

Effects of nest-site characteristics and parental activity on cowbird parasitism and nest predation in Brown-and-yellow Marshbirds

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ABSTRACT. Nest-site selection and nest defense are strategies for reducing the costs of brood parasitism and nest predation, two selective forces that can influence avian nesting success and fitness. During 2001–2002, we analyzed the effect of nest-site characteristics, nesting pattern, and parental activity on nest predation and brood parasitism by cowbirds (*Molothrus* spp.) in a population of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*) in the Buenos Aires province, Argentina. We examined the possible effects of nest detectability, nest accessibility, and nest defense on rates of parasitism and nest predation. We also compared rates of parasitism and nest predation and nest survival time of marshbird nests during the egg stage (active nests) with those of the same nests artificially baited with passerine eggs after young fledged or nests failed (experimental nests). Most nests (45 of 48, or 94%) found during the building or laying stages were parasitized, and 79% suffered at least one egg-predation event. Cowbirds were responsible for most egg predation, with 82 of 107 (77%) egg-predation events corresponding to eggs punctured by cowbirds. Nests built in thistles had higher rates of parasitism and egg predation than nests in other plant, probably because cowbirds were most active in the area where thistles were almost the only available nesting substrate. Parasitism rates also tended to increase as the distance to conspecific nests increased, possibly due to cooperative mobbing and parental defense by marshbirds. The proportion of nests discovered by cowbirds was higher for active (95%) than for experimental (29%) nests, suggesting that cowbirds used host parental activity to locate nests. Despite active nest defense, parental activity did not affect either predation rates or nest-survival time. Thus, although nest defense by Brown-and-yellow Marshbirds appears to be based on cooperative group defense, such behavior did not reduce the impact of brood parasites and predators.

RESUMEN. Efectos de las características del sitio de nidificación y actividad parental en el parasitismo de cría por tordos y depredación de nidos en *Pseudoleistes virescens*

La selección del sitio de nidificación y defensa del nido son estrategias que reducen los costos del parasitismo de cría y depredación de nidos, dos fuerzas selectivas que pueden afectar el éxito reproductivo y la eficacia biológica de las aves. Durante 2001–2002, analizamos el efecto de las características del sitio de nidificación, patrón de nidificación, y actividad parental en la depredación de nidos y parasitismo de cría por tordos (*Molothrus* spp.) en una población de *Pseudoleistes virescens* en la provincia de Buenos Aires, Argentina. Examinamos los posibles efectos de la detectabilidad, accesibilidad y defensa del nido en las tasas de parasitismo y depredación de nidos. Asimismo, se compararon las tasas de parasitismo, depredación, y tiempo de supervivencia de los nidos entre los estadios de huevo (nidos activos) con los de los mismos nidos cebados artificialmente con huevos de passerinos (nidos experimentales). La mayoría de los nidos (45 de 48, o 94%) hallados durante los estadios de construcción y puesta fueron parasitados, donde el 79% de los nidos sufrieron al menos un evento de depredación de huevos. Los tordos fueron responsables de la mayoría de los eventos de depredación de huevos, donde 82 de 107 (77%) eventos de depredación correspondieron a huevos picados por tordos. Los nidos construidos en cardos tuvieron tasas de depredación y parasitismo más altas que las correspondientes a nidos construidos en otros sustratos, probablemente debido a que los tordos exhiben una mayor actividad en el área donde los cardos son el único sustrato de nidificación disponible. La tasa de parasitismo mostró una tendencia a crecer con la distancia al nido más próximo, probablemente debido a la defensa parental y los despliegues de defensa comunales de *Pseudoleistes virescens*. La proporción de nidos descubiertos por tordos fue mayor para nidos activos (95%) que para nidos experimentales (29%), lo cual sugiere que los tordos utilizaron la actividad parental para detectar los nidos. A pesar de la activa defensa del nido, descubrimos que la actividad

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parental no afectó ni la tasa de predación ni el tiempo de supervivencia de los nidos. De esta forma, a pesar de que la defensa del nido en *Pseudoleistes virescens* aparenta estar basada en la defensa cooperativa grupal, tal comportamiento no redujo el impacto de los parásitos de cría o predadores de nidos.

