frequently, nesting performance and reproductive traits have been related to mating systems and reproductive behavior (but see Post 1986, Larsen et al. 1996).

Chick and egg predation have been suggested to be the main causes of nesting failure in terrestrial birds (Ricklefs 1969, Picman 1988, Martin 1995). Nest predation reduces parental fitness and might be expected to select for parental breeding traits and strategies to reduce the predation risk (Meilvang et al. 1997). Accordingly, several researchers have recognized predation as a major factor affecting such diverse aspects of breeding strategies as the spacing pattern of nesting (Lack 1968, Post 1986, Martin 1988) and parent investment on nesting attempts (Skutch 1949, 1985; Martin 1992).

Different benefits and costs have been proposed relating to the spacing pattern of nests. Nesting in a territorial pattern with a high intra- and interspecific defense of the territory has been suggested to reduce brood parasitism (Robertson and Norman 1977) and losses from predators by reducing conspicuousness (Lack 1968). On the other hand, clumping of nests could be advantageous because it increases the detection of predators from a greater distance (Burger 1974), clumping nests also makes possible defense by cooperative mobbing (Wiklund and Anderson 1980) or by dilution effect (Robertson 1973).

Intraspecific comparisons have shown that traits such as timing of breeding or even

[1] Lab. de Biología del Comportamiento, Instituto de Biología y Medicina Experimental (CONICET). Vuelta de Obligado 2490, (1428) Buenos Aires, Argentina.

[2] Lab. de Ecología, Programa de Ecología Matemática. Univ. Nacional de Luján. Rutas 5 y 7. (6700) Luján. Buenos Aires, Argentina.

[3] Depto. de Ecología y Comportamiento Animal. Instituto de Ecología, A.C. Km. 2.5, Antigua Carretera a Coatepec. Apdo postal 63, 91000 Xalapa, Veracruz, México.

[4] Corresponding author: E-mail: mermoz@dna.uba.ar

TABLE 1. Comparison of breeding strategies of Brown-and-yellow Marshbirds and Scarlet-headed Blackbirds. Sources: Orians et al. 1977; Orians 1980; Mermoz and Reboreda 1998.

Behavior	Brown-and-yellow Marshbird	Scarlet-headed Blackbird
Mating system	monogamous	monogamous
Nesting habitat	marshes, edges of marshes and humid grasslands	marshes
Mate guard after nest is built	yes	no
Territorial defense	no	yes
Presence of helpers at the nest	yes (usually at nestling stage)	no
Chick feeding	both parents and helpers	both parents

clutch size could vary with environmental conditions (Murphy 1983, Brawn 1991). Studies of species that breed simultaneously could control for variance because these species experience the same general predator assemblage and the same macroclimate conditions (Martin and Ghalambor 1999). Thus, contemporaneous studies of sympatric, closely related and ecologically similar species are particularly useful for characterizing reproductive patterns and identifiying an ecological basis for life history differences (Murphy 1988, Ramstack et al. 1998).

In this work we compare the nesting success and reproductive traits of two sympatric, closely related Neotropical marshbirds breeding in the same area during 1995–1997; the Scarlet-headed Blackbird (*Amblyramphus holosericeus*) and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*). Both species are monogamous open cup-nesters and have similar morphological and ecological characters, but differ in their reproductive strategies. The Scarlet-headed Blackbird performs an active territorial defense; the Brown-and-yellow Marshbird is a non-territorial breeder that performs mate guarding and has helpers at the nest (Orians 1980). The cooperatively breeding Brown-and-yellow Marshbird may experience higher predation rates than the non-cooperatively breeding Scarlet-headed Blackbird (Orians et al. 1977, Orians 1980). Although helpers collaborate in nest defense, predation affects more than 80% of Brown-and-yellow Marshbird nests (Mermoz and Reboreda 1998).

Our objective was to determine whether differences in life histories and breeding strategies between these species account for differences in their nesting success. Territorial defense performed by Scarlet-headed Blackbirds might reduce nest predation risk and cowbird parasitism; however, it could reduce the food delivery to nestlings once they hatched. Brown-and-yellow Marshbird mate guarding behavior could increase the time that a nest remains unattended exposing it to greater nest predation. Helpers at the nest in this species could increase the amount of food delivery to nestling.

METHODS

Study species.—The Scarlet-headed Blackbird inhabits marshes of southern Brazil, Paraguay, Uruguay, and eastern and northeastern Argentina (Ridgely and Tudor 1989). They are gregarious during the non-reproductive season (Sclater and Hudson 1898, Gibson 1918), but they form individual breeding pairs during early spring (August–September). Each nesting pair defends a large territory (up to 50 ha) against all conspecifics and, occasionally, from individuals of other coexisting species (Orians 1980).

