NESTING SUCCESS IN BROWN-AND-YELLOW MARSHBIRDS: EFFECTS OF TIMING, NEST SITE, AND BROOD PARASITISM

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Abstract.—The Brown-and-yellow Marshbird (*Pseudoleistes virescens*) is a nonterritorial blackbird with helpers at the nest that inhabits temperate marshy areas and humid grasslands of Argentina, Uruguay, and Brazil. We estimated nesting success of marshbirds throughout the breeding season (late September to mid-December) and analyzed the effects of brood parasitism and nest-site selection (i.e. nesting substrate) on daily survival rates at different stages of the nesting cycle. Most nests were started in November, and these nests had a higher daily survival rate than those initiated in October or December. Only 13.3% of the nests fledged chicks. Predation accounted for 77% of nest losses, whereas the other failures resulted from nest desertion, in most cases after the loss of several eggs. Sixty-five percent of the nests were parasitized by Shiny Cowbirds (*Molothrus bonariensis*), but brood parasitism did not reduce nest survival. Daily survival rates increased from egg laying and incubation to the brood-rearing stage. Nesting success was three times higher in nests built in native black rushes and pampa grasses than in nests built in two exotic species of thistle. Eighty-nine percent of the nests were built in thistles, which were the most abundant plants in the study area. However, many black rushes and pampa grasses remained unoccupied. *Received 6 June 1997, accepted 18 February 1998.*

Food Limitation is an important factor that shapes life-history variation in birds (Lack 1968, Drent and Daan 1980). Nesting success, in particular nest predation, also may exert an important influence on life-history variation (Slagsvold 1982, Martin 1995). Several factors affect nesting success in birds. Most species show a decline in nesting success as the breeding season progresses (Perrins 1970, Daan et al. 1988). This decline is thought to result from seasonal variation in the environment (Hochachka 1990), differences in quality between early and late breeders (Nilsson 1994), or a combination of both factors (Verhulst et al. 1995). The site at which the nest is built affects its detectability and therefore the probability of predation (Best and Stauffer 1980, Martin and Roper 1988). In addition, brood parasitism may influence nesting success in some species. Some hosts abandon the nest when parasitized (Rothstein 1990), whereas others desert the nest as a consequence of egg losses (removals or punctures) caused by the parasite (Zimmerman 1983, Wiley 1985, Sedgwick and Knopf 1988, Hill and Sealy 1994). Moreover, the louder begging calls of some parasite chicks (Briskie et al. 1994, Lichtenstein 1997) could increase the detection of parasitized nests by predators (Hudson 1874).

Predation risk is not constant through the nesting cycle. Most studies of nesting success have found that nest loss is highest during the brood-rearing stage and have attributed these losses to the higher frequency of visits by adults and to the begging activities of nestlings, both of which could make the nest more conspicuous to predators (Skutch 1949, Nice 1957, Redondo and Castro 1992, Schaub et al. 1992). However, a few studies have found that nest loss is highest during the laying and incubation stages (Roseberry and Klimstra 1970, Best and Stauffer 1980). This effect has been attributed to increased nest defense by the parents as the nesting season progresses (Andersson et al. 1980).

Several studies have analyzed nest predation in the tropics and in north temperate areas (Skutch 1949, 1985; Martin 1995), but almost no information is available on nesting success in south temperate areas (see Martin 1996). In this paper, we present data on nesting success of the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) and examine the effects of brood parasitism and nest-site selection on daily survival rates at different stages of the nesting cycle. The Brown-and-yellow Marshbird is an insectivorous blackbird that inhabits marshy areas and

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humid grasslands in northeastern Argentina, Uruguay, and southern Brazil (Ridgely and Tudor 1989). During the nonbreeding season, Brown-and-yellow Marshbirds are highly gregarious and feed in dense groups on the ground (Hudson 1920). During the breeding season, they are monogamous, nonterritorial breeders (Orians et al. 1977, Orians 1980). The female alone builds the nest and incubates, whereas the male accompanies the female during feeding trips and usually feeds her while she is incubating. At this time, other individuals, the helpers, may bring food to the female. The number of birds that attend the nest increases after the young hatch, and all of these attending birds provision the nestlings (Orians et al. 1977). Brown-and-yellow Marshbirds are frequent hosts of the Shiny Cowbird (*Molothrus bonariensis*; Gibson 1918, Hudson 1920, Orians 1980, Mermoz and Reboreda 1994).

