

# Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by shiny cowbirds on chalk-browed mockingbirds

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## Summary

We investigated the association between brood parasitism by shiny cowbirds (*Molothrus bonariensis*), and behaviour and nest-site characteristics of chalk-browed mockingbirds (*Mimus saturninus*). This host builds nests on trees, it is aggressive against intruders and it is larger than shiny cowbirds. We conducted focal observations of mockingbird nests, and registered mockingbird activity and attentiveness around the nest. To characterize nest sites, we measured nest cover, nest height, and distance from the nest to the closest perch, and included host laying date and year as additional predictor variables. We also evaluated experimentally host agonistic behaviours directed towards a female cowbird and a control model, and the association between aggressive behaviour and parasitism. Nest attentiveness, nest cover and laying date were associated with parasitism. These results contradict the host-activity hypothesis, because more attentive pairs were less parasitized, and the nest-exposure hypothesis, because more concealed nests were more parasitized. Experiments showed that unparasitized pairs were more aggressive against cowbird models than were parasitized ones. Our findings indicate that shiny cowbirds prefer to parasitize more concealed nests, where they could lay undetected by the host, and that mockingbird nest attentiveness and aggression towards cowbirds are effective first lines of defence against brood parasitism.

**Keywords:** brood parasitism, host behaviour, *Molothrus bonariensis*, *Mimus saturninus*, nest-site characteristics.

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## Introduction

Brood parasitism generally has significant costs to host fitness (Payne, 1977; Rothstein, 1990; Ortega, 1998; Rothstein & Robinson, 1998; Davies, 2000; Krüger, 2007) and, thus, exerts a strong selective pressure on host species to evolve antiparasite defences (Davies & Brooke, 1988; Sealy, 1996). Because parasites must find host nests in which to lay their eggs, one antiparasite defence would be to select nest sites that are difficult to find. A second defence would be to avoid giving behavioural cues that allow parasites to find nests (Sealy et al., 1998).

There has been considerable effort to identify cues and search modes that brood parasites use to find nests (Thompson & Gottfried, 1981; Gill et al., 1997; Clotfelter, 1998; Teuschl et al., 1998; Moskát & Honza, 2000; Banks & Martin, 2001; Antonov et al., 2007). A major motivation to understand which cues are used by brood parasites in locating host nests are frequent observations that brood parasitism is not random within and across host populations (Lindholm, 1999; Krüger, 2007). Such non-random parasitism has been widely documented for host nest-site characteristics (Øien et al., 1996; Grim, 2002). Røskoft et al. (2002) found that the host breeding habitat explains the rate of parasitism by the common cuckoo (*Cuculus canorus*) and Hauber (2001) found that brown-headed cowbirds (*Molothrus ater*) preferentially parasitize eastern phoebe (*Sayornis phoebe*) nests under eaves versus those under bridges. Other characteristics such as host age and/or experience (Brooker & Brooker, 1996), host quality (Soler et al., 1995), and host behaviours around nests (Clotfelter, 1998) also affect the probability of parasitism.

There are at least four non-exclusive hypotheses for mechanisms and cues used by parasites to find host nests (Clotfelter, 1998; Hauber & Russo, 2000). The host-activity hypothesis states that vocal and visible activities of hosts attract brood parasites and thereby increase probability of parasitism (Uyehara & Narins, 1995; Banks & Martin, 2001). The nesting-cue hypothesis asserts that parasites use nest-defence responses by hosts directed towards them as a cue to locate hosts' nests. Thus, hosts that respond more aggressively towards parasites would be parasitized more often than less aggressive ones (Robertson & Norman, 1976, 1977; Smith et al., 1984). The nest-exposure hypothesis proposes that brood parasites find more easily those host nests that are visually conspicuous. According to this hypothesis, nests with little cover are more likely to be parasitized (Larison et al., 1998; Moskát &

Honza, 2000). Finally, the perch-proximity hypothesis states that brood parasitic females are better able to locate host nests they can observe from above at nearby perches (Freeman et al., 1990; Øien et al., 1996; Clotfelter, 1998; Larison et al., 1998).

