

LACK OF EFFECTS OF MICROHABITAT CHARACTERISTICS ON NEST PREDATION AND BROOD PARASITISM IN THE CREAMY-BELLIED THRUSH (*TURDUS AMAUROCHALINUS*)

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Resumen. – Ausencia de efectos de características del microhabitat sobre la depredación de nidos y el parasitismo de cría en el Zorzal Chalchalero (*Turdus amaurochalinus*). – La depredación de nidos y el parasitismo de cría son factores clave que afectan la supervivencia de nidos de aves pase-riformes. Como resultado, las aves pueden seleccionar sitios de nidificación que minimicen la probabi-lidad de que un nido sea encontrado por un depredador o un parásito de cría. Sin embargo, la evidencia es confusa. Mi objetivo fue determinar la relación entre algunas características del microhabitat de los nidos (cobertura, distancia al camino más cercano, distancia al canal más cercano y sustrato) y las tasas de depredación o parasitismo de cría en el Zorzal Chalchalero. No encontré una relación entre las varia-bles estudiadas y las tasas de depredación o parasitismo de nidos. Este estudio, al igual que muchos estudios previos, no puede apoyar la hipótesis de que el sitio de nidificación afecte la tasa de depre-dación o de parasitismo de cría.

Abstract. – Nest predation and brood parasitism are key factors affecting nest survival in passerine birds. As a result, birds may select nest sites that minimize the probability of nests being found by predators or by brood parasites. Nevertheless, evidence remains equivocal. My objective was to deter-mine the relationship between nest microhabitat characteristics (nest concealment, distance to a road, distance to water, and substrate) and nest predation rates or brood parasitism rates in the Creamy-bellied Thrush. I found no relationship between the microhabitat characteristics studied and nest preda-tion or brood parasitism rates. This study, in concordance with several previous studies, fails to support the hypothesis that nest-site selection affects nest predation or brood parasitism rates. *Accepted 31 October 2013.*

Key words: Creamy-bellied Thrush, *Turdus amaurochalinus*, Shiny Cowbird, *Molothrus bonariensis*, brood parasitism, nest concealment, nest predation, nest site.

INTRODUCTION

Nest predation typically results in the loss of entire clutches (Martin *et al.* 2000). Many researchers have studied the relationship between nest-site microhabitat and nest pre-dation rates (e.g., Lahti 2001, Latif *et al.* 2012). One of the microhabitat characteristics that has received most attention is nest conceal-

ment. The concealment hypothesis (Cresswell 1997) states that more conspicuous nests are easier to find by predators, resulting in selec-tion for more concealed nests. On the other hand, the edge-effect hypothesis (Gates & Gysel 1978) suggests that nest predation is more frequent when nests are closer to an edge. Some authors have considered roads as edges, but they did not find an effect on nest

predation rates (Mankin & Warner 1992, Huhta 1995, Pasitschinskiak-Arts *et al.* 1998). Roads have also been considered as corridors that facilitate movement of predators between patches, having a high incidence in nest predation (Weldon 2006, Pescador & Peris 2007, Crino *et al.* 2011). In addition, tall trees growing along roads have been reported to favor predation because they can be used by predatory birds as perches to detect nests through parental activity (Bergin *et al.* 1997, Sheldon *et al.* 2007). Besides, shrubs growing along roads can be used as shelters by predator (Brzezinski *et al.* 2012).

Brood parasitism by cowbirds, on the other hand, is frequently associated with partial brood reduction (Sealy 1992, McMaster & Sealy 1997, Rothstein & Robinson 1998, Astié & Reboresda 2006). Brood reduction can be caused by: 1) egg puncture or removal of eggs or nestlings (Post & Wiley 1977, Astié & Reboresda 2006), 2) reduced hatchability of the hosts eggs (Carter 1986, Petit 1991), and 3) starvation of host nestlings due to competition with the parasite nestlings (King 1973, Marvil & Cruz 1989).

