**CSIRO** PUBLISHING
*Emu*, 2012, **112**, 55–59
http://dx.doi.org/10.1071/MU11038

***Short Communication***

# Dense canopy cover over House Wren (*Troglodytes aedon*) nests increases latency of brood parasitism by Shiny Cowbirds (*Molothrus bonariensis*)

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**Abstract.** Obligate brood parasites must find host nests in which to lay their eggs. The search for a suitable host nest is predicted to be more difficult if the host nest is well-concealed by vegetation (nest-concealment hypothesis) and brood parasitism of better concealed nests should be less common than parasitism of less well-concealed nests. We experimentally tested this hypothesis by placing nest-boxes used by House Wrens (*Troglodytes aedon*) in woodland sites with sparse and dense canopy cover and measuring the frequency (proportion of nests parasitised), latency (days elapsed since laying of the first host egg and parasitism), and intensity (number of parasite eggs in parasitised nests) of parasitism by Shiny Cowbirds (*Molothrus bonariensis*). The frequency and intensity of parasitism did not differ between sites with sparse or dense canopy cover, but the latency of parasitism was shorter in sites with sparse cover than in sites with denser cover. Brood parasites that find host nests more quickly have higher reproductive success, whereas House Wrens have higher reproductive success when parasites lay their eggs later during the incubation period, owing to reduced mortality of host nestlings. Because woodland degradation is associated with sparser canopy cover, host species nesting in degraded woodlands may suffer more from parasitism than those nesting in protected woodlands.

**Additional keywords:** nest-concealment hypothesis, nest cover.

Received 16 May 2011, accepted 19 September 2011, published online 24 February 2012

## Introduction

Obligate avian brood parasites, such as cowbirds (Passeriformes : Icteridae) and cuckoos (Cuculiformes : Cuculidae), lay their eggs in the nests of host species, which subsequently act as foster parents, incubating eggs and then feeding young parasites (Ortega 1998; Rothstein and Robinson 1998; Davies 2000). Hosts within and between populations are not parasitised with equal probability (Krüger 2007) and some habitat features and nest-site characteristics can influence the probability of parasitism (Øien *et al*. 1996; Grim 2002; Honza *et al*. 2002). Parasites can locate nests by observing the activity of hosts (Wiley 1988; Honza *et al*. 2002), but vegetation structure around nests may conceal movements of hosts and therefore influence the probability that brood parasites will find the nest (Sharp and Kus 2006). Hosts are therefore predicted to build their nests in areas with high levels of concealment by vegetation (or other material) to reduce the probability of detection by brood parasites. Accordingly, the nest-concealment hypothesis predicts that nests with greater vegetative cover have a lower probability of parasitism than those with sparse vegetative cover (Burhans 1997; Clotfelter 1998; Larison *et al*. 1998; Grieef and Sealy 2000; Moskát and Honza 2000; Saunders *et al*. 2003). There is support for this prediction: studies on hosts of Common Cuckoos (*Cuculus canorus*) and Brown-headed Cowbirds (*Molothrus ater*) found a negative association between the probability of parasitism and vegetative cover of the host nest (Burhans 1997; Larison *et al*. 1998; Saunders *et al*. 2003; Antonov *et al*. 2007). However, some studies have found the opposite pattern: some hosts of Brown-headed Cowbirds had a higher incidence of parasitism at better concealed nests (Brittingham and Temple 1996; Grieef and Sealy 2000; Mclaren and Sealy 2003). Mclaren and Sealy (2003) suggested that one possible explanation for the latter results would be that brood parasites may have selectively adapted to lay in more concealed nests, as these nests are less likely to be discovered by predators.

Few studies have analysed the relationship between habitat characteristics and brood parasitism by Shiny Cowbirds (*M. bonariensis*). Shiny Cowbirds typically spend morning hours on breeding grounds watching the behaviour of hosts (Hoy and Ottow 1964; Wiley 1988) and use the activity of hosts to find host nests (Wiley 1988) and to parasitise them (Fiorini and Reboreda 2006). As with parasitism by Brown-headed Cowbirds, studies of Shiny Cowbirds and their hosts have provided mixed support for the nest-concealment hypothesis. Svagelj *et al*. (2009) did not find an association between cover of nests of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*) and parasitism by Shiny Cowbirds. However, Fiorini *et al*. (2009*a*) found that parasitism was higher at better concealed nests of Chalked-browed Mockingbirds (*Mimus saturninus*), perhaps because female Shiny Cowbirds had a better chance to approach the host nest unnoticed.