Factors that influence probability of parasitism have been extensively studied in common cuckoos (*Cuculus canorus*) and brown-headed cowbirds (*Molothrus ater*). Most studies indicate that common cuckoo and brown-headed cowbird parasitism increase with nest visibility, suggesting that poorly concealed nests are easier to find by parasites (Brittingham & Temple, 1996; Burhans, 1997; Larison et al., 1998; Saunders et al., 2003; Antonov et al., 2007). Additionally, nests closer to potential perches experience more parasitism than those far from perches (Alvarez, 1993; Clotfelter, 1998; Hauber & Russo, 2000; Antonov et al., 2007). Furthermore, nests with more parental activity around them may be more likely to be parasitized by brown-headed cowbirds (Uyehara & Narins, 1995; Banks & Martin, 2001). Other observational and experimental studies support the idea that brown-headed cowbirds use host aggression directed to them as a cue to find host nests (Strausberger, 1998; Smith et al., 1984), although evidence of brown-headed cowbirds exploiting nest-defence behaviour has been equivocal (Folkers & Lowther, 1985; Gill et al., 1997; Grief & Sealy, 2000).

In contrast, few studies have explored cues used by shiny cowbirds to find host nests (but see Wiley, 1988; Kattan, 1997; Fiorini & Reboreda, 2006; Svagelj et al., 2009). In this paper we investigate using a multivariate approach the association between shiny cowbird parasitism and behaviour and nest-site characteristics of chalk-browed mockingbirds (*Mimus saturninus*), one of its common hosts. If shiny cowbirds use host activity to find nests, we should observe a positive association between probability of parasitism and mean level of host activity. If the probability of parasitism was affected by nest concealment, we expected a negative association between these variables. Finally, if parasitism is associated with the use of perches by shiny cowbirds, we expect that nests nearer potential perches will be more parasitized than those further away from such perches. Parasitism could vary also with height of host nests because if cowbirds search for host nests from a perch, higher nests would be easier to find (Briskie et al., 1990; Martin, 1993; Barber & Martin, 1997). Therefore, we expected a positive association between nest height and probability of parasitism. Because date of host

laying influences probability of parasitism in other host-brood parasite systems (Wyllie, 1981; Payne & Payne, 1998; Mermoz & Reboreda, 1999), we also included this variable in our analyses. We also tested experimentally if shiny cowbird parasitism is associated with host aggressiveness. If female cowbirds use host agonistic behaviours directed to them to locate host nests, we expected that pairs that responded more aggressively to cowbird models close to nests would be more parasitized than less aggressive pairs.

## Methods

### *Study site*

The study was carried out at Reserva El Destino, near the town of Magdalena (35°08'S, 57°23'W) in the province of Buenos Aires, Argentina. Data collection was done during the breeding seasons (September–January) 2002–2003, 2003–2004 and 2005–2006. The study area is nearly flat, marshy grassland, with planted pastures and old and second growth stands dominated by tala (*Celtis tala*) and coronillo (*Scutia buxifolia*).

### *Study species*

Chalk-browed mockingbirds breed from late September until mid-January. Adult weight is approx. 70–75 g. This species is commonly parasitized by shiny cowbirds (Fraga, 1985; Sackmann & Reboreda, 2003; Fiorini & Reboreda, 2006). This host build their nests in talas, coronillos and molles (*Schinus longifolius*) at an average height of 1.5 m. The nest is a large open cup of twigs (outer diameter 20–25 cm) lined with fibres and horsehair. Shiny cowbirds breed from early October until late January and adult weight is approx. 45 g for females and 55 g for males.

We found mockingbird nests by focusing on individual activity and then inspecting potential nesting sites within the territory of breeding pairs. Nests were visited daily or every other day to detect parasitism. Because this host has high abandonment rates as a result of egg punctures associated with shiny cowbird parasitism, which mainly occurs during laying (Fiorini & Reboreda, 2006), we considered for our analyses nests that were active for at least the first two days of the laying period.