Several researchers have studied the relationship between nest-site microhabitats and brood parasitism rates. Evidence for an association between nest concealment and brood parasitism rates has been equivocal. Less concealed nests have been reported to be parasitized at higher rates (Burhans 1997, Larison *et al.* 1998, Saunders *et al.* 2003), lower rates (McLaren & Sealy 2003, Fiorini *et al.* 2009), or rates similar to those of more concealed nests (Smith 1981, Brittingham & Temple 1996, Burhans 1997, Svagelj *et al.* 2009). Similarly, parasitism rates can have a positive association (Freeman *et al.* 1990, Hauber & Russo 2000, Rodewald 2009) or have no association (Brittingham & Temple 1996, Fiorini *et al.* 2009) to distance from perches (cowbirds use perches to watch host activity and locate nests). Besides, the effect of nest concealment

on brood parasitism rates seem to be affected by habitat type, host species, or the placement of concealment (Burhans 1997, Larison *et al.* 1998).

My objective is to describe the effects of substrate, nest concealment, distance to the closest road and distance to the closest canal on nest predation and brood parasitism by the Shiny Cowbird (*Molothrus bonariensis*) on the Creamy-bellied Thrush (*Turdus amaurochalinus*) in a population breeding in Mendoza, Argentina. Although several investigators have addressed the question of how nest-site selection can affect rates of nest predation or brood parasitism separately (e.g., Martin 1993, Brittingham & Temple 1996, Lahti 2001, Rodewald 2009), new insights may be obtained by considering the effect of different microhabitat characteristics on both variables in the same area (Best & Stauffer 1980). Nest predation and brood parasitism may select for nest-sites that may be in conflict, e.g., concealment may protect nests from predation (Cresswell 1997), but favor parasitism (Fiorini *et al.* 2009). This may result in an evolutionary tug-of-war for selection of nest placement. On the other hand, closer distances to roads or canals could increase nest predation and parasitism because they could be acting as corridors or shelters for predators and tall trees along them could act as perches to predator birds and parasites. However, canals are the only source of water in this semiarid land, so, longer distances could increase travel time from and to the nest and, thereby, increase the time exposed to visual predators.

METHODS

Study area. Field work was carried out at Guaymallén Department, Mendoza Province, Argentina (68°43'W, 32°55'S). Mendoza is located in the Monte desert region of Argentina, dominated by shrubland. The desert landscape matrix displays large areas of

land irrigated for agricultural use, locally named oasis. Oasis occur mostly in the center and in the western sides of the Province, and they occupy less than 6% (~ 8900 km²) of the province of Mendoza. Creamy-bellied Thrushes occur primarily in these irrigated areas.

The study area was a 100 ha field cultivated with vineyards (*Vitis* sp.), olives (*Olea europaea*), and poplar (*Populus nigra*) groves. Landscape architecture was fairly similar throughout oasis areas: land is crisscrossed by a network of canals for irrigation and by roads. Commonly, roads are bordered by a line of tall trees on both sides and shrubs grow under them. Those trees are usually more than 15 m tall. They are mostly poplars (*Populus* sp.), mulberrys (*Morus* sp.), and plane trees (*Platanus* sp.). Bigger canals are also bordered by tall trees, mostly by poplars, but arranged in groups, not in a line. This arrangement produces areas inside barriers of tall trees, which are occupied by plantations of vine (~1.7 m tall), and olive (~ 5 m tall). Given that Mendoza lies in a semi-desert region, canals provide main sources of water. Tall trees at the sides of roads and canals can act as perches for predator birds and for cowbirds.

Study species. The breeding season of Creamy-bellied Thrushes extends from October to December in the study area (Astié & Luchesi 2012). They lay three eggs (Astié & Reboreda 2005) and usually have two nesting attempts per season (Astié 2004). Incubation period is 11.5 days and nestling period is 12 days (Astié & Reboreda 2005).