The Brown-and-yellow Marshbird inhabits temperate marshy areas and humid grasslands in northeastern Argentina, Uruguay, and neighboring areas of southern Brazil (Ridgely and Tudor 1989). During the non-breeding season they are highly gregarious and feed in dense groups on the ground (Hudson 1920). During the breeding season they are non-territorial breeders and monogamous. Once chicks hatched, helpers at the nest might deliver food to the chicks (Orians et al. 1977, Orians 1980). Table 1 summarizes the main breeding behaviors of the two species.

Study area.—Nesting data were collected during 1995–1997 breeding seasons (October–December). Nest searching was performed along the sides of an unpaved road (about 15 km long), parallel to an artificial drainage (Canal 2) and along the sides of the route 11 at General Lavalle (36° 20′ S, 56° 54′ W), Buenos Aires Province, Argentina. The habitat is flat and low, characterized by numerous small wetlands and scattered shallow marshes (about 60% of the area), with little of the land rising more than 4 m above sea level. The marshes consisted of mixed patches of bulrush (*Scirpus californicus*), cattails (*Thypha* spp.), *Cyperus* spp., and in some cases broad pure patches of *Solanum malacoxylon.* Water depth was generally 0.3–0.5 m throughout the study period although three marshes were completely dry. On the upland areas, exotic thistles (*Cynara cardunculus, Carduus* sp.) 0.5–1.5 m tall grew along the sides of the road in a continuous row. Flooded areas and marshes surrounded these small upland areas. Native bushes [black-rushes (*Juncus acutus*) and pampa grasses (*Cortaderia selloana*)] were clumped on flooded areas. The study site was surrounded by open fields, used primarily for livestock rearing on natural pastures. Potential nest predators in our study area were Chimango Caracara (*Milvago chimango*), Long-winged Harrier (*Circus buffoni*), opossums (*Lutreolina crassicaudata*), ferrets (*Galictis* spp.), Barn owls (*Tyto alba*), skunks (*Conepatus* spp.), small snakes, and rodents.

We found most of Brown-and-yellow Marshbirds' nests (61.5%) built in thistles in uplands, 23.1% of the nests were built on black rushes in flooding areas (edges of marshes) and 15% were on cattails in marshes. We classified nests as being built on marshes, uplands, or flooding areas (Mermoz and Reboreda 1998).

Nesting biology.—Each nest located was mapped and marked nearby with an inconspicuous coded tag. When the nest was found during incubation, we used the date found, number of eggs, and incubation stage (Hays and LeCroy 1971) to estimate the date of the first egg. Most nests were checked every other day until the young fledged or the nest failed. Each egg was marked with waterproof ink and checked for cracks or punctures. The presence of egg fragments or missing eggs was attributed to partial predation or interspecific brood parasitism by cowbirds (Shiny Cowbird, *Molothrus bonariensis*; Screaming Cowbird, *M. rufoaxilliaris*). Most nests were abandoned after one or several eggs had been removed. To be conservative, we considered those nests that had cowbird eggs or nestlings at any stage to be parasitized. Nests showing either total egg or nestling loss were considered depredated.

Nest survival.—Nest survival was estimated using Mayfield's exposure method, which is based on nest losses over the total number of days nests were under observation (Mayfield 1975, Johnson 1979). The daily nest mortality rate was defined by the number of nests lost or failed divided by the total number of days those nests were under observation (nest losses/nest $\times$ day). To calculate nest exposure time we assumed that the length of the interval at which nest loss occurred was one-half of its length (i.e., nest loss occurred in the middle of the interval between our visits; Mayfield 1975). This nest mortality rate was calculated for three nest stages: egg laying, incubation, and nestling. A nest was considered in the egg laying stage when the females were laying eggs. The incubation stage lasted from the day after the laying of the last egg until the hatching of the first (host or parasite) chick. The chick rearing stage lasted from the day the first chick hatched to the day the last nestling of either species fledged. We estimated the variance of this daily nest mortality rate (V) from Johnson's (1979) equation $V = [(\text{ND} - \text{losses}) \times \text{losses}]/\text{ND}^3$, where ND is the number of nest-days of exposure and losses the number of nests that failed. Nest survival at each nesting stage was calculated as $(1 - DNMR)^t$, t being the time of each nesting stage and *DNMR* the respective daily nest mortality rate. We assumed that daily nest mortality rates remained constant over each stage. Nesting success was defined as the product of the probability of nest survival at each stage (Mayfield 1975). We compared stage-specific nest survival rates using the program CONTRAST (Hines and Sauer 1989).