STUDY AREA AND METHODS

The study was carried out near the town of General Lavalle (36°26′S, 56°25′W) in the province of Buenos Aires, Argentina, from late September until mid-December, 1992 to 1994. The study area is within the so-called "flooding pampas," a flat region with elevations of no more than 4 m above sea level. The area includes marshes and humid grasslands with scattered patches of native woodland of *Celtis tala* and *Jodina rhombifolia* in the higher areas. The climate is temperate subhumid with mean monthly temperatures of 23°C in January (summer) and 13°C in July (winter); the average annual rainfall is about 1,500 mm (Soriano 1991).

Brown-and-yellow Marshbirds build open cup nests 0.5 to 1.5 m above the ground in thistles (*Cynara cardunculus, Carduus* spp.), black rushes (*Juncus acutus*), and pampa grasses (*Cortaderia selloana*). Thistles are exotic and usually grow along roadsides. We found most nests along the sides of a 20-km stretch of unpaved secondary road parallel to an artificial drainage canal (Canal 2). The nearest-neighbor distance between most nests was 20 to 40 m.

For each nest, we recorded the plant species in which it was built and the start date (i.e. first Brown-and-yellow Marshbird egg). In nests found during the laying stage, we estimated the start date by the number of eggs in the nest. In nests found during the incubation stage, the start date was estimated by egg flotation (as an index of embryo development; Hays and LeCroy 1971). We tagged the nests inconspicuously with a number placed in the plant and marked the nest location with a colored flag placed more than 10 m away. In most cases (91%), nests were checked daily or every other day until either fledging

or nest failure. In fewer cases (9%), nests were visited every five to seven days. Eggs were marked with waterproof ink, and chicks were marked with waterproof ink or color bands and were weighed with Pesola scales daily until fledging (10 to 13 days after hatching).

We considered a nest as parasitized if it had a cowbird egg or nestling at any stage; a nest was considered successful if it fledged at least one chick. Because the aim of the study was to analyze nest desertion and nest predation, nests that fledged only parasite chicks were considered to be successful (Smith 1981). Nests that contained undamaged eggs or nestlings but were no longer attended by adult marshbirds were considered to be abandoned. In some cases, the nest was abandoned after high winds blew the nest from its substrate. However, most nests were abandoned after one or several eggs had been removed. Nests that showed no signs of disturbance but from which eggs or chicks had been removed were considered to have been depredated by birds, snakes, or small mammals, whereas nests in which the bowl was torn apart and/or the nest was pulled from its original position were considered to have been depredated by large mammals (Best and Stauffer 1980). Potential nest predators in our study area included Chimango Caracara (*Milvago chimango*), Long-winged Harrier (*Circus buffoni*), Barn Owl (*Tyto alba*), opossums (*Didelphis* spp.), skunks (*Conepatus* spp.), and small snakes.

We estimated nesting success using Mayfield's exposure method (Mayfield 1975, Johnson 1979). We calculated daily survivorship separately for the laying, incubation, and brood-rearing periods. The incubation stage lasted from the day after the laying of the last Brown-and-yellow Marshbird egg until the hatching of the first chick (host or parasite). The brood-rearing stage lasted from the day the first chick hatched to the day the last nestling of either species fledged.

We estimated daily mortality rate (DMR) by dividing the number of failed nests by the total number of days all nests were under observation (Mayfield 1975). We compared stage-specific mortality using the statistic:

$$\hat{s}_2 - \hat{s}_1 / [V(\hat{s}_1) + V(\hat{s}_2)]^{1/2}, \qquad (1)$$

where $\hat{s}$ and $V(\hat{s})$ are the estimator and variance of the daily survival rate (DSR), respectively (DSR = 1 − DMR; Johnson 1979). When Johnson's statistic exceeds $Z_{0.025}$, the null hypothesis of equal survival probabilities among different stages is rejected.

To test the effect of brood parasitism on nest survival, we compared the DMR of parasitized and nonparasitized nests within each nesting stage using Johnson's statistic. The Mayfield method considers both predation and desertion as nest losses. To ascertain if there was an effect of brood parasitism on the probability of a nest being depredated or desert-

ed, we constructed a contingency table with nests found during the building or egg-laying stages. Within each stage, we compared the observed and expected frequency of success, abandonment, and predation in parasitized and nonparasitized nests with a log-likelihood G-test (Zar 1996).