Nests of Creamy-bellied Thrush are heavily predated (67% of the nests, Astié & Luchesi 2012) and parasitized by Shiny Cowbirds (frequency = 60% of nests, intensity = 1.6 eggs per nest; Astié & Reboreda 2006). Nest predation accounts for the loss of the entire clutch, as in the study area there is no

evidence of partial predation or brood reduction caused by chick starvation (Astié & Luchesi 2012). Nest predation is constant throughout the season and is not associated with the time a nest is initiated (Astié & Luchesi 2012). On the other hand, egg punctures by Shiny Cowbird are an important cause of reproductive loss in this host. At least one thrush egg was punctured in 71% of parasitized nests (Astié & Reboreda 2009a). They also punctured eggs in 42% of non-parasitized nests, probably to assess the degree of embryonic development to decide whether to parasitize that nest (Astié & Reboreda 2009a). Because parasitized nests have a higher frequency of eggs punctured and a lower hatching success than non-parasitized nests, they produce 20–25% fewer fledglings (Astié & Reboreda 2006, 2009a). Rates of nest parasitism are constant throughout the season (Astié & Reboreda 2006). All these citations (Astié & Reboreda 2005, 2006, 2009a; Astié & Luchesi 2012) refer to the same study site and years of study.

Data collection. During the breeding seasons of 2000–2002 (October–December), I searched for thrush nests systematically and using behavioral cues. To ensure that search effort was uniform independently of microhabitat characteristics, I divided my study area into five plots (20 ha). I searched for nests in one of these plots each day in a pre-determined order so each plot was visited every five days. Plots were gridded, and I walked at a regular speed while I searching for nests by eye. When I heard alarm calls from adult Creamy-bellied Thrushes, I stopped the systematic search and searched carefully around following the alarm calls. I determined nest stage (building, laying, incubation, or nestling). Once I found a nest, I visited it every 1–2 days until young fledged or nests failed. For each visit, I recorded the number of host and parasite eggs and if any eggs had been punc-

tured. I considered a nest was located by a Shiny Cowbird when I found a parasite egg or a thrush egg punctured in the nest between two consecutive visits (see Astié & Reboresda 2006 for details). I considered a nest predated when all eggs or chicks disappeared between two consecutive visits.

For each nest, I recorded the substrate (olive or vine), distance to the closest road, distance to the closest canal, and nest concealment. I estimated nest concealment by eye as the proportion of the nest cup ($\pm 5\%$) not visible from 0.5 m above the nest (Clotfelter 1998). All parameters were measured the day they were predated or parasitized.

Statistical analyses. I only included in the analysis nests found during building or egg laying and that survived until three days after the start of the incubation. I used this criterion to be more conservative because: 1) nests found later may bias the sample to nests less vulnerable to predation, and 2) more than 80% of parasitism occurred on or before the third day after laying (Astié & Reboresda 2009b).

A correlation analysis (Polycor Package, Fox 2007) showed no values higher than 0.70 ($P < 0.05$) among any pair of the independent microhabitat variables mentioned above. So I included all of them in subsequent analyses.

To determine if microhabitat variables affected the probability that a nest would be found by a predator or a Shiny Cowbird, I applied Generalized Linear Models (GLM) with a binomial distribution (link function = logit) using R software, version 2.15.1 (R Development Core Team 2012). In the first analysis, nest predation (predated or not) was the response variable. Year, substrate, distance to the closest road, distance to the closest canal, and concealment were the explanatory variables. In the second analysis, nest parasitism (nest was found by a brood parasite or not) was the response variable. Explanatory

variables were the same as in the first analysis.

I evaluated the models and parameter estimates following information-theoretic procedures (Burnham & Anderson 2002). This method allows model uncertainty to be included in both model evaluation and derivation of parameter estimates (Burnham & Anderson 2002). Models with all possible combinations of predictor variables were considered because there was no *a priori* basis to eliminate models. This resulted in 32 candidate models. Due to sample size ($N = 67$) I used Akaike's information criterion corrected for small sample size (AICc). I performed model comparisons with ΔAICc , which is the difference between the lowest AICc value (i.e., best of suitable models) and AICc from all other models. 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. I also calculated parameter estimates to supplement parameter-likelihood evidence of important effects, 95% confidence intervals.

RESULTS

During my three-year study (2000–2002), I found 237 nests. I recorded substrate, type of plantation, distance to the closest road and canal, and nest concealment for 67 nests. Forty-six of them were predated and 50 were parasitized. The rest of the nests were located in inaccessible places and I was unable to measure all the parameters. Predators I observed at nests during visits included rats (*Rattus* sp.), snakes (*Philodryas* sp.), Guira Cuckoos (*Guira guira*), and Chimango Caracaras (*Milvago chimango*).