To control for differences in nest site habitat, interspecific comparisons of nest survival and nesting success were performed considering daily nest mortality rates for each stage of the Scarlet-headed Blackbird and the Brown-and-yellow Marshbird nests built in marshes. We also compared daily nest mortality rates of Brown-and-yellow Marshbirds for nests built in marshes, upland, and flooding areas because this species builds nests in different habitats.

Because brood parasitism was found to have no influence on nest survival (Mermoz and Reboreda 1998), we included all nests we found regardless of parasitism in our analyses. Nests that produced only cowbird fledglings and were not depredated or abandoned were considered successful for this analysis.

Nest attention.—To estimate nest attentiveness during each stage of the nesting cycle, we recorded whether at least one parent was in or near the nest (less than 10 m) on each nest visit during 1996–1997. We made 149 observations at 100 nests of Brown-and-yellow Marshbirds and 140 observations at 36 nests of Scarlet-headed Blackbirds.

Clutch size, egg survival, hatching and fledging success.—Clutch size (total number of eggs laid) was measured from nests found at building or early laying stages. Egg survival was measured as the proportion of the clutch size that remained in the nest until the first egg hatched. Hatching success was estimated as the number of chicks that hatched divided by the total number of eggs present at the end of incubation (Koenig 1982). In some nests, the smallest chick disappeared and we considered this loss as brood reduction (Mock 1994). In 6 Brown-and-yellow Marshbirds' nests and 1 Scarlet-headed Blackbird's nest, we found the smallest chick dead in the nest. In most of those nests, the growth rate of the smallest chick was lower than any of their larger nestmates (Mermoz 1996). Predation was considered as a more probable cause of chick disappearance when the larger ones were missing (Mock 1994). Fledging success was estimated as the number of chicks that fledged divided by the total number of chicks that hatched in successful nests. The effect of cowbird parasitism on egg survival, hatching, and fledging success was evaluated in the Brown-and-yellow Marshbird by comparing these variables in parasitized and non-parasitized nests. The same analysis could not be done in the Scarlet-headed Blackbird because of the small number of parasitized nests.

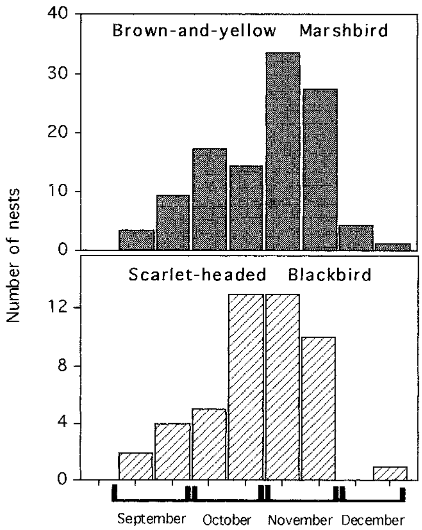

FIG. 1. Total number of nests initiated at different times of the breeding season (15 day interval) of Brown-and-yellow Marshbirds (*n* = 108) and Scarlet-headed Blackbirds (*n* = 48).

All measures are presented as mean ± SE of the mean. Statistical analyses were performed using the software StatView 4.51 for Macintosh (1996 Abaccus Concepts Inc.).

RESULTS

General breeding biology.—Scarlet-headed Blackbird pair bonds were first observed 20–30 August, but nests were not found until September (earliest nest found 10–20 September). Similarly, Brown-and-yellow Marshbirds showed breeding activity early in the season and nesting attempts started in September (earliest nest found 1–10 September). For both species, breeding lasted until December (latest nest found 20–30 December).

We found 49 Scarlet-headed Blackbirds' and 129 Brown-and-yellow Marshbirds' nests during the 1995–1997 breeding seasons. The nesting pattern was similar for both species, with the number of nests initiated peaking during November and declining through December (Fig. 1).

Eight of the 49 Scarlet-headed Blackbird nests were renesting attempts and were built on the same territory as the previous failed nest. We observed one instance of two renesting attempts, but most breeding pairs made only one renesting attempt after desertion or depredation. Consequently, 41 Scarlet-headed Blackbird's breeding pairs were followed during this study. The gregarious nesting of the Brown-and-yellow Marshbirds precluded us from assigning renesting attempts because we did not color mark the individuals.

Brown-and-yellow Marshbirds had a larger mean clutch than Scarlet-headed Blackbirds (4.61 ± 0.14 eggs, $n = 18$, 3.05 ± 0.06 eggs, $n = 23$, respectively; Mann-Whitney test: $Z = 5.9$, $P < 0.001$). Both species laid eggs at daily intervals and incubation began with the laying of the penultimate egg. The eggs usually hatched after 13–14 full days of incubation and nestlings remained in the nest for about 12 days.