The occurrence of parasitism is an approximate indicator of how easy it is for female Shiny Cowbirds to find host nests. Other variables that better indicate detectability of host nests are the latency of parasitism (days elapsed between the laying of the first egg by the host and parasitism) and the intensity of parasitism (number of parasite eggs in parasitised nests). These variables are more appropriate to study the relationship between nest concealment and brood parasitism because the nest-concealment hypothesis predicts that less-well concealed host nests would be found and parasitised earlier and by more Cowbirds than better concealed nests. To our knowledge, no previous study has tested the predicted relationship between concealment of the host nest and latency of brood parasitism.

In this work we experimentally analysed the effect of concealment of House Wren (*Troglodytes aedon*) nests on the frequency, latency and intensity of parasitism by Shiny Cowbirds. This host is an appropriate model system to test the nest-concealment hypothesis because its nests are frequently parasitised by Shiny Cowbirds (Kattan 1997; Tuero *et al*. 2007) and it uses nest-boxes, which can be experimentally located in sites with different vegetative cover. Based on the nest-concealment hypothesis, we expected higher frequency and, higher intensity of parasitism and shorter latency of parasitism by brood parasites at host nests with lower levels of vegetation concealment.

## Materials and methods

### Study site

The study was carried out at Reserva El Destino (35°08′S, 57°23′W) in the province of Buenos Aires, Argentina, during a single breeding season, between October 2009 and January 2010. The reserve encompasses a mosaic of grasslands, marshes and patches of xeric thorny woodlands arranged in bands of vegetation 20–100 m wide and up to several kilometres in length running parallel to the edge of the Rio de la Plata. Woodlands are dominated by Tala (*Celtis tala*) and Coronillo (*Scutia buxifolia*). Woodland stands of Talas were selectively logged until 1960 (Ribichich and Protomastro 1998) and, as a result, some areas of Talas woodland have dense canopy cover (i.e. contiguous vegetation with no open spaces in the canopy) whereas others have sparse canopy cover (i.e. with openings in the canopy).

### Study species

At our study site, House Wrens are a common host of Shiny Cowbirds; from previous studies, the overall prevalence of parasitism was 60% and the intensity was 1.7 eggs per parasitised nest (Tuero *et al*. 2007). House Wrens had a modal clutch size of five eggs, and 57% of parasitism occurred during the laying period of the Wren (Fiorini *et al*. 2009*b*). Both species breed from early October to mid-January (Tuero *et al*. 2007). House Wrens are cavity nesters and normally use nest boxes to build their nests.

### General methodology

We placed 88 nest boxes (height × width × depth: 25 × 17 × 13 cm) supported in trunks of the trees, at a height of 1.5–1.8 m and at least 20 m apart. The woodland patches of the study have sites with sparse canopy cover (low levels of concealment) and dense canopy cover (high levels of concealment), but there were fewer sites with sparse vegetation cover: 33 nest-boxes were placed in sites with sparse cover and 55 in sites with dense cover. We selected woodland locations where we could place both types of nest box in a spatially mixed pattern, alternating one nest-box in sparse cover with two in denser cover. We estimated cover categories by eye (Clotfelter 1998), using the estimated percentage of sky concealed by the vegetation in a 5-m radius centred on the nest-box (Fiorini *et al*. 2009*a*). Canopy cover was estimated by the same observer (V. D. Fiorini) for all sites. Mean percentage canopy cover for sparse-cover sites was 62 ± 3% (s.e.) and 98 ± 1% for dense-cover sites (Mann–Whitney test, $U = 36$, $P < 0.0001$, $n = 88$ nests; Table 1). We selected places for nest-boxes at sparse- and dense-cover sites before the beginning of the breeding season (October). At the end of the breeding season (January), we re-estimated canopy cover to ascertain that the sites had the same cover category at the end of the season, and confirmed no difference in our initial nest-cover category.