To determine whether laying date affected nesting success, nests were assigned to month (October, November, or December) according to their start date. We compared DMRs for each month with the T-statistic for comparison among more than two categories of nests (Johnson 1990). Johnson's (1990) method does not allow for determining which groups are different. To solve this problem, we compared observed and expected nest losses per month with a χ^2 test for homogeneity (Hoel 1954). The expected nest losses per month were estimated as the product of the average DMR (throughout the breeding season) and the exposure time of each month. This analysis allows for multiple comparisons by subdividing the contingency table (Zar 1996).

When the interval between nest visits was less than two days, we assumed that nest loss occurred in the middle of the interval. When the interval was five to seven days, we assumed that nest loss occurred at 40% the interval length (Johnson 1979). Mayfield's method assumes that the length of each nesting stage is the same for all nests (Hensler and Nichols 1981). Shiny Cowbird chicks usually hatch one day before host chicks (Mermoz and Reboreda 1994). Therefore, parasitized nests had, on average, an incubation stage that was one day shorter than nonparasitized nests; we assumed that this difference was negligible.

To analyze the effect of our visits on nesting success, we compared the survival of nests that were visited weekly ($n = 19$) with that of nests visited at intervals of 1 to 2 days ($n = 243$; analysis confined to nests built in thistles). DMR did not differ between nests in the two groups (Johnson's statistic, $P > 0.1$ for the comparison within the three nesting stages).

The mean clutch size in nonparasitized nests was $4.3 \pm$ SE of 0.11 eggs (range 3 to 6 eggs, $n = 59$ complete clutches found during the building or laying stage). Thus, to estimate nesting success, we considered the laying period to be 4.3 days.

RESULTS

We monitored a total of 418 nests (73 in 1992, 129 in 1993, and 216 in 1994); 70% of the nests were found during the building ($n = 144$) or egg laying ($n = 145$) stages, and only 3.3% ($n = 14$) were found during the brood-rearing stage. Eighty-nine percent of the nests were built in thistles (mainly *Cynara cardunculus*), 9% in black rushes, and 2% in pampa grasses. Pre-
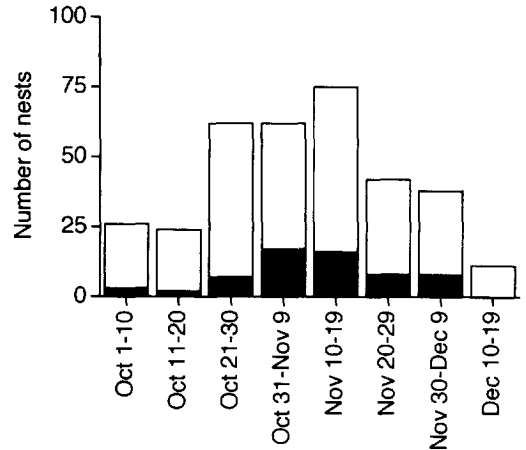

FIG. 1. Number of Brown-and-yellow Marshbird nests initiated by 10-day period (bars) and number of those nests that fledged chicks (black portion of the bars). Data correspond to 345 nests found during the 1993 to 1994 breeding seasons.

dation accounted for 76.9% ($n = 256$) of nest losses, 16.5% of which ($n = 42$) were attributed to large mammals. Sixty-six nests (15.8%) were abandoned, in most cases after the loss of several eggs. In 10 cases, nests were abandoned after being knocked down by heavy winds.

The breeding season of Brown-and-yellow Marshbirds lasted from late September through mid-December, with most nesting attempts occurring in November (Fig. 1). We estimated nesting success and daily survival rates from nests found during the building or laying stages ($n = 289$). Daily survival rates differed among months (October, 0.942 $\pm$ SD of 0.009; November, 0.973 $\pm$ 0.004; December, 0.959 $\pm$ 0.009; $T = 13.99$, df = 2, $P < 0.001$, $\chi^2 = 13.47$, df = 2, $P < 0.005$). Survival rates were lower in nests that started in October than in those started in November and December ($\chi^2 = 11.2$, df = 1, $P < 0.005$). Likewise, nests that started in November had a higher daily survival rate than those that started in October or December ($\chi^2 = 10.84$, df = 1, $P < 0.005$).