Key words: concealment, egg losses, experimental nests, host activity, *Molothrus* spp., nest-searching method, partial nest predation

Strategies to reduce the costs of brood parasitism and nest predation include nest-site selection and nest defense (Montgomerie and Weatherhead 1988, Weidinger 2002). Nest-site characteristics can influence both nest detectability and accessibility by brood parasites and predators (Martin 1993, Cresswell 1997, Clotfelter 1998). For example, rates of parasitism and nest predation may increase with increasing nest visibility because poorly concealed nests are more easily found by parasites and predators (Martin and Roper 1988, Brittingham and Temple 1996, Burhans 1997).

Breeding adults can also distract and repel potential parasites and predators (Martin 1992). Birds that vigorously defend nests or perform group defense of nests, such as colonial birds or cooperative breeders, can exhibit high nesting success (Robinson 1985). However, parental activity may also attract parasites and predators to nests (Gill et al. 1997, Martin et al. 2000, Banks and Martin 2001; see also Sealy et al. 1998). For example, Brown-headed (*Molothrus ater*) and Shiny (*M. bonariensis*) cowbirds use host activity during nest building to find nests (Wiley 1988, Banks and Martin 2001).

Although several investigators have examined the effects of either parental activity or nest-site characteristics on rates of brood parasitism and nest predation, few have analyzed both factors simultaneously (Clotfelter 1998, Martin et al. 2000, Banks and Martin 2001, Weidinger 2002). However, an integrative analysis is recommended because, when considered separately, the results of partial analyses could produce biased or contradictory conclusions (Weidinger 2002). For example, the absence of any relationship between concealment and nest survival could indicate that vegetation cover has no effect of nest detectability or could be the result of an independent effect of parental defense (see Weidinger (2002) for a more detailed description concerning interactive effects between nest concealment and parental activity on nest survival).

Weidinger (2002) examined the interaction between parental behavior and nest-site selection in four open-nesting passerine species. Using experimental and natural nests, Weidinger (2002) concluded that larger species based their defense strategy against predators on effective and vigorous nest defense, whereas smaller species selected nest sites that minimized detection by predators. The effectiveness of nest defense may also depend on the nesting behavior of a species. Colonial or group-nesting species may benefit from cooperative defense against predators or brood parasites (Burger 1974, Wiklund and Anderson 1980, Poiani and Pagel 1997, Massoni and Reboreda 2001). Therefore, for species with clumped nesting, nest survival may depend primarily on parental nest defense.

Our objective was to evaluate the effects of nest-site characteristics and parental activity (presence vs. absence) of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*) on the ability of cowbirds and nest predators to detect nests. Brown-and-yellow Marshbirds are relatively large (80 g) and nest in grasses and small shrubs, with their open-cup nests typically 0.5–1.5 m above the ground and clutches usually consisting of four to five eggs (Orians et al. 1977, Mermoz and Reboreda 1994, 1998). These marshbirds have a cooperative breeding system, with helpers that assist in rearing young and defending nests against predators and brood parasites (Orians et al. 1977). In our study area, marshbirds are frequently parasitized by Shiny (*M. bonariensis*) and Screaming (*M. rufoaxillaris*) cowbirds (Mermoz and Reboreda 1999, Mermoz and Fernández 2003), and suffer high rates of nest predation (Mermoz and Reboreda 1999, Fernández and Mermoz 2000). We measured nest-site characteristics related to nest detectability, accessibility, nesting gregariousness, and nest defense to evaluate the relationships between these characteristics and rates of brood parasitism and nest predation. We also assessed the effect of parental activity on the probability of nest detection by cowbirds

and predators, comparing active marshbird nests to the same nests (once they were predated or abandoned) baited with artificial clutches (i.e., without parental care).

METHODS

Our study was conducted from October to December 2001–2002 near the town of General Lavalle (36°26'S, 56°25'W), Buenos Aires province, Argentina. This area is within the "flooding pampas," a flat region less than 4 m asl that includes marshes and humid grasslands (Soriano 1991). Open fields, used primarily for livestock grazing, surround the area. We searched for marshbird nests in a 13-km stretch of land bordering both sides of an unpaved road (Mermoz and Reboreda 1998, 1999). Nests were found by systematic nest searching and observing marshbird behavior.