Nest survival.—Twenty-five Scarlet-headed Blackbird's nests (25/41, 60.97%) and 72 Brown-and-yellow Marshbird nests (72/92, 78.26%) were depredated or deserted, in most cases after several eggs were removed from a nest. We excluded the fates of 37 Brown-and-yellow Marshbird and 8 Scarlet-headed Blackbird nests because visit intervals to those nests at the end of nestling stage were more than 5 days (mostly caused by adverse weather). Therefore, we were unable to determine the fate of those nests.

Daily nest mortality rates did not differ with time for the Scarlet-headed Blackbird and the Brown-and-yellow Marshbird ($\chi^2_2 = 3.1$, $P > 0.05$; $\chi^2_2 = 5.46$, $P > 0.05$, respectively). Also, we found no differences between the daily nest mortality rates of Scarlet-headed Blackbirds nests and Brown-and-yellow Marshbirds nests built on marshes at any stage ($\chi^2_1 = 0.03$, $P > 0.05$ for laying; $\chi^2_1 = 0.05$, $P > 0.05$ for incubation; and $\chi^2_1 = 0.23$, $P > 0.05$ for nestling; Fig. 2A). However, nesting success (measured as the product of the nest survival for each stage) was higher for Scarlet-headed Blackbird's nests than for Brown-and-yellow Marshbird nests ($\chi^2_1 = 4.81$, $P = 0.03$; Fig. 2B). Considering a clutch size of 3 eggs, an incubation period of 13 days and a nestling period of 12 days for Scarlet-headed Blackbird's nests, the probability of a nest surviving the entire nesting cycle was 0.25. Similarly, for Brown-and-yellow Marshbird's nests with a laying period of 4.6 days, a 13 days of incubation, and a 12 days of nestling period, the nest survival probability was 0.11. Because we did not detect differences in daily nest mortality rates for any stage of the nest-

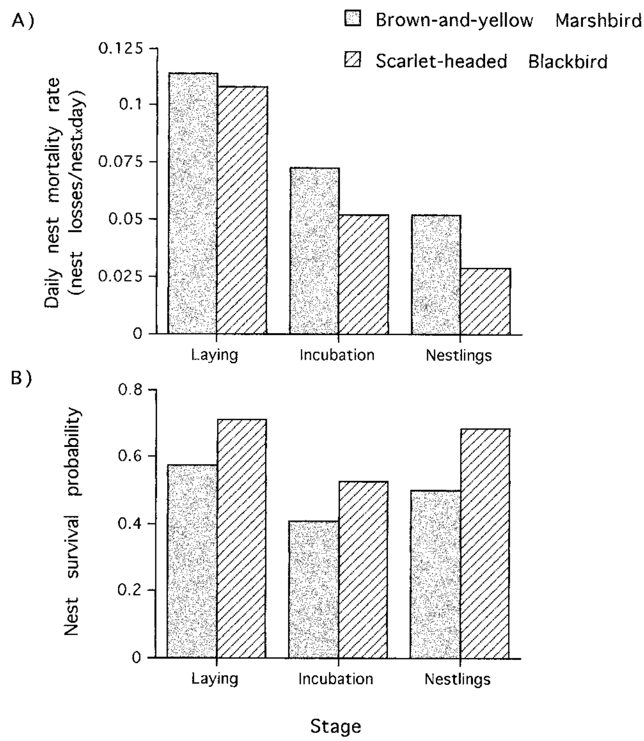

FIG. 2. A. Daily nest mortality rates estimated by Mayfield method (DNMR = nests losses/nest.day). B. Nest survival probability at laying, incubation, and nestling stages of the Brown-and-yellow Marshbird and the Scarlet-headed Blackbird nests. Nesting survival probability were estimated as $(1 - \text{DNMR})^t$, where t is the time involved on each nesting stage.

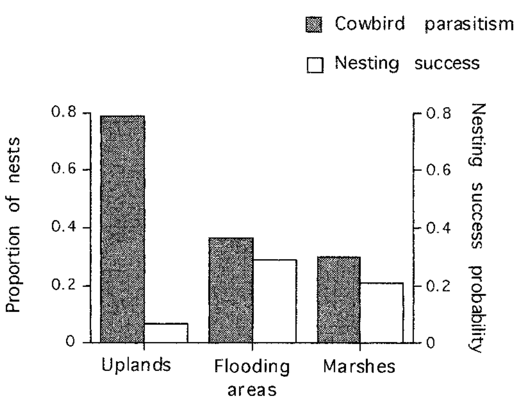

FIG. 3. Proportion of nests parasitized by cowbirds (shaded bars) and nesting success (open bars) of Brown-and-yellow Marshbird nests built in different habitats. Nesting success was estimated as the product of nest survival at each nesting stage [$(1 - DNMR)^t$, with t being the time involved on each nesting stage and *DNMR* the respective daily mortality rate].

ing cycle, we assumed that this difference in the nest survival probability was the result of a longer laying period for the Brown-and-yellow Marshbird. When we recalculated nest survival probabilities for a 3 egg laying period, expected nest losses were similar to those of the Scarlet-headed Blackbird (nest survival probability 0.25 vs 0.14, respectively; $\chi^2_1 = 2.34$, $P > 0.05$).