*Nest-site characteristics*

To test the nest-exposure hypothesis, we measured nest cover and height. Nest cover was estimated by eye (Clotfelter, 1998). We averaged six cover measurements from the tree border: four at nest-height level in the cardinal directions, one at the upper border (overhead) of the tree in the nest line, and one at the lower border below the nest. We estimated percentage of nest cover (to the nearest 5%) as the proportion of the nest cup not visible from borders (Clotfelter, 1998). For nests too high to measure overhead cover by standing directly above, we looked from the nest to the sky and estimated the percentage of sky not visible. Nest height was measured to the nearest cm from the ground to the base of the nest cup.

To test the perch-proximity hypothesis we measured distance between the edge of the tree where the nest was built and the nearest tree (defined as any woody vegetation higher than 1.5 m). We measured this distance to the nearest cm with a measuring tape. To reduce risk of nest abandonment by investigator activity, we collected nest-site measurements after nests failed or the chicks fledged (McLaren & Sealy, 2003).

*Host behaviour*

To test if host behaviour was associated with parasitism, we performed focal nest observations during laying. They were made from a blind located at least 30 m away from nests and using 10 × 50 binoculars. Observations lasted from 55 to 90 min, were conducted from 06:30 to 11:00 h, and were performed always at different nests.

To test the host-activity hypothesis, we estimated mockingbird activity with two variables: (1) nest activity: number of times per hour that one member of a pair crossed a 10-m radius circle around a nest, and (2) nest attentiveness: proportion of time during observations that at least one member of a pair was <10 m from their nest.

*Experiment*

During the 2003–2004 breeding season, we performed an experiment to test the nesting-cue hypothesis. We evaluated recognition of parasitic females by hosts, and host agonistic behaviours directed to parasites. To distinguish host responses towards shiny cowbirds from generalized responses to nest intruders, we quantified nest defence by presenting simultaneously taxidermic

mounts in a life-like position of a female shiny cowbird and a control model cattle tyrant (*Machetornis rixosus*), each at a distance of 1 m from the nest and level with it (Mark & Stutchbury, 1994). We used a cattle tyrant (*Machetornis rixosus*) model because it is common in our study area, is about the same size and shape as a female shiny cowbird (cattle tyrant 17 cm and shiny cowbird 19 cm), it is not a threat for our host species, and differs in plumage from female shiny cowbirds. Both models were clipped directly to the vegetation and one was presented on one side of the nest, and the second on the opposite side; presentation sides were alternated at successive nests. Each nest was tested only once between 8:30 and 11:30 during the laying stage.

We observed host responses from a blind located  $\geq 30$  m away from the nest using  $10 \times 50$  binoculars and videotaped the experiment for later analysis. A 5-min testing interval began when a nest owner arrived at the tree nest. If after 30 min no individual had arrived, or if they approached but did not respond to a model, the session finished and the nest was excluded from analyses (4 of 15 cases). Once one nest owner responded, we quantified two variables: (1) time that at least one member of the pair was  $< 1$  m from each model, and (2) number of strikes with the bill, body, or legs by hosts to each model.

### *Statistical analyses*

To evaluate associations between parasitism and both nest-site and host behaviour, we used 41 nests at which we performed focal observations and measured nest-site variables. Effects of different predictor variables on parasitism were examined by fitting generalized linear models with a binomial error structure and logit link function (Crawley, 2007). Year and host laying date (October 1 = day 0 of the three breeding seasons) were also included as predictor variables because these factors might influence frequency of parasitism (e.g., Briskie et al., 1990; Petit, 1991; Øien et al., 1996; Brooke et al., 1998; Mermoz & Reboreda, 1999). Models were evaluated and parameter values estimated with information-theoretic procedures (Burnham & Anderson, 1998; Crawley, 2007). Due to sample size ( $N = 41$  nests), our analyses were restricted a priori to models containing a maximum of three predictors. We included all models with one variable, all models with two variables, and three models with three variables that we considered could