Nest monitoring. Nests were checked daily during the laying and incubation (length = 13 d, Mermoz and Reboreda 1998) periods. Previous studies of this population revealed no effect of nest visitation on nest survival, with nests visited every 1–2 d having similar mortality rates as nests checked weekly (Mermoz and Reboreda 1998). We monitored nests until they were predated or young fledged. For each nest, we assigned an initiation date corresponding to the laying of the first marshbird egg and recorded the exposure time (in days) for both laying and incubation stages. We noted the number of cowbird eggs laid in each nest, and eggs were inspected during each visit to determine if any were missing or damaged. We considered eggs predated if missing, broken, or pecked. Eggs pecked by Shiny Cowbirds usually have one or more small punctures (Massoni and Reboreda 2002). Shiny Cowbirds do not remove eggs from host nests (Massoni and Reboreda 2002). Thus, for predated eggs, we unambiguously identified the subset of eggs lost by cowbird pecks.

Nest-site assessment. In 2001, we recorded the plant species in which each nest was built. Thistles were the most abundant plant substrate and most were located along the road. Because other substrates were less abundant and more broadly distributed, we categorized substrates as either thistles or other substrates. We also quantified visibility for each nest using a grid (15 × 15 cm) with 85 regularly spaced circles inside. This grid was placed

above nests and nest visibility estimated as the number of visible circles recorded in images taken with a digital camera (Sony Mavica FD-92, Sony Corporation, Tokyo, Japan). We estimated two visibility indices for each nest, with top visibility measured 1 m above nests and lateral visibility being the mean visibility from images taken 1 m from nests in four directions (northeast, southeast, southwest, and northwest). All visibility measures were recorded either during the incubation period or immediately after nests were predated.

Marshbirds calls induce collective mobbing behavior by conspecifics from nearby nests (Orians et al. 1977). Thus, we measured the distance from focal nests to the nearest active marshbird nest. Active neighbors were considered those that started egg laying within 2 d of the start-laying date of the focal nest (Westneat 1992). Distance to the nearest edge (distance to the nearest edge of the patch of vegetation of the same species as the nest substrate surrounding the nest) and nest height above the ground were also measured. Distance to the nearest road was also measured because roads, as linear edges of vegetation, could facilitate nest searching by predators and parasites (Gates and Gysel 1978, Brittingham and Temple 1983). Because parasitism and predation pressure could vary during the breeding season (Mermoz and Reboreda 1999), we included the start-laying day as another variable (with day 1 = 7 October 2001, the date when the first egg was laid in that breeding season). Most distance measurements were rounded to the nearest meter; nest height and distance to the nearest edge were measured to the nearest 0.05 m. For nests >100 m from the nearest active nest, distance was estimated using GPS coordinates.

Parental activity. We assessed the effect of parental activity (as presence or absence) by comparing parasitism and predation rates and nest survival time of marshbird nests attended by adults (hereafter active nests) with the same nests (after they were predated or abandoned) baited with artificial clutches (i.e., without parental care; hereafter experimental nests). Thus, differences between active and experimental treatments could be attributed to the presence or absence of parental activity. Experimental nests were left where built and baited with two fresh Shiny Cowbird eggs of the spotted morph that were similar in appearance to host eggs, but

slightly smaller (22.7×18.1 mm and 26.0×19.1 mm for Shiny Cowbird and Brown-and-yellow Marshbird eggs, respectively; Mermoz and Reboresda 1994). We baited 25 experimental nests (14 in 2001 and 11 in 2002) at least 10 days after the particular nesting attempt had finished.

To assess for a possible reuse effect (i.e., nest odors or predator memory), we also baited 10 marshbird nests that were completely built, but abandoned before egg laying (hereafter, unused nests). We avoided the use of experimental and unused nests less than 50 m from the nearest active nest. Experimental and unused nests were checked for 12 consecutive days or until predated. All nests were checked daily.

Finally, the hypothesis that cowbirds use host activity to locate nests was tested by comparing the proportion of active and experimental treatments nests discovered by cowbirds. We considered the presence of either parasite eggs or eggs punctured by cowbirds as evidence that cowbirds had discovered a nest.

Data analysis. For nests found during building or egg laying, parasitism intensity was calculated by determining the number of cowbird eggs laid in them during the marshbird egg-laying period. To avoid underestimating parasitism intensity, we only considered nests with at least two days of exposure at laying. During the laying and incubation stages, we determined the number of egg-predation events, that is, the number of times nests lost at least one egg (either host or parasite).