We detected differences in the nesting success of Brown-and-yellow Marshbirds related to nest-site ($\chi^2_2 = 7.88$, $P = 0.02$). Nests built on flooding areas and marshes had a lower daily nest mortality rates than nests built on upland areas ($\chi^2_1 = 4.82$, $P = 0.03$; Fig. 3). When analyzed by nesting stages, no differences were found ($\chi^2_1 = 0.27$, $P > 0.05$, for laying; $\chi^2_1 = 3.73$, $P > 0.05$, for incubation; and $\chi^2_1 = 4.89$, $P > 0.05$, for nestling stage).

Nest attentiveness.—The Brown-and-yellow Marshbird's nest attentiveness increased over the nesting cycle (Homogeneity G-test:

G_2 = 6.6, P = 0.03). During the laying and incubation stages, 71.3% of the time at least one parent remained near the nest (n = 87 observations) and increased to 87.1% (n = 62 observations) after the chicks hatched (Homogeneity G-test: G_1 = 6.52, P = 0.01). We detected differences in nest attentiveness at any stage related to the nest habitat (Homogeneity G-test: 2 df, $P > 0.05$ for all comparisons).

Neither was there any difference in nest attentiveness by the Scarlet-headed Blackbird among different nesting stages (Homogeneity G-test: G_2 = 0.04, $P > 0.05$). At least one parent was near the nest on 93.2% of the visits during laying and incubation (n = 74) and on 92.4% of the visits during chick rearing stage (n = 66). Furthermore, Scarlet-headed Blackbirds were significantly more attentive to the nest during both egg laying and incubation than Brown-and-yellow Marsbirds (Homogeneity G-test: G_1 = 5.85, P = 0.01; G_1 = 7.65, P = 0.006 respectively). However, their nest attentiveness were similar during chick rearing (Homogeneity G-test: G_1 = 1, $P > 0.05$).

Egg survival, hatching, and fledging success.—Twenty-four Scarlet-headed Blackbird nests hatched but six were depredated at hatching. Of the 18 surviving nests, 16 produced fledglings (one produced one cowbird and one host chick) and the fates of the other 2 were unknown.

Forty-six Brown-and-yellow Marshbird nests had nestlings and 22 of these nests fledged young. Of the nests with nestlings, 18 were depredated or deserted, and we did not know the fate of the 6 remaining nests.

Egg survival was higher in Scarlet-headed Blackbird than in Brown-and-yellow Marshbird nests (Mann-Whitney test: Z = 3.74, n_1 = 19, n_2 = 22, $P < 0.001$). About 94.7% (± 3.8, n = 19) of the eggs survived in Scarlet-headed Blackbird nests whereas 74.8% (±6.4, n = 22) of the eggs survived the incubation period in Brown-and-yellow Marshbird nests. Hatching success was also higher in Scarlet-headed Blackbird nests (Mann-Whitney test: Z = 3.63, n_1 = 18, n_2 = 28, $P < 0.001$). Hatching success averaged 0.94 ± 0.04 chick/egg (n = 18); whereas Brown-and-yellow Marshbird hatching success averaged 0.59 ± 0.06 (n = 28). Fledging success was similar for both species (0.82 ± 0.06, n = 14, for Scarlet-headed Blackbirds, and 0.84 ± 0.07, n = 20, for Brown-and-yellow Marshbirds; Mann-Whitney test: Z = 0.82, $P > 0.05$). Differences in egg survival and hatching success resulted in fewer Brown-and-yellow Marshbirds nestlings (Mann-Whitney test: Z = 2.94, n_1 = 18, n_2 = 28, P = 0.003) in spite of their larger clutch size, but a similar number of fledglings produced per successful nest (Mann-Whitney test: n_1 = 14, n_2 = 20, Z = 0.96, $P > 0.05$, Fig. 4). Taking into account total nest losses, Scarlet-headed Blackbirds had a higher breeding success per egg than Brown-and-yellow Marshbirds. For all nests pooled that were found at laying and early incubation for each species, only 8.3% (28/337) of the eggs laid by Brown-and-yellow Marshbird produced fledglings, but 30.8% (29/94) of Scarlet-headed Blackbird's eggs fledged (Homogeneity G-test: G_1 = 27.6, $P < 0.001$). No differences were detected in brood reduction frequency between the study species where 2 or more chicks had hatched (Fisher Exact test: P = 0.14). Scarlet-headed Blackbirds suffered brood reduction on 50% of their nests (6/12 nests), but Brown-and-yellow Marshbirds suffered chick loss on 22.7% of the nests (5/22 nests).