Brood parasitism occurred in 189 nests (65.4%), and chicks fledged from 38 nests (13.1%). The remaining nests were abandoned or preyed upon (Table 1). Nesting success did not differ between nonparasitized (11/100) and parasitized (27/189) nests (Fisher exact test, $P = 0.47$). Among the successful parasitized nests, 10 fledged only Brown-and-yellow

TABLE 1. Number of nest losses from predation or desertion relative to nesting stage and nest parasitism in Brown-and-yellow Marshbird nests. Data are from 100 nonparasitized nests (11 successful and 89 unsuccessful) and 189 parasitized nests (27 successful and 162 unsuccessful) that were found during the building or laying stages.

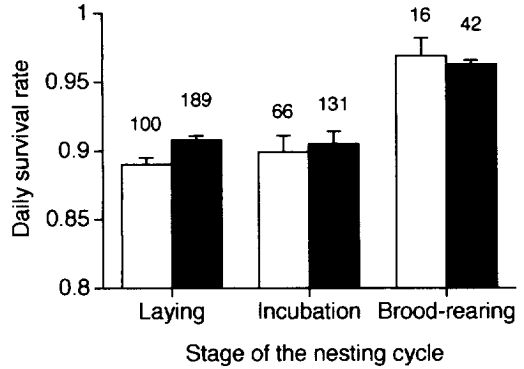| Nesting stage	Nonparasitized		Parasitized	
	Depredated	Deserted	Depredated	Deserted
Building	—	—	0	2
Laying	27	7	46	10
Incubation	38	12	57	32
Brood rearing	4	1	13	2

FIG. 2. Daily survival rate ($\pm$ SD) at different stages of the nesting cycle for nonparasitized (empty bars) and parasitized (black bars) Brown-and-yellow Marshbird nests. Numbers above bars indicate sample sizes.

Marshbird chicks, 5 fledged only Shiny Cowbird chicks, and 12 fledged chicks of both species. The numbers of nonparasitized and parasitized nests that were depredated or abandoned at different stages of the nesting cycle are shown in Table 1. Two nests were abandoned during the building stage as a consequence of early multiple parasitism. For statistical analysis, we grouped these nests with parasitized nests deserted during the laying stage. The frequency of nest predation and nest desertion did not differ between nonparasitized and parasitized nests (building and laying, G = 0.33, df = 2, P = 0.89; incubation, G = 3.48, df = 2, P = 0.17; brood rearing, G = 0.23, df = 2, P = 0.89). Likewise, DSR did not differ between nonparasitized and parasitized nests within the same nesting stage (Johnson statistic = −0.63, −0.49, and 0.33 for the laying, incubation, and brood-rearing stages, respectively; P > 0.5 for all comparisons; Fig. 2). DSRs were lower during the laying and incubation stages than during the brood-rearing stage, both in nonparasitized (Johnson statistic = 3.28 for laying vs. brood rearing and −3.46 for incubation vs. brood rearing; P < 0.001; Fig. 2) and in parasitized nests (Johnson statistic = 3.61 for laying vs. brood rearing and −4.03 for incubation vs. brood rearing; P < 0.0004). Given a laying period of 4.3 days, an incubation period of 13 days, and a brood-rearing period of 11 days (see Methods), the average probability of a nest surviving the entire nesting period was 0.133.

We detected a significant effect of nest site (i.e. plant species as substrate) on nesting success. Because of the small sample size for nests built in pampa grasses (n = 3), we grouped these nests with those built in black rushes (n

= 23). Nesting success was 11% for nests built in thistles and 33.3% for nests built in black rushes or pampa grasses (29/263 vs. 9/26; Fisher exact test, P = 0.003). This effect was also observed when we restricted the analysis to nests found during the building stage (10/126 vs. 8/18; Fisher exact test, P = 0.0002). The number of nests in black rushes or pampa grasses found during building or laying that reached incubation or brood rearing was less than 20, so we added exposure data of nests found during the incubation stage for the analysis of DSRs (Hensler and Nichols 1981). Nests built in black rushes or pampa grasses had higher DSR during the laying, incubation, and brood-rearing stages than those built in thistles (Johnson statistic = 3.22, 1.96, and 2.27, respectively; $P \leq 0.02$ in each case; Fig. 3). The average probability that a nest survived the entire nesting period was 0.08 in thistles and 0.297 in black rushes or pampa grasses.