explain variation in nest parasitism. This resulted in 33 candidate models, including one fully specified general model with all predictors (global model), and a base model without predictors (null model). We evaluated goodness of fit of global model following Hosmer & Lemeshow (2000). We calculated for each model Akaike's Information Criterion corrected for small sample size (AICc, Burnham & Anderson, 1998). Model comparisons were made with  $\Delta\text{AICc}$ , which is the difference between the lowest AICc value (i.e., best of suitable models) and AICc from all other models. Models with  $\Delta\text{AICc} \leq 2$  have substantial support from the data (Burnham & Anderson, 1998). The AICc 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, AICc model weights were summed across all models that contained a parameter (parameter likelihood; Burnham & Anderson, 1998). Parameters with good support have high parameter-likelihood values (near 1). Parameter estimates were calculated using model-averaged parameter estimates based on AICc model weights for all candidate models. Unconditional variances were used to calculate standard errors (Burnham & 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 SE, respectively (Burnham & Anderson, 1998). Statistical tests were performed using STATISTICA 6.0 (StatSoft, 2001) and SPSS 11.5.1 (SPSS, 2002) and were two-tailed.

For the analysis of the experiment we first determined if mockingbirds recognized female cowbirds, and second if more aggressive pairs had a higher probability of parasitism. To test parasite recognition we evaluated if the amount of time the host spent close to the cowbird model and the aggression directed to it was higher than those for the cattle tyrant model. To determine if parasitized pairs were more aggressive to cowbirds than non-parasitized ones, we compared the amount of time hosts spent close to female cowbird models and aggression directed to it in unparasitized versus parasitized pairs. When possible we used parametric statistical tests. Otherwise, we used non-parametric tests (Siegel & Castellan, 1988).

## **Results**

Our dataset included 41 nests, 29 of which (70%) were parasitized. A goodness-of-fit test (Hosmer & Lemeshow, 2000) indicated that the global

**Table 1.** Generalized linear models explaining variation in parasitism of shiny cowbirds (*Molothrus bonariensis*) on chalk-browed mockingbird (*Mimus saturninus*) nests.

Model	Number of parameters	$\Delta$ AICc	AICc weight	$R^2$
Laying date + nest cover + nest attention	4	0.00	0.667	0.364
Laying date + nest cover	3	4.50	0.071	0.246
Laying date + nest attention	3	4.60	0.068	0.245
Global	9	5.20	0.051	0.496
Laying date + nest cover + nest activity	4	5.90	0.035	0.266
Null	1	11.50	0.002	

Only the null model, the global model, the best model and the next three models are shown. Models are listed in decreasing order of importance.

model fit the observed data ( $\chi_{39}^2 = 48.5$ ,  $p = 0.14$ ). The model that best described variation in parasitism included laying date, nest cover, and nest attention as explanatory variables ( $w_i = 0.667$ ; likelihood ratio test, comparison with null model involving intercept only:  $\chi_3^2 = 9.27$ ,  $p < 0.005$ ; Table 1) and accounted for 36.4% of variation in parasitism (Table 1). None of the other models had a  $\Delta$ QAICc  $\leq 2$ . The three variables included in the best fitting model were important predictors of parasitism because they had high likelihood parameter values and confidence intervals of their parameter estimates excluded zero (Table 2). Parasitism was positively associated with laying date (parasitized nests: mean  $\pm$  SE =  $55.62 \pm 29.20$  days, non-parasitized nests: mean  $\pm$  SE =  $31.42 \pm 5.95$  days) and nest cover (parasitized nests: mean  $\pm$  SE =  $79.33 \pm 2.44\%$  cover, non-parasitized nests: mean  $\pm$  SE =  $66.60 \pm 6.47\%$  cover) and negatively associated with nest attentiveness (parasitized nests: mean  $\pm$  SE =  $0.61 \pm 0.05$  proportion of attentiveness, non-parasitized nests: mean  $\pm$  SE =  $0.73 \pm 0.07$  proportion of attentiveness) (Table 2). The relationship between parasitism and nest cover could arise if nests initiated later in the breeding season were more concealed than those initiated earlier. However, laying date and nest cover were not associated ( $R^2 = 0.05$ ,  $p = 0.65$ ,  $N = 41$ ). Thus, the relationship between parasitism and nest cover was not a by-product of the relationship between laying date and nest cover. As indicated by low parameter-likelihood values and confidence intervals including zero, other explanatory variables were not related to parasitism (Table 2).