To evaluate the relationship between nest-site characteristics and the intensity of parasitism and egg predation, we used generalized linear models with the Poisson error structure and log-link function (Crawley 2007). Models were evaluated and parameter values estimated using information-theoretic procedures (Burnham and Anderson 1998, Crawley 2007). This method allows model uncertainty to be included in both model evaluation and derivation of parameter estimates (Burnham and Anderson 1998). Therefore, inferences were not based on a model or set of models, but relative strength of parameter estimates derived from all models were used (Esler *et al.* 2001, Folk and Hepp 2003). Models with all possible combinations of predictor variables were considered because there was no a priori basis to eliminate models. Size of candidate models (measured as the number of parameters to be

estimated) must be related to the amount of data and information available (Burnham and Anderson 1998). Thus, due to sample size ($N = 48$ and $N = 66$ for parasitism intensity and number of egg-predation events, respectively), our analyses were restricted a priori to models containing up to three predictors as maximum. This resulted in 94 candidate models, with 92 models corresponding to all possible combinations of eight predictors including up to three predictors per model, one fully specified general model with all predictors (global model) and a base model without predictors (null model). A null model was useful for assessing the relative explanatory power of models containing predictors of interest. We assessed goodness of fit for global models and estimated the variance inflation factor ($\hat{\epsilon}$) as residual deviance divided by degrees of freedom (Burnham and Anderson 1998). As Hazler (2004) noted, if $\hat{\epsilon} > 1$ (even if it is not significant), it should be used to adjust the standard errors of the estimates. Thus, Akaike's information criterion corrected for $\hat{\epsilon}$ and small sample size (QAICc) was calculated for each model (Burnham and Anderson 1998). Model comparisons were made with ΔQAICc , which is the difference between the lowest QAICc value (i.e., best of suitable models) and QAICc from all other models. Models with $\Delta\text{QAICc} \leq 2$ have substantial support from the data (Burnham and Anderson 1998). The QAICc weight of a model (w_i) signifies the relative likelihood that the specific model is the best of the suite of all models. To evaluate support for estimates of predictor variables, QAICc model weights were summed across all models that contained the parameter being considered (parameter likelihood; Burnham and Anderson 1998). Parameters with good support have high parameter likelihood values (near 1). Parameter estimates were calculated using model-averaged parameter estimates based on QAICc model weights for all candidate models. Unconditional variances were used to calculate standard errors (Burnham and Anderson 1998). To supplement parameter likelihood evidence of important effects, we also calculated 95% confidence intervals of parameter estimates. Upper and lower confidence limits intervals were calculated by adding or subtracting $2 \times \text{SE}$, respectively (Burnham and Anderson 1998). Nest-exposure time was neither related to parasitism intensity nor to egg-predation events (likelihood

ratio tests: $\chi_1^2 = 1.9$, $P = 0.17$ and $\chi_1^2 = 1.3$, $P = 0.26$, respectively), so inclusion of nest-exposure time as an offset term was not justified in our analyses.

Parental activity. We compared the proportion of active and experimental nests that were parasitized or predated. Because cowbirds typically parasitize marshbird nests during egg laying (Mermoz and Reboresda 1999), we only included nests with at least two exposure days ($N = 21$ nests) to avoid underestimating levels of parasitism. A nest was considered predated if one or more eggs were lost or damaged (Zanette and Jenkins 2000), regardless of whether egg losses were caused by brood parasites or predators. Successful nests were those that were not predated. In addition, for each experimental and unused nest, we calculated nest-survival time as the time elapsed until it was either predated or observed for 12 d. Because our measure of nest survival time was right censored, the effect of parental activity on nest survival time was assessed by applying Cox Proportional Hazards regression with the Efron handling ties method (Therneau and Grambsch 2000, Kalbfleisch and Prentice 2002). Treatment (active, experimental, and unused) was included as a categorical variable. The plant species in which nests were built and laying date were included as covariates controlling for differences between nest substrates and possible seasonal variation; nest identity was included as a random effect to account for different risks between nests (Therneau and Grambsch 2000).