For nests built in thistles, DSR was lower during the laying and incubation stages than during the brood-rearing stage (Johnson statistic = −4.6 and −4.9, respectively; P < 0.002 in both cases). Similarly, DSR for nests built in black rushes or pampa grasses was lower during the incubation stage than during the brood-rearing stage (Johnson statistic = −2.75, P = 0.006).

DISCUSSION

Nesting success in Brown-and-yellow Marshbirds was notably lower than the average values
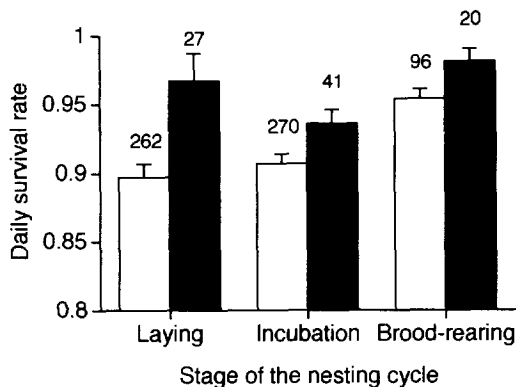
FIG. 3. Daily survival rate (± SD) at different stages of the nesting cycle for Brown-and-yellow Marshbird nests built in thistles (empty bars) and black rushes and pampa grasses (black bars). Numbers above bars indicate sample sizes.

for 49 Neartic species that build open nests in shrubs, grasslands, and marshes (i.e. 41%; Martin 1995) or for open nesters in the humid Neotropics (40%; Skutch 1985). This low nesting success is not exclusive for this species, because similar values were found for two other open-nesting blackbird species that inhabit marshes near our study area. Nesting success of the colonial Yellow-winged Blackbird (*Agelaius thilius*) was 14.5% (Massoni and Reboreda 1998), and nesting success of the territorial Scarlet-headed Blackbird (*Amblyramphus holosericeus*) was 12.8% (Fernández and Mermoz unpubl. data).

The low nesting success that we estimated for Brown-and-yellow Marshbirds could be because some individuals may have been included more than once in the same year owing to renesting attempts. These putative repeat nests could not be identified because birds were not banded, and this species is not territorial. Because of the possible effect of renesting attempts, unsuccessful pairs might have occurred more often in our sample of nests than individuals whose first clutches were successful. Therefore, our DSR estimate must be considered strictly as the daily survival probability of an average nest (Johnson 1979, Hensler and Nichols 1981).

One explanation for the differences between our results and those reported by Skutch (1985) and Martin (1995) is that most of the estimates reported in those studies were calculated using the apparent estimator (i.e. successful nests/ total nests found). These values could be over-

estimates of nesting success if nests are found after the first day of the nesting attempt (Mayfield 1975, Johnson 1979, Hensler and Nichols 1981).

We observed an effect of laying date (by month) on nesting success of Brown-and-yellow Marshbirds. In most bird species, reproductive success declines through the breeding season (Perrins 1970, Hochachka 1990, Nilsson 1994, Verhulst et al. 1995). In contrast, nesting success in Brown-and-yellow Marshbirds was higher in nests initiated in November (midseason) than in those initiated in October (early season) or December (late season). One interpretation for this result could be that during November (when most nests were initiated), nest defense is enhanced by the presence of neighbors (Clark and Robertson 1979, Robinson 1985). This hypothesis would also explain the drastic decline in nesting success during the second half of December, when there was a notable decrease in the number of active nests.

Nest predation and nest desertion were similar in nonparasitized and parasitized nests throughout the nestling cycle. A few cases of nest desertion were associated with the puncture of several eggs by the nest parasite and with the occurrence of multiple parasitism before the laying of the first marshbird egg. Otherwise, we did not observe nest abandonment as a consequence of the presence of parasitic eggs. Our results indicate that neither the event of parasitism nor the presence of a parasite's egg substantially increased the probability of nest failure. We also did not observe an effect of the presence of a Shiny Cowbird chick on nest predation probability, as suggested by Hudson (1874, Gochfeld 1979).