The entrance hole in nest-boxes was 4.5 cm in diameter, which allowed female Shiny Cowbirds to enter, and the nest-boxes had an opening in the roof that allowed researchers to monitor progress of the nest. We checked nest-boxes during the morning (0900 to 1200 hours), because previous study had shown that both House Wrens and Shiny Cowbirds finish laying by 0900 hours. We checked nest-boxes every 1–2 days.

We analysed parasitism that occurred from Day 0 (day the first host egg was laid) to Day 6. We used this criterion because ~70% of all parasitism occurs during this period (Fiorini *et al*. 2009*b*), and we can estimate the intensity of parasitism without the combined effect of nest predation during the incubation period, which can be very high. The sample size for analysis would be smaller if we were to extend the sampling period of parasitism into the incubation period owing to such predation.

In 11 cases, brood parasitism occurred between nest inspections separated by 2 days; in these cases, we estimated the date

**Table 1. Number of House Wren nests that survived until Day 6, the number of those nests that were parasitised, mean clutch-size, latency of parasitism and intensity of parasitism for nests with sparse and dense cover over nests (mean percentage canopy cover)**

Means are presented ± s.e.

| | Nest cover | |
|---|---|---|
| | Sparse | Dense |
| Number of nests that survived until Day 6 | 13 | 26 |
| Number of nests parasitised | 6 | 13 |
| Percentage canopy cover over nest | 62 ± 3 | 98 ± 1 |
| Clutch-size | 5.15 ± 0.13 | 5.00 ± 0.16 |
| Latency of parasitism | 1.00 ± 0.45 | 2.92 ± 0.43 |
| Intensity of parasitism | 1.33 ± 0.33 | 1.23 ± 0.12 |

of parasitism indirectly. In four of these cases we estimated it from the date of hatching of the parasitic egg, assuming an incubation period for Shiny Cowbird eggs of 13 days (Tuero *et al*. 2007). In the other seven cases, we did not know the date of hatching of the parasite egg and assumed that in half of the cases the parasitic egg was laid the day before we visited the nest and in the other half the same day that we visited the nest.

### *Statistical analyses*

We tested statistical differences in the frequency and latency of parasitism between nests with sparse and dense cover using Chi-square and *t*-tests respectively. We tested differences in parasite intensity using a Mann–Whitney test because this variable did not have a normal distribution, even after transformation (Siegel and Castellan 1988). Statistical analyses were done with STATISTICA 6.0 (StatSoft 2001). All analyses were two-tailed.

## Results

In sites with sparse cover, Wrens occupied 15 of 33 (45.5%) nest-boxes; 13 nests survived to Day 6, and six nests were parasitised during the observation period. In sites with dense cover, Wrens occupied 31 of 55 (56.4%) nest-boxes; 26 nests survived to Day 6, and 13 nests were parasitised during the observation period (Table 1). We did not find significant differences in frequency of parasitism (6 of 13 *v.* 13 of 26 nests; $\chi^2 = 0.05$, $P = 0.82$; Fig. 1*a*) or intensity of parasitism ($U = 38$, $P = 0.93$, $n = 19$; Fig. 1*b*) between nests in sites with sparse or dense cover, but sites with sparse cover were parasitised more quickly than sites with dense cover ($t_{17} = -2.71$, $P = 0.01$; Fig. 1*c*). There was no significant difference in initiation of clutches by Wrens: in sites of sparse cover, laying started between 20 October and 26 December whereas in sites of dense cover laying started between 17 October and 20 December (for Julian day of laying: $t_{(1,37)} = 0.94$, $P = 0.34$).

## Discussion

Our results provide partial support for the nest-concealment hypothesis. Our results show that the latency of parasitism by Shiny Cowbird in nests of House Wrens was affected by percentage canopy cover: sites with sparse cover, which are more conspicuous nests with low levels of vegetative concealment, were parasitised sooner than nests with denser canopy cover and that are better concealed. However, vegetative cover did not influence the frequency or intensity of parasitism.