To control for any effect of reusing nests, we compared parasitism and predation rates and nest survival time of experimental and unused nests. Survival analyses met the proportional hazard assumption required by the Cox regression (Therneau and Grambsch 2000, Kalbfleisch and Prentice 2002). Finally, the proportion of nests losing at least one egg due to cowbird pecks was compared between treatments. The proportion of predated nests and nests suffering egg loss by cowbird pecks did not differ between 2001 and 2002 (M. E. Mermoz, unpubl. data), so we pooled data from both breeding seasons. Because of small sample sizes, we analyzed frequency data using a Fisher exact test, except for matched-pairs comparison of frequency data where the binomial test was used (Sokal and Rohlf 1995). Results are presented as mean \pm SE, and statistical tests

were considered significant at $\alpha = 0.05$. All tests were two-tailed unless otherwise indicated. All statistical analyses were carried out using R software (Version 2.5.1, R Development Core Team 2007).

RESULTS

Parasitism and predation. We found, monitored, and measured the characteristics of 66 marshbird nests in 2001, with 16 (24%) found during building, 32 (49%) during laying, and 18 (27%) during incubation. Forty nests (61%) were in thistles (*Cynara cardunculus*), 13 (20%) in black rushes (*Juncus acutus*), four (6%) in pampa grasses (*Cortaderia selloana*), and nine (13%) in other plants. Most nests (45/48, or 94%) found during the building or laying stages were parasitized, and the mean number of cowbird eggs per nest was 3.04 ± 0.31 (range = 0–10).

For 66 nests, we noted 107 egg-predation events, and at least one egg was predated in 52 (79%) nests. The mean number of egg-predation events per nest was 1.62 ± 0.15 (range = 0–4). Most predation was caused by cowbirds, with 82 (77%) egg-predation events corresponding to cowbird-punctured eggs. Two-thirds (44/66) of marshbird nests had at least one egg punctured by cowbirds. Indeed, parasitism intensity and number of egg-predation events were positively correlated ($r = 0.38$, $r^2 = 0.14$, $t = 2.8$, $N = 48$, $P = 0.008$).

Parasitism. The global model explaining parasitism intensity (number of cowbird eggs per marshbird nest) fit our data ($\chi_{39}^2 = 48.5$, $P = 0.14$), but the variance inflation factor ($\hat{c} = 1.24$) indicated slight overdispersion. None of the models with $\Delta\text{QAICc} \leq 2$ accounted more than 28% of the variation in parasitism intensity (Table 1A). The model that best described the variation in parasitism intensity included the substrate and distance to the nearest active marshbird nest as explanatory variables ($w_i = 0.085$; likelihood ratio test, comparison with the null model involving intercept only: $\chi_2^2 = 17.9$, $P = 0.0001$; Table 1A). These two variables were important predictors of parasitism intensity because both had high likelihood parameter values (Table 2A), being included in all models with $\Delta\text{QAICc} \leq 1$ (Table 1A). The substrate was the most important single predictor of parasitism intensity (confidence interval excluding zero,

Table 1. Generalized linear models explaining variation in (A) parasitism intensity and (B) number of egg-predation events. The null model, the global model, and models with strong support ($\Delta\text{QAICc} \leq 2$) are provided. Models are listed in decreasing order of importance.

Response variable	Model	Explanatory variables ^a	Number of parameters	ΔQAICc	QAICc weight	R^2
(A) Parasitism intensity $N = 48$	1	SUBS NEAR	3	0.0	0.085	0.253
	2	SUBS NEAR HEIG	4	0.9	0.054	0.279
	3	SUBS NEAR PATD	4	1.0	0.053	0.278
	4	SUBS	2	1.2	0.047	0.192
	5	SUBS PATD	3	1.9	0.033	0.219
	6	SUBS NEAR ROAD	4	2.0	0.031	0.259
	Null	–	1	9.9	0.000	–
Global	All variables	9	12.6	0.000	0.315	
(B) Egg-predation events $N = 66$	1	SUBS LAYD	3	0.0	0.082	0.140
	2	SUBS	2	0.4	0.068	0.102
	3	LAYD	2	1.0	0.050	0.093
	4	SUBS NEAR	3	1.7	0.034	0.114
	5	SUBS ROAD LAYD	4	1.8	0.033	0.146
	6	SUBS LATV	3	1.9	0.032	0.112
	7	SUBS LATV LAYD	4	1.9	0.031	0.145
	Null	–	1	5.1	0.006	–
Global	All variables	9	13.7	0.000	0.157	

^aSUBS = substrate (thistle or not thistle), TOPV = superior visibility, LATV = lateral visibility (see the text for details), NEAR = distance to the nearest simultaneously active Brown-and-yellow Marshbird nest, PATD = distance to nearest patch-edge of homogeneous vegetation, HEIG = nest height, ROAD = distance to unpaved road, and LAYD = julian date of laying initiation.