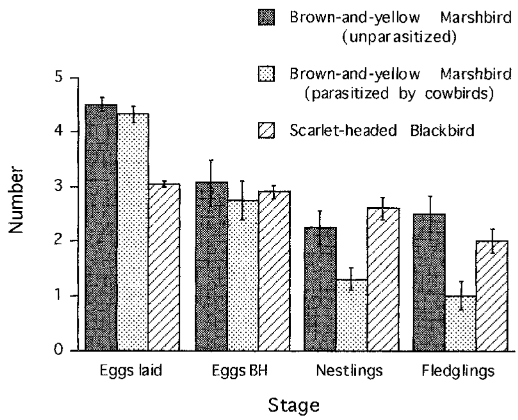

FIG. 4. Number (mean ± SEM) of eggs laid, eggs present before hatching (eggs BH), nestlings hatched, and fledglings produced in Brown-and-yellow Marshbird and Scarlet-headed Blackbird nests. In the Brown-and-yellow Marshbird, dark bars represent unparasitized nests and stippled bars indicate parasitized nests.

Missing eggs and hatching failures we observed in Brown-and-yellow Marshbird nests may be attributed to high cowbird parasitism.

Thus, we repeated the analysis excluding parasitized nests. Taking into account only unparasitized nests, egg survival was similar in Scarlet-headed Blackbird and Brown-and-yellow Marshbird nests (0.94 ± 0.04, $n = 18$, and 0.89 ± 0.06 %, $n = 9$ respectively; Mann-Whitney test: $Z = 1.21$, $P > 0.05$). Nevertheless, hatching success was higher in Scarlet-headed Blackbird nests (0.94 ± 0.04 chick/egg, $n = 17$ vs 0.73 ± 0.08 chick/egg, $n = 13$ for Brown-and-yellow Marshbirds; Mann-Whitney test: $Z = 2.65$, $P = 0.008$). On the other hand, fledging success was similar for both species (0.86 ± 0.06, $n = 13$ for Scarlet-headed Blackbirds, 0.92 ± 0.06, $n = 10$ for Brown-and-yellow Marshbirds; Mann-Whitney test, $Z = 0.8$, $P > 0.05$). Consequently, even when taking into account the higher brood parasitism it suffered, Brown-and-yellow Marshbirds produced a similar number of nestlings and fledglings per nest as did Scarlet-headed Blackbirds (Mann-Whitney test: $Z = 0.11$, $n_1 = 17$, $n_2 = 13$, $P > 0.05$ and $Z > 0.05$, $n_1 = 13$, $n_2 = 10$, $P > 0.05$, respectively; Fig. 4).

Cowbird brood parasitism.—Only 6 out of 39 (15.4%) of the Scarlet-headed Blackbird nests with completed clutches were parasitized by Shiny Cowbirds. Of these, only one fledged a cowbird. Seventy-seven of 123 Brown-and-yellow Marshbird nests that remained active for at least three days during egg laying were parasitized (62.6%). Fifty-six nests were parasitized with Shiny Cowbird eggs only (45.5 %) and 9 were parasitized with Screaming Cowbird eggs (7.3%). The remaining 12 nests (9.7%) were parasitized by both cowbird species. Of the 77 parasitized nests, 21 hatched cowbird chicks (14 only by Shiny Cowbirds, 4 only by Screaming Cowbirds, 3 by both). Cowbird fledglings were successfully reared in at least 6 nests.

Incidence of cowbird parasitism varied among habitats containing the Brown-and-yellow Marshbird nests. Nests built on uplands (thistles) suffered higher cowbird parasitism than nests built in marshes and flooding areas (Homogeneity G-test: $G_2 = 26.1$, $P < 0.001$; Fig. 3). However, Brown-and-yellow Marshbird nests in marshes and flooding areas were more heavily parasitized than Scarlet-headed Blackbird nests (Homogeneity G-test: $G_1 = 5.72$, $P = 0.02$).