Previous studies on the role of nest concealment in brood parasitism by Brown-headed Cowbirds found a negative relationship between the frequency of parasitism and nest cover (Brittingham and Temple 1996; Larison *et al.* 1998; Clarke *et al.* 2001; Saunders *et al.* 2003; Sharp and Kus 2006). Sharp and Kus (2006) also found that conspicuous nests of Bell's Vireos (*Vireo bellii pusillus*) had a higher frequency of parasitism than concealed nests with high microhabitat cover. Sharp and Kus (2006) suggested that high microhabitat cover may have concealed the movements of hosts near the nest, thus reducing the chance of nest detection by searching Cowbirds. In contrast, other studies did not find a relationship between intensity of parasitism by Brown-headed (Mclaren and Sealy 2003) and Shiny (Svagelj *et al.* 2009) Cowbirds and vegetation cover. Svagelj *et al.* (2009) proposed that the lack of a correlation between concealment and parasitism in some studies could be explained by differences in density of Cowbirds. On this

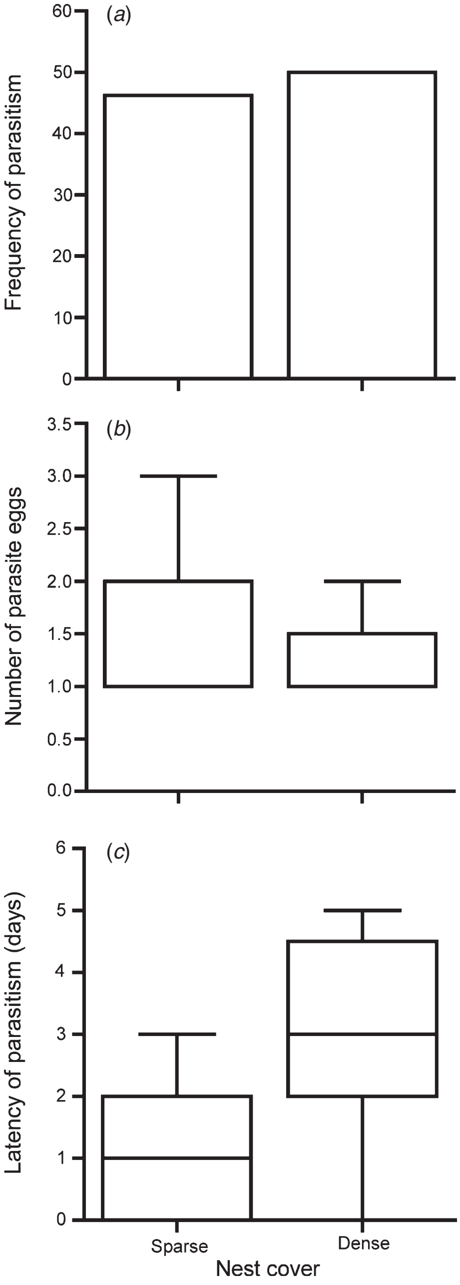

**Fig. 1.** Parasitism by Shiny Cowbirds in House Wren nests in sites of dense ($n = 13$) and sparse ($n = 6$) vegetation cover: (*a*) frequency of parasitism and (*b–c*) plots showing the median, lower and upper quartiles (boxes), and smallest and largest observations (whiskers) of: (*b*) intensity of parasitism and (*c*) latency of parasitism. The frequency of parasitism was estimated as the number of parasitised nests as a proportion of the total number of nests; intensity of parasitism was estimated as the number of parasite eggs per parasitised nest; and latency of parasitism was estimated as the number of days between laying of the first host egg and the laying of the Cowbird eggs.

interpretation, high density of Cowbirds would override measurable effects of nest-site characteristics if Cowbirds use behaviour of other Cowbirds as indicators of the location of a nest, for example.

Differences in latency of parasitism between House Wren nests built in sites with low and high percentage canopy cover and thus low and high levels of concealment may reflect nest-searching strategies used by Shiny Cowbirds. Shiny Cowbirds locate host nests primarily by watching nest-building activity (Wiley 1988). A more open canopy would potentially give Shiny Cowbirds a clearer view of the activity of hosts, and thus increasing the likelihood of finding host nests. However, Shiny Cowbirds can also locate host nests by systematic searching (Kattan 1997; Svagelj *et al*. 2003; Fiorini and Reboreda 2006), which could explain the absence of differences in frequency and intensity of parasitism between nests with high and low percentage canopy cover. Lack of differences in frequency and intensity of parasitism between sites of low and high levels of concealment may also result if Wrens that nest in sites with low levels of concealment compensate for this by providing more parental care. However, we did not find an association between nest attentiveness and nest cover (V. D. Fiorini, unpubl. data).