Table 2A), accounting for 19% of the variation (Table 1A). Cowbirds laid more eggs ($\chi_1^2 = 13.6$, $P = 0.0002$) in nests built in thistles ($\bar{x} = 3.64 \pm 0.39$ eggs per nest, $N = 33$) than in nests in other substrates ($\bar{x} = 1.73 \pm 0.25$, $N = 15$).

Although parasitism intensity tended to be positively related to the distance to the nearest active marshbird nest (increasing as distance increased), the 95% confidence interval of parameter estimate encompassed zero (Table 2A). The relationship between parasitism intensity and distance to the nearest active nest may have been influenced by the plant substrate where nests were built (e.g., if nests in thistles were closer to conspecific nests than those in other substrates). However, this distance did not differ (Mann–Whitney two-tailed U -test, $U = 510.5$, $P = 0.83$) between thistles (median = 76 ± 33 m, $N = 39$) and other substrates (median = 88 ± 35 m, $N = 27$). Thus, the relationship between parasitism intensity and distance to the nearest active nest was not a byproduct of the substrate. As indicated by low parameter likelihood values and confidence intervals including

zero, other explanatory variables were not related to parasitism intensity (Table 2A).

Egg predation. The global model describing the number of egg-predation events was well fitted to our data ($\hat{c} = 1.12$; $\chi_{57}^2 = 63.7$, $P = 0.25$). Nest-site characteristics were poor descriptors of egg predation, with none of the models with $\Delta\text{QAICc} \leq 2$ accounting for more than 15% of the variation (Table 1B). The best model accounting for the variation in egg-predation events included the substrate and start-laying date as explanatory variables ($w_i = 0.082$; likelihood-ratio test, comparison with the null model involving intercept only: $\chi_2^2 = 10.6$, $P = 0.005$; Table 1B). The substrate was the most important predictor (confidence interval excluding zero, see Table 2B), being included in six of the seven best models ($\Delta\text{QAICc} \leq 2$; Table 1B). The mean number of egg-predation events for nests in thistles (1.97 ± 0.19 , $N = 39$) was higher ($\chi_1^2 = 7.7$, $P = 0.006$) than for nests in other substrates (1.11 ± 0.21 , $N = 27$). Although egg predation also exhibited a tendency to be positively related to start-laying date (increasing as breeding season progressed),

Table 2. Parameter estimates (\pm SE) from generalized linear models describing variation in (A) parasitism intensity and (B) number of egg-predation events. Parameter likelihoods are QAICc weights summed across all models that contained the parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using model QAICc weights) from all models, and standard error (SE) is calculated from all candidate models using unconditional variances. Upper and lower confidence limits intervals (95%) were calculated by adding or subtracting $2 \times$ SE, respectively. Explanatory variables with confidence intervals excluding zero are shown in bold font. Explanatory variables are listed in decreasing order of importance.