**Table 2.** Parameter estimates ( $\pm$ SE) from generalized linear models describing variation in parasitism.

Explanatory variable	Parameter likelihood	Parameter estimate $\pm$ SE	Confidence interval	
			Lower	Upper
Intercept		$-2.77 \pm 2.65$	-2.53	8.07
<b>Laying date</b>	<b>0.95</b>	<b><math>0.06 \pm 0.02</math></b>	<b>-0.11</b>	<b>-0.01</b>
<b>Nest cover</b>	<b>0.86</b>	<b><math>0.07 \pm 0.03</math></b>	<b>-0.132</b>	<b>-0.005</b>
<b>Nest attentiveness</b>	<b>0.81</b>	<b><math>-5.55 \pm 2.77</math></b>	<b>0.01</b>	<b>11.10</b>
Nest activity	0.10	$0.05 \pm 0.07$	-0.19	0.08
Distance to perch	0.08	$0.003 \pm 0.003$	-0.009	0.002
Nest height	0.07	$0.0007 \pm 0.0167$	-0.03	0.03
Year 2002	0.06	$-0.86 \pm 1.07$	-1.29	3.01
Year 2003	0.06	$-1.26 \pm 1.02$	-0.78	3.31

Parameter likelihoods are AICc weights summed across all models that contained that parameter and are indicative of the importance of the variable. Parameter estimates are weighted averages (using model AICc weights) from all models and standard errors (SE) are calculated from all candidate models using unconditional variances. Upper and lower confidence limits intervals (95%) were calculated 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.

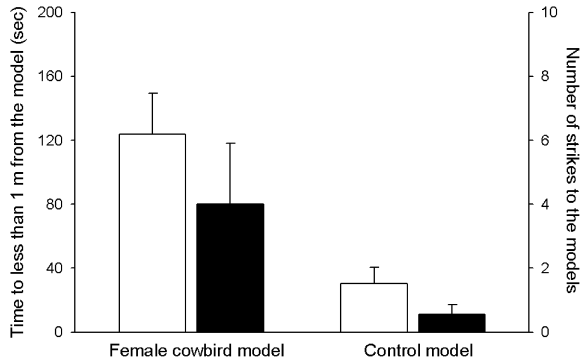
### Experiment

Chalk-browed mockingbirds spent more time near female shiny cowbird models than near control models (Wilcoxon paired-sample test,  $Z = -2.58$ ,  $p < 0.01$ , Figure 1). They also were more aggressive towards parasitic models than towards control models (Wilcoxon paired-sample test,  $Z = -2.50$ ,  $p = 0.01$ , Figure 1).

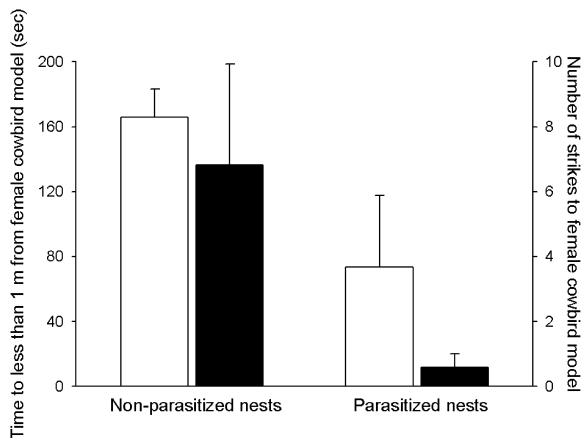
Parasitized pairs were less aggressive towards female shiny cowbird models than non-parasitized ones (ANOVA  $F_{1,9} = 13.19$ ,  $p = 0.005$ , Figure 2). There were also a marginal difference in the proportion of time that parasitized and non-parasitized pairs spent near the parasitic model (ANOVA  $F_{1,9} = 4.38$ ,  $p = 0.065$ , Figure 2).