House Wrens have a modal clutch size of five eggs and they start incubation with the laying of the penultimate egg (Tuero *et al*. 2007), equivalent to Day 3 of our analysis. When parasitism is synchronised with host laying (i.e. it occurs before the onset of incubation), Shiny Cowbird chicks hatch 2–3 days before the host chicks (Tuero *et al*. 2007). This early hatching by Cowbirds reduces the hatching success of House Wren eggs by ~25% (from 0.97 to 0.73) and the fledging success of House Wren chicks by ~50% (from 0.8 to 0.42) (Tuero *et al*. 2007). On the contrary, when Shiny Cowbird eggs are laid 2–3 days after the start of incubation, they do not reduce hatching and fledging success of House Wren eggs and chicks (Tuero *et al*. 2007). Our results show that when House Wrens nest in nest-boxes placed in well-concealed sites (sites of high canopy cover), some parasitism occurs after the onset of incubation (Days 4–6), whereas when they used nest-boxes in less well-concealed sites (low canopy cover), all parasitism occurred before the onset of incubation. Therefore, it is likely that the use of nest-boxes at well-concealed sites increases the reproductive success of House Wrens. Because woodland degradation is generally associated with lower levels of vegetative cover, our results suggest that host species nesting in degraded woodlands may suffer more from parasitism than those nesting in protected woodlands with intact and denser canopy cover.

## Acknowledgements

We thank the 'Fundación Elsa Shaw de Pearson' for allowing us to conduct this study at Estancia El Destino. We are grateful to two anonymous reviewers for helpful comments on a previous version of this manuscript. We specially appreciate the improvements in English usage made by Sonia Kleindorfer. V. D. Fiorini and D. T. Tuero were supported by fellowships from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). V. D. Fiorini and J. C. Reboreda are Research Fellows of the CONICET. This work was supported by grants of the Agencia Nacional de Promoción Científica y Tecnológica and University of Buenos Aires.

## References

Antonov, A., Stokke, B. G., Moksnes, A., and Røskaft, E. (2007). Factors influencing the risk of Common Cuckoo *Cuculus canorus* parasitism on Marsh Warblers *Acrocephalus palustris. Journal of Avian Biology* **38**, 390–393.

Brittingham, M. C., and Temple, T. A. (1996). Vegetation around parasitised and non-parasitised nests within deciduous forest. *Journal of Field Ornithology* **67**, 406–413.

Burhans, D. E. (1997). Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* **99**, 866–872. doi:10.2307/1370136

Clarke, A. L., Øien, I. J., Honza, M., Moksnes, A., and Røskaft, E. (2001). Factors affecting Reed Warbler risk of brood parasitism by the Common Cuckoo. *Auk* **118**, 534–538. doi:10.1642/0004-8038(2001)118[0534:FARWRO]2.0.CO;2

Clotfelter, E. D. (1998). What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests? *Animal Behaviour* **55**, 1181–1189. doi:10.1006/anbe.1997.0638

Davies, N. B. (2000). 'Cuckoos, Cowbirds and Other Cheats.' (Oxford University Press: Oxford, UK.)

Fiorini, V. D., and Reboreda, J. C. (2006). Cues used by Shiny Cowbirds (*Molothrus bonariensis*) to locate and parasitise Chalk-browed Mockingbird (*Mimus saturninus*) nests. *Behavioral Ecology and Sociobiology* **60**, 379–385. doi:10.1007/s00265-006-0175-3

Fiorini, V. D., Tuero, D. T., and Reboreda, J. C. (2009*a*). Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by Shiny Cowbirds on Chalk-browed Mockingbirds. *Behaviour* **146**, 1387–1403. doi:10.1163/156853909X433338

Fiorini, V. D., Tuero, D. T., and Reboreda, J. C. (2009*b*). Shiny Cowbirds synchronize parasitism with host laying and puncture host eggs according to host characteristics. *Animal Behaviour* **77**, 561–568. doi:10.1016/j.anbehav.2008.11.025

Grieef, P. M., and Sealy, S. G. (2000). Simulated host activity does not attract parasitism by Brown-headed Cowbirds (*Molothrus ater*). *Bird Behaviour* **13**, 69–78.