Response variable	Explanatory variable ^a	Parameter likelihood	Parameter estimate \pm SE	Confidence interval	
				Lower	Upper
(A) Parasitism intensity <i>N</i> = 48	Intercept		0.6230 \pm 0.4399	-0.2568	1.5027
	SUBS	0.683	0.6585 \pm 0.3059	0.0466	1.2703
	NEAR	0.455	0.0008 \pm 0.0004	-4.6E-05	1.6E-03
	ROAD	0.315	0.0147 \pm 0.0100	-5.2E-03	3.5E-02
	PATD	0.280	-0.0030 \pm 0.0024	-7.8E-03	1.7E-03
	HEIG	0.259	-0.0117 \pm 0.0124	-3.6E-02	1.3E-02
	TOPV	0.179	-0.0056 \pm 0.0149	-3.5E-02	2.4E-02
	LATV	0.171	0.0072 \pm 0.0060	-4.8E-03	1.9E-02
	LAYD	0.163	0.0052 \pm 0.0075	-9.9E-03	2.0E-02
(B) Egg-predation events <i>N</i> = 66	Intercept		0.0063 \pm 0.3507	-0.6951	0.7077
	SUBS	0.658	0.5682 \pm 0.2829	0.0025	1.1340
	LAYD	0.534	0.0150 \pm 0.0081	-1.2E-03	3.1E-02
	NEAR	0.205	0.0004 \pm 0.0005	-6.5E-04	1.4E-03
	ROAD	0.201	0.0031 \pm 0.0121	-2.1E-02	2.7E-02
	TOPV	0.195	-0.0016 \pm 0.0052	-1.2E-02	8.7E-03
	LATV	0.191	-0.0043 \pm 0.0126	-3.0E-02	2.1E-02
	PATD	0.164	0.0000 \pm 0.0022	-4.3E-03	4.3E-03
	HEIG	0.162	-0.0005 \pm 0.0053	-1.1E-02	1.0E-02

^aSUBS = substrate (thistle or not thistle), TOPV = superior visibility, LATV = lateral visibility (see the text for details), NEAR = distance to the nearest simultaneously active Brown-and-yellow Marshbird nest, PATD = distance to nearest patch-edge of homogeneous vegetation, HEIG = nest height, ROAD = distance to unpaved road, and LAYD = julian date of laying initiation.

the 95% confidence interval encompassed 0 (Table 2B), suggesting no effect of laying date on predation events. Moreover, the median start-laying date differed between thistles and other substrates (Mann-Whitney two-tailed *U*-test, *U* = 294.0, *P* = 0.002), with marshbirds nesting in thistles starting egg laying, on average, 12 days later in the season (median date: 8 November 2001, *N* = 39) than those nesting in other substrates (median date: 27 October 2001, *N* = 27). Thus, the relationship between egg predation and start-laying date was probably a byproduct of the plant substrate where nests were built. No other explanatory variable was related to the number of egg-predation events (Table 2B).

Effect of parental activity. Experimental nests (2 of 21, or 10%) were less likely to be parasitized than active nests (20 of 21, or 95%; one-tailed binomial test, *P* < 0.0001).

Parasitism rates for experimental and unused nests did not differ (unused nests: 20%, 2/10; Fisher exact test, *P* = 0.18). Four artificially baited nests were parasitized by Shiny Cowbirds.

Predation rates for active and experimental nests (16/25 in both cases; binomial test, *P* = 1.0) and for experimental and unused nests (unused nests: 8/10; Fisher exact test, *P* = 0.45) did not differ. In addition, we found no difference in nest survival times of either active (5.74 ± 0.94 days) and experimental (4.68 ± 0.76 days) nests (Cox Proportional Hazards regression, *N* = 25; *z* = 0.0, *P* = 0.98) or experimental and unused nests (unused nests: 4.40 ± 1.21 days, *N* = 10; *z* = 0.3, *P* = 0.78). The proportion of active and experimental nests that lost at least one egg due to cowbird pecking did not differ (9/21 vs. 5/21, respectively; one-tailed binomial test, *P* = 0.17). Experimental and unused nests did not differ in the proportion that lost eggs due

to cowbird pecking (unused nests: 4/10; Fisher exact test, $P = 0.42$).

Nest searching by cowbirds. Twenty of 21 active nests (95%) were parasitized by cowbirds. Cowbirds discovered 6 of 21 (29%) experimental nests. Four nonparasitized nests had punctured eggs, one nest without punctured eggs was parasitized, and one nest was parasitized and had punctured eggs. Therefore, the proportion of nests discovered by cowbirds was higher for active than for experimental nests (one-tailed binomial test, $P < 0.0001$). The proportion of experimental and unused nests discovered by cowbirds did not differ (unused nests: 4/10; Fisher exact test, $P = 0.69$).

DISCUSSION

Cowbirds parasitized 94% of Brown-and-yellow Marshbird nests in our study and were responsible for at least 77% of the egg-predation events. Indeed, this is probably an underestimate because hosts may have removed punctured eggs from nests before nest inspection (Mermoz 1996). Similarly high rates of parasitism and loss of eggs due to cowbirds have been reported by other investigators in our study area (Mermoz and Reboreda 1998, Fernández and Mermoz 2000, Svagelj et al. 2003).