When we compared parasitized and unparasitized nests of Brown-and-yellow Marshbirds, we found nearly significant differences in egg survival (0.89 ± 0.06, $n = 9$ for unparasitized nests; 0.65 ± 0.09, $n = 13$, for parasitized nests; Mann-Whitney test: $Z = 1.9$, $P = 0.052$). The number of eggs that remained at hatching did not differ between parasitized and unparasitized nests (Mann-Whitney test: $Z = 1.75$, $P > 0.05$; Fig. 4). Hatching success was higher in unparasitized than in parasitized nests (0.73 ± 0.08, $n = 13$, and 0.47 ± 0.09, $n = 15$, respectively; Mann-Whitney test: $Z = 2.08$, $P = 0.04$) resulting in more nestlings (Mann-Whitney test: $Z = 2.56$, $P = 0.01$; Fig. 4). However, fledging success was similar in parasitized and unparasitized nests (0.78 ± 0.13, $n = 10$, and 0.92 ± 0.06, $n = 10$, respectively Mann-Whitney test: $Z = 0.65$, $P > 0.05$). Overall, unparasitized nests produced more fledglings than parasitized nests (Mann-Whitney test: $Z = 2.52$, $P = 0.01$; Fig. 4). Frequency of brood reduction in parasitized and unparasitized Brown-and-yellow Marshbird's nests where 2 or more chicks hatched was similar (Fisher Exact test: $P > 0.99$). Unparasitized nests suffered brood reduction of 28.6% of their nests (2/7 nests), whereas parasitized nests suffered chick loss of 20% of the nests (3/15 nests).

DISCUSSION

Nest survival and cowbird parasitism.—About 20–25% of the nesting attempts by Brown-and-yellow Marshbirds and Scarlet-headed Blackbirds were neither depredated nor abandoned despite differences in their breeding systems. Territorial defense and higher nest attention in the Scarlet-headed Blackbird apparently do not improve the nesting success of this species compared to the Brown-and-yellow Marshbird. On the other hand, compared to Scarlet-headed Blackbird, non-territorial nesting and cooperative defense against potential predators in Brown-yellow Marshbirds apparently is not an effective strategy for reducing nest predation. The nest losses we observed were similar to those previously reported for the nesting success of the Brown-and-yellow Marshbird (Mermoz and Reboreda 1998) and the Yellow-winged Blackbird (*Agelaius thilius*; Massoni and Reboreda 1998), another sympatric marshbird species nesting in the same area. All are monogamous, but Brown-and-yellow Marshbirds and Yellow-winged Blackbirds are not territorial. In these two species males guard their mates when away from the nest, leaving the nest unattended most of the time, especially during egg laying (Mermoz 1996, this study). We found no clear relationship between the nests' spacing pattern or territorial defense and predation rate.

Cowbird parasitism was significantly higher in Brown-and-yellow Marshbirds. More than 60% of their nests were parasitized (by Shiny Cowbirds and/or Screaming Cowbirds) compared to less than 15% parasitism by Shiny Cowbirds in the Scarlet-headed Blackbird nests.

Selection of nesting sites appears to affect breeding success and cowbird parasitism rates of Brown-and-yellow Marshbirds. Comparative studies on the reproductive success of coexisting blackbirds have shown that marsh nesting birds usually experience lower nest predation rates than those in adjacent upland habitats (Case and Hewitt 1963, Robertson 1972, Picman 1988; but see Ricklefs 1969). We also found that success of Brown-and-yellow Marshbirds nesting on thistles (uplands) was lower than those nesting in marshes and flooded areas. Furthermore, nests on thistles suffer a higher cowbird parasitism and subsequently greater hatching failure, resulting in fewer fledglings per nest. A similar site effect was detected previously. In a 3-year study, Mermoz and Reboreda (1998) found that nests built in flooded areas were likely to be about 3 times more successful than those built in the uplands and suffered lower cowbird parasitism. They suggested that these differences in nest predation and cowbird parasitism could be the result of the differential distribution of plants (Mermoz and Reboreda 1998). Thistles usually grow as hedges along the sides of unpaved roads. Therefore, nests built on these plants could be detected easily by cowbirds and predators that travel along roads (Camp and Best 1994). Nests built on upland areas are vulnerable to terrestrial predators like skunks, ferrets, and rodents, which rarely could depredate nests built on flooded areas or marshes. However, Brown-and-yellow Marshbirds nest preferentially on uplands near the marshes, about 60% of the nests were built on thistles along the roads. Because similar differences on nesting success related to nest site were consistently found between Mermoz and Reboreda (1998) and our study, it is unlikely that variation in nesting success among years could explain this nesting site preference (Hatchwell et al. 1999). Further, Brown-and-yellow Marshbirds are apparently unconstrained in their choice of suitable nesting sites because they are not territorial and more than 60% of the study area is vegetated marshes. It is possible that nest building in unsuccessful sites might be maintained by gene flow (Hatchwell et al. 1999). Because we have no data about nesting success of Brown-and-yellow Marshbird elsewhere, we could not dismiss that possibility.