Grim, T. (2002). Why is mimicry in cuckoo eggs sometimes so poor? *Journal of Avian Biology* **33**, 302–305. doi:10.1034/j.1600-048X.2002.330312.x

Honza, M., Taborsky, B., Taborsky, M., Teuschl, Y., Vogl, W., Moksnes, A., and Røskaft, E. (2002). Behaviour of female Common Cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radiotelemetry study. *Animal Behaviour* **64**, 861–868. doi:10.1006/anbe.2002.1969

Hoy, G., and Ottow, J. (1964). Biological and oological studies of the molothrine cowbirds (Icteridae) of Argentina. *Auk* **81**, 189–203.

Kattan, G. H. (1997). Shiny Cowbirds follow the 'shot-gun' strategy of brood parasitism. *Animal Behaviour* **53**, 647–654. doi:10.1006/anbe.1996.0339

Krüger, O. (2007). Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* **362**, 1873–1886. doi:10.1098/rstb.2006.1849

Larison, B., Laymon, S. A., Williams, P. L., and Smith, T. B. (1998). Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. *Condor* **100**, 93–101. doi:10.2307/1369900

Mclaren, C. M., and Sealy, S. G. (2003). Factors influencing susceptibility of host nests to brood parasitism. *Ethology Ecology and Evolution* **15**, 343–353. doi:10.1080/08927014.2003.9522661

Moskát, C., and Honza, M. (2000). Effect of nest and nest site characteristics on the risk of Cuckoo *Cuculus canorus* parasitism in the Great Reed Warbler *Acrocephalus arundinaceus. Ecography* **23**, 335–341. doi:10.1111/j.1600-0587.2000.tb00289.x

Øien, I. J., Honza, M., Moksnes, A., and Roskaft, E. (1996). The risk of parasitism in relation to the distance from reed warbler nests to cuckoo perches. *Journal of Animal Ecology* **65**, 147–153. doi:10.2307/5717

Ortega, C. (1998). 'Cowbirds and Other Brood Parasites.' (University of Arizona Press: Tucson, AZ.)

Ribichich, A. M., and Protomastro, J. (1998). Woody vegetation structure of xeric forest stands under different edaphic site conditions and disturbance histories in the Biosphere Reserve 'Parque Costero del Sur', Argentina. *Plant Ecology* **139**, 189–201. doi:10.1023/A:1009718819857

Rothstein, S. I., and Robinson, S. K. (1998). The evolution and ecology of avian brood parasitism. In 'Parasitic Birds and Their Hosts, Studies in Coevolution'. (Eds S. I. Rothstein and S. K. Robinson.) pp. 3–56. (Oxford University Press: New York.)

Saunders, C. A., Arcese, P., and O'Connor, K. D. (2003). Nest site characteristics in the Song Sparrow and parasitism by Brown-headed Cowbirds. *Wilson Bulletin* **115**, 24–28. doi:10.1676/02-057

Sharp, B. L., and Kus, B. E. (2006). Factors influencing the incidence of cowbird parasitism of Least Bell's Vireos. *Journal of Wildlife Management* **70**, 682–690. doi:10.2193/0022-541X(2006)70[682:FITIOC]2.0.CO;2

Siegel, S., and Castellan, N. J. J. (1988). 'Nonparametric Statistics for the Behavioral Sciences.' (McGraw-Hill International Editions: New York.)

StatSoft (2001). 'STATISTICA', Version 6. (Statsoft: Tulsa, OK.)

Svagelj, W. S., Mermoz, M. E., and Fernández, G. J. (2003). Effect of egg type on the estimation of nest predation in passerines. *Journal of Field Ornithology* **74**, 243–249.

Svagelj, W. S., Fernández, G. J., and Mermoz, M. E. (2009). Effects of nest-site characteristics and parental activity on cowbird parasitism and nest predation in Brown-and-yellow Marshbirds. *Journal of Field Ornithology* **80**, 9–18. doi:10.1111/j.1557-9263.2009.00200.x

Tuero, D. T., Fiorini, V. D., and Reboreda, J. C. (2007). Effects of Shiny Cowbird parasitism on different components of House Wren reproductive success. *Ibis* **149**, 521–529. doi:10.1111/j.1474-919X.2007.00676.x

Wiley, J. W. (1988). Host selection by the Shiny Cowbird. *Condor* **90**, 289–303. doi:10.2307/1368557