Nests in black rushes and pampa grasses had an average nesting success (33.3%) that was three times higher than nests in thistles. This value is similar to those reported for two Neartic marshbirds (30.7% in Red-winged Blackbirds [*Agelaius phoeniceus*] and 30% in Yellow-headed Blackbirds [*Xanthocephalus xanthocephalus*]; Martin 1995). The lower success for nest placed in thistles could be attributed in part to the fragility of these plants. All nests that fell (i.e. were blown) from their substrates were built in thistles, whereas none of the nests built in black rushes or pampa grasses were deserted as a consequence of weather conditions. Predation also was higher in nests built in this-

tles. This different pattern of nest predation could be the result of the different spatial distribution of plants. Thistles usually grow in clumps, forming hedges along the sides of unpaved secondary roads (i.e. higher places). Black rushes and pampa grasses also are clumped, but they are not associated with road edges. Therefore, nests built in thistles could be detected more easily by predators that travel along roads as they search for prey items (Camp and Best 1994). The use of thistles may reflect recent changes in the availability of nest sites for Brown-and-yellow Marshbirds. The first studies of this species (Gibson 1918, Hudson 1920) reported that nests were found mainly in young *Celtis tala,* bushes, and pampa grasses. These plant species declined sharply throughout the "flooding pampas" as a consequence of habitat transformation, mainly for livestock grazing (Vervoost 1967). At present, our study area contains no young *Celtis tala* or shrubs, and black rushes and pampa grasses are approximately 50 times less abundant than thistles. However, because many black rushes and pampa grasses were not used in all years, the use of thistles could not be explained exclusively as a consequence of a shortage of other nest sites.

Regardless of substrate, nests were less vulnerable to loss during brood rearing than during the earlier nesting stages. The increase in daily survival rate over the nesting cycle could be the result of some nests being more visible to predators and therefore more likely to be detected by them earlier in the nesting cycle. Alternatively, this result could be related to the presence of helpers at the nest in this cooperative-breeding species. Adult Brown-and-yellow Marshbirds are very aggressive, and parents and helpers routinely mob nest predators (Mermoz 1996). Roughly 50% of the nests, whether built in thistles or black rushes, appear to have helpers (i.e. more than two adults mobbed us during nest visits). Helpers may become associated with the nest during the incubation stage, but the number of helpers increases after hatching (Orians et al. 1977, Mermoz 1996). Accordingly, nest attendance increased as the nesting stages progressed from egg laying through brood rearing. During egg laying and incubation, three or more adults often attended the nest, but they usually arrived and departed together, leaving the nest unat-

tended. In contrast, nests seldom were left unattended during the brood-rearing period (Mermoz 1996).

Nest predation has been suggested as a selective force that could affect life-history traits such as clutch size (Skutch 1949; Martin 1995, 1996). Under this view, small clutch sizes would be favored in species with high rates of nest predation. The high nest-predation rate we observed in Brown-and-yellow Marshbirds does not support this hypothesis. The modal clutch size of Brown-and-yellow Marshbirds is 4 to 5 eggs (Mermoz 1996), which is higher than clutch sizes of other temperate South American marshbirds: Yellow-winged Blackbird, 3 eggs (Massoni and Reboreda 1998); Chestnut-capped Blackbird (*Agelaius ruficapillus*), 3 eggs (Klimaitis 1973); and Scarlet-headed Blackbird, 3 eggs (Fernández and Mermoz unpubl. data).

The presence of helpers in Brown-and-yellow Marshbird nests increases the number of food deliveries and therefore could increase the number of chicks that can be reared. Thus, in agreement with Lack's (1968) hypothesis, the high clutch size in this species might be related to the maximum number of chicks that can be raised rather than to the high rate of nest predation that it suffers. However, the high rate of predation in Brown-and-yellow Marshbirds may not be indicative of the selective pressures that this species has experienced in the past. As mentioned above, the low nesting success in our sample was mainly due to the use of thistles, an exotic species introduced in the eighteenth century (E. Rapoport pers. comm.). If predation rates in native plant species like pampa grasses and black rushes are indicative of historical rates, then nesting success in this species would be higher. If so, both higher levels of food delivery to the nest (Lack 1968) and lower predation pressure (Skutch 1949; Martin 1995, 1996) could have influenced clutch size in Brown-and-yellow Marshbirds.

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Associate Editor: L. J. Petit