Levels of parasitism and egg predation in our study were higher for marshbird nests in thistles than for nests in other substrates. Although not quantified, our observations indicated that cowbird activity was highest along the road where thistles were almost the only available nesting substrate. Indeed, distance to the unpaved road was inversely related to parasitism intensity ($\chi^2_1 = 10.7$, $P = 0.001$) when the nest substrate was excluded from the analysis. Other studies have also revealed that the frequency and intensity of cowbird parasitism are related to cowbird density at both local (Brittingham and Temple 1983, Goguen and Mathews 2000) and regional (McGeen 1972, Hoover and Brittingham 1993) scales. Burhans (1997) noted that the effects of nest-site characteristics on parasitism may be less important than differences in cowbird density or abundance. Therefore, the lack of a relationship between most nest-site characteristics and parasitism intensity could be due to differences in cowbird densities and habitat preferences in our study area.

Parasitism levels in our study tended to increase as the distance to conspecific nests increased. Brown-and-yellow Marshbirds defend nests vigorously against brood parasites and potential predators (Mermoz 1996). Freeman et al. (1990) proposed that aggregated (in time and space) nests may provide an antiparasitic advantage arising from group defense. Other investigators have also found that rates of brood parasitism increased with distance to nearest neighbors and decreased with host density (Westneat 1992, Clotfelter and Yasukawa 1999, Massoni and Reboreda 2001). Thus, group defense may have reduced levels of cowbird parasitism in our study. Nearest distance to neighbors, however, did not affect egg-predation rates, suggesting that cooperative mobbing may not be an efficient strategy for avoiding predation.

Although activity at nests may influence detection by brood parasites and predators (Skutch 1949, Martin et al. 2000), we found no differences between active and experimental nests in predation rates, nest-survival time, and the proportion of nests with eggs punctured by cowbirds. So, the net effect of parental activity in nest detection by cowbirds and predators was neutral, regardless of vigorous nest defense by marshbirds against parasites and potential predators. Previous studies on comparable species with relatively high potential for nest defense have produced contrasting results. Cresswell (1997) found no differences between active and experimental nests in predation rates (i.e., neutral influence of parental activity) in Blackbirds (*Turdus merula*). In contrast, Weidinger (2002) found a positive net effect of parental activity for both Song Thrushes (*T. philomelos*) and Blackbirds, with active nests surviving better than experimental nests. In our study, parental behavior of marshbirds apparently did not affect nest detection by predators or cowbirds. However, the neutral effect of parental activity may also be a consequence of the combination of positive (parental defense) and negative (nest disclosure) effects of parental activity, with positive and negative effects offsetting each other (Martin et al. 2000, Weidinger 2002).

Female cowbirds may not require the presence of adult hosts, but may locate nests by searching a habitat (Thompson and Gottfried 1981, Wiley 1988). In our study, cowbirds found 32% (10/31) of nests without marshbird activity. However, cowbirds also find nests by watching

host behavior, especially during nest building (Norman and Robertson 1975, Wiley 1988, Banks and Martin 2001). In our study, 95% of active nests were found by cowbirds and only 29% of these same nests were found when there was no parental activity, indicating that cowbirds use host activity to find nests. In addition, such activity may determine whether a nest is actually parasitized. For example, we found that cowbirds discovered 32% of nests without host activity, but only 13% (4/31) were parasitized. Similarly, Fiorini and Rebores (2006) found that Shiny Cowbirds located nests without host activity, but the decision to parasitize a nest depended on host activity.

In summary, nest concealment did not affect rates of parasitism or nest predation for Brown-and-yellow Marshbirds. Instead, nest defense appears to be based on cooperative group defense. However, such defense did not reduce the impact of brood parasites and predators. Furthermore, although cooperative defense could deter parasites and predators, increased activity at the nest would disclose nest location. Indeed, cowbirds used parental activity at the nests of Brown-and-yellow Marshbirds as the main cue to locate nests. This fact, in addition to the apparently high density of cowbirds and predators in our study area, appears to be the main factor explaining rates of brood parasitism and nesting success of Brown-and-yellow Marshbirds. Further studies evaluating the cues used by brood parasites and predators to find nests could improve our understanding of their effects on the nesting success of Brown-and-yellow Marshbirds.

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