Instead of the nest site effect, we found that cowbird parasitism was higher in Brown-and-yellow Marshbird nests built on flooding areas and marshes than in Scarlet-headed Blackbird nests. It has been suggested that high nest attentiveness and interspecific territorial defense performed by Scarlet-headed Blackbird may preclude nests from being parasitized. In turn, mate guarding during most of the nesting cycle (mainly during the egg laying stage) in the Brown-and-yellow Marshbird could increase the chances of being parasitized (Mermoz 1996, Mermoz and Fernández 1999).

Most researchers recorded the highest nest mortality during the nestling stage, attributing it to the higher frequency of visits by adults delivering food and to the sounds of nestlings begging (Skutch 1949, Nice 1957, Young 1963, Robertson 1972, Redondo and Castro 1992, Schaub et al. 1992). A few researchers found the highest nest mortality during the laying and incubation stages (Roseberry and Klimstra 1970, Caccamise 1976, Best and Stauffer 1980, Roper and Goldstein 1997, Mermoz and Reboreda 1998). This could be attributed to increased nest defense and nest attention by the parents through the nesting cycle (Caccamise 1976, Andersson et al. 1980). However, despite the increased time parents spend near the nest throughout the nesting cycle in Brown-and-yellow Marshbirds, we were unable to find differences in nesting survival among nesting stages. Nevertheless, in a previous study on this species, a pattern of increasing nest-survival over the nesting cycle was found (Mermoz and Reboreda 1998). Consequently, the increase of parental attention to the nest could reduce the nest predation risk. On the other hand, Scarlet-headed Blackbirds were more attentive to their nests than the Brown-and-yellow Marshbirds during the egg-stage (laying and incubation), but this behavior did not increase the daily survival of their nests. The high nest mortality observed in these species appears to indicate that nest attention might not be enough to drive all potential predators away.

Helpers at the nest could contribute to nest survival mostly during the chick rearing stage by serving as sentinels or by mobbing potential predators (Orians et al. 1977, Mermoz 1996, Poiani and Pagel 1997). However, the cooperative chick rearing system in the Brown-and-yellow Marshbird does not seem to enhance nest or chick survival relative to the non-cooperative Scarlet-headed Blackbird. Helping at the nest may be only compensating for predation risk, as was found in other comparative studies (Koenig 1982, Poiani and Pagel 1997).

Clutch size, hatching and fledging success.—Brown-and-yellow Marshbirds have a larger clutch size than Scarlet-headed Blackbird. Eggs within Brown-and-yellow Marshbirds' clutches were more similar in sizes, color, and marking pattern than eggs of different clutches. Consequently, we discard the idea that their larger clutch size was the consequence of more than one female (e.g., a helper) was laying in the nest. Thus, in spite of the higher clutch size of the Brown-and yellow Marshbird (4–5 eggs vs 3 eggs for the Scarlet-headed Blackbird), hatchability was higher in the Scarlet-headed Blackbird. As a result, both species produced similar numbers of fledglings. This result could be attributable to the higher cowbird parasitism found in Brown-and-yellow Marshbird nests. In this species, cowbird parasitism effectively reduced the number of eggs hatched and chicks fledged. Cowbird eggs hatched earlier than Brown-and-yellow Marshbird eggs, and therefore the female discontinued incubation earlier thus reducing the hatching success of the eggs. Frequently cowbird chicks also could outcompete the host chicks (Mermoz and Reboreda 1994, Mermoz 1996). However, when we omitted parasitized nests from the analysis, the Scarlet-headed Blackbird showed higher hatching success than the Brown-and-yellow Marshbird. Shiny and Screaming cowbirds peck host eggs and some of their egg-pecking behavior occurs in unparasitized nests (Fraga 1998, Massoni and Reboreda 1998). Therefore, we could not dismiss the possibility that at least some of the differences in egg survival and hatching success found between Scarlet-headed Blackbirds and Brown-and-yellow Marshbirds continue to be attributable to the differences in cowbird parasitism. If cowbird egg pecking activities in unparasitized nests are negligible, differences found between the two species could be the consequence of some other phenomenon, perhaps the social complexity of their reproductive strategy. It has been suggested that in cooperative bird species, more social interactions could reduce the female's nest attentiveness and so, egg incubation efficiency (Koenig 1982). The Brown-and-yellow Marshbird could be wasting its reproductive effort because of the greater egg losses suffered during laying and incubation, and the lower hatching success of the remaining eggs. Hence, the cooperative Brown-and-yellow Marshbird and the non-cooperative, territorial Scarlet-headed Blackbird had a similar nesting success and produced the same number of fledglings. Because we have no data on adult survival, we cannot discard the possibility that the benefits of the presence of helpers in the Brown-and-yellow Marshbird increased parental lifetime fitness by reducing parental costs during breeding. Further studies on the role of food limitation in these species and the role of helpers in the Brown-and-yellow Marshbird seem to be necessary to understand the evolution of their life history strategies.

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