### Discussion

Shiny cowbird parasitism in chalk-browed mockingbird nests was negatively associated with nest attentiveness. This result contradicts the host-activity



**Figure 1.** Chalk-browed mockingbird behaviour associated with female shiny cowbird and with control cattle tyrant models presented during a 5-min testing interval. White and black bars show the time that hosts were near models and the number of strikes directed at models, respectively. The number of experimental nests was 11. Values are mean  $\pm$  SE.



**Figure 2.** Behaviour of non-parasitized ( $N = 5$ ) and parasitized ( $N = 6$ ) chalk-browed mockingbird pairs towards a female shiny cowbird model presented during a 5-min testing interval. White and black bars show the time that hosts were near the model and the number of strikes directed to the model, respectively. Values are mean  $\pm$  SE.

hypothesis and indicates that host attentiveness limits shiny cowbirds parasitism rather than draws attention and acts as a cue to nest location. Therefore, our results support the nest-guarding hypothesis in which time near the nest aids hosts in detecting brood parasites and facilitates nest defence (Moller, 1989; Sealy et al., 1998). Arcese & Smith (1988) also found that song sparrows that were more vigilant at their nests were parasitized less

frequently. In contrast, Banks & Martin (2001) found in a comparative study with four different brown-headed cowbird hosts that parasitized pairs tended to spend more time around their nests than did unparasitized pairs.

We also evaluated host activity as another variable to test the host-activity hypothesis, but we did not find a relationship between this variable and probability of parasitism. Similarly, Banks & Martin (2001) found that females of different brown-headed cowbird hosts whose nests were parasitized visited their nests less frequently than those that were not parasitized. Other studies have found some support for the host-activity hypothesis (Clotfelter, 1998; McLaren & Sealy, 2000) but they used host songs or nest mass to quantify activity.

Contrary to the nest-exposure hypothesis, we found that the probability of parasitism was higher in more concealed nests. In contrast, others (Brittingham & Temple, 1996; Larison et al., 1998; Clarke et al. 2001; Saunders et al., 2003) have found that more concealed nests were parasitized less often than those more exposed. In the latter cases, cover might conceal movements of hosts near their nests and reduce the chance of detection by searching cowbirds. Our finding of a positive relationship between parasitism and nest cover is consistent with previous works with brown-headed cowbirds (Grieff & Sealy, 2000; McLaren & Sealy, 2003). The latter authors found that multiply parasitized song sparrow (*Melospiza melodia*) nests tended to have more ground cover than singly parasitized or unparasitized nests. These authors stated that more concealed nests may provide cowbirds a better chance to lay unmolested by hosts. Another possibility is that cowbirds assess chances of successful reproduction by nest characteristics. More concealed nests may be less obvious to predators and may provide a better return on investment for the parasite. When we analyzed the association between nest cover and number of days that nests were active we found a positive (although weak) association between them ( $R^2 = 0.09$ ,  $F = 5.09$ ,  $p = 0.03$ ). Therefore, it is possible that by choosing nests with more cover, parasitic females are also selecting pairs with a lower risk of predation or higher parental quality. In support of this, Soler et al. (1995) found that great spotted cuckoos (*Clamator glandarius*) preferred to parasitize large nests of magpies (*Pica pica*) and a large nest apparently indicates high parental quality.

We found a seasonal increase in probability of parasitism, as did Sackman & Reboreda (2003) in a study also carried out with chalk-browed mockingbirds, and Mermoz & Reboreda (1999) in another frequent host of the shiny cowbird host, the brown and yellow marshbird (*Pseudoleistes virescens*).

In our study area, the height of chalk-browed mockingbird nests did not explain differences in frequency of shiny cowbird parasitism. Previous works in other host-parasite systems also failed to support this prediction (Moskát & Honza, 2000; Saunders et al., 2003). Banks & Martin (2001) studied the four most abundant brown-headed cowbird hosts in riparian habitat in Montana. They found that the two most heavily parasitized species built the highest nests, but within species, there were no differences in height of parasitized and unparasitized nests. These authors suggest that nest height may affect vulnerability of host species to parasitism by cowbirds, but it rarely explains which nests are parasitized within species.

Our results did not support the perch-proximity hypothesis either, as there were no differences in proximity to perches between parasitized and unparasitized nests. The perch-proximity hypothesis has received some support for ground nesters in open habitats. In these cases, trees from which the parasites can observe potential nest sites may be important because they provide parasites an extensive view of host activities (Øien et al., 1996; Clotfelter, 1998; Hauber & Russo, 2000; Moskát & Honza, 2000; Saunders et al., 2003; Patten et al., 2006; Antonov et al., 2007). In contrast, Brittingham & Temple (1996) studied effects of songbird nest-site characteristics on brown-headed cowbird parasitism and did not find support for the perch-proximity hypothesis. The latter study was carried out in a forest, where availability of potential perches is high. Similarly, our study area is grassland with open patches of woodland where mockingbirds build their nest. These patches of woodland provide shiny cowbird females a high availability of potential perches that allow them to observe mockingbird nests. Another possibility is that shiny cowbird females prefer to observe host nests from perches further away than are the closest vantage points. Accordingly, Honza et al. (2002) radiotracked common cuckoo females and found that they used perches almost four times further from the nest than the closest possible one, and they suggested that female cuckoos may prefer these perches to avoid being detected or attacked by hosts.

Experimental presentation of models of a female shiny cowbird and a control species beside mockingbird nests revealed that aggression towards parasite models was higher in non-parasitized than in parasitized pairs. This result contradicts the nesting-cue hypothesis and supports the idea that mockingbird aggression is an effective first line of defence against brood parasitism. Chalk-browed mockingbirds are considerably larger in body size

than shiny cowbirds and they are very aggressive (Fiorini, 2007). Therefore, access of shiny cowbird females to mockingbird nests could be particularly dangerous for parasites. Sealy et al. (1998) experimentally tested the nesting-cue hypothesis in two hosts of the brown-headed cowbird: the yellow warbler (*Dendroica petechia*) and the red-winged blackbird (*Agelaius phoeniceus*). Generally, parasitized and unparasitized pairs of the two hosts responded similarly to models, but unparasitized yellow warblers uttered more chip calls toward cowbird models than did parasitized nest owners. Clotfelter (1998) found that redwings whose nests were parasitized were not more aggressive towards a female brown-headed cowbird mount than unparasitized red-wing blackbirds, contrary to the nesting-cue hypothesis. Neudorf & Sealy (1992) suggested that cowbirds attacked by hosts could be injured and, therefore, it could be dangerous for them to depend on nest defence when searching for nests, particularly when searching for nests of large hosts. In contrast to nest defence, cowbirds would be exposed to little risk of injury when they observe host activities. Accordingly, Wiley (1988) observed that in 70% of cases, shiny cowbirds watched activities of prospective hosts to locate their nests. In the other 30% of cases, shiny cowbirds used active searches or flushing behaviour. In a previous study we found that although shiny cowbirds do not parasitize nests if they do not observe a mockingbird, they are able to locate nests without the presence of mockingbirds (Fiorini & Reboreda, 2006). In this case they probably use the “active search strategy” (Wiley, 1988), which involves female cowbirds quietly moving through the habitat in short flights and hops through the vegetation. Therefore, it is probable that cowbirds use a combination of strategies when searching for nests.

In conclusion, shiny cowbird females parasitize more concealed nests and nests with hosts that were less attentive and less aggressive. These results indicate that mockingbirds reduce the likelihood of parasitism through nest attentiveness and that shiny cowbird females choose safer nests. However, other host characteristics such as phenotypic quality (Soler et al., 1995; Polacikova et al., in press) may be important influences on nest selection by shiny cowbirds and this topic should be investigated in future studies.

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