The model that best described variation in predation included distance to the closest road ($w_i = 0.189$; Table 1). However, the 95% confidence interval encompassed 0 (Table 2), suggesting no effect of distance to the closest road on the likelihood of nest predation.

TABLE 1. GLM analysis of the predated and not predated nests (binomial distribution and logit link function). Models are listed in decreasing order of importance. The null model and models with support $w_i > 0.05$ are shown. Number of observations used = 67 nests. ^aDROA = distance to closest road, SUBS = substrate (olive/frutal or vine), CONC = concealment, and DCAN = distance to closest canal.

Model ^a	k	AICc	Δ AICc	w_i
DROA	2	83.55	0.00	0.189
DROA SUBS	3	85.19	1.64	0.084
SUBS	2	85.28	1.73	0.080
Null model	1	85.39	1.84	0.076
CONC DROA	3	85.60	2.05	0.068
DCAN DROA	3	85.61	2.06	0.068

Thus, no explanatory variable was related to predation (Table 2).

The model that best described variation in parasitism included year and concealment ($w_i = 0.151$; Table 3). However, as in the previous case, 95% confidence intervals encompassed 0 (Table 4), indicating no effect of year and concealment on parasitism. In consequence, no explanatory variable was related to parasitism (Table 4).

DISCUSSION

Most nests of Creamy-bellied Thrushes in the study area were predated. Distance to the closest road was the only variable included in the model that best explained the likelihood of nest predation. Although rates of predation tended to increase for nests closer to road, this model also demonstrates that there was no clear effect of this variable in the variation observed (Table 2). This result suggests that there are no edge, shelter, or corridor effects and also no relation between distance to nearest perches (tall trees growing along roads or canals) and predation rates. My results also do not support the concealment hypothesis

(greater rates of nest predation in less concealed nests; Cresswell 1997). In addition, I did not find an effect of substrate on predation. Therefore, none of the microhabitat characteristics I examined explained differences in nest predation rates in my study.

Correlations between microhabitat characteristics and nest predation rates remains equivocal. Although some studies did find some relationships, others did not (Latif *et al.* 2012). For instance, empirical evidence has shown that nest concealment has a negative (Colombelli-Négrel & Kleindorfer 2009, Matsui & Takagi 2012) or a null relationship with predation rates (Filliater *et al.* 1994, Colombelli-Négrel & Kleindorfer 2009). Similarly, authors that considered roads as edges, did not find an effect on nest predation rates (Mankin & Warner 1992, Huhta 1995, Pasitschiniak-Arts *et al.* 1998). In addition, road sides have been considered as shelters to protect terrestrial and arboreal predators from humans because of the presence of tall trees and the dense shrubs (Brzezinski *et al.* 2012). Several studies have demonstrated that understanding the interaction among variables is a central issue. Nest predation may or may not be affected by nest concealment depending on nest height (Colombelli-Négrel & Kleindorfer 2009), by the distance to an edge depending on the year (Svobodová *et al.* 2011), or by the distance to a road depending on human activity (Pescador & Peri 2007). In this work I found that predation tended to increase for nests closer to a road but correlation was not strong enough to support edge, shelter or corridor effect. However, sample size in this work is small and I can not discard that the power of this analysis have affected the results. Futures works will need to increase sample size in order to provide a better estimation of the effect of distance to a road.

Nest predators can use different cues (visual or olfactory) to find nests. The fre-

TABLE 2. Parameter estimates (\pm SE) from generalized linear models of the predated and not predated nests. Parameter estimates are weighted averages from all models, and standard errors (SE) are calculated from all candidate models using unconditional variances. Upper and lower confidence limits intervals (95%) are shown. Explanatory variables are listed in decreasing order of importance. aDROA = distance to closest road, SUBS = substrate (olive/frutal or vine), CONC = concealment, DCAN = distance to closest canal, and YEAR (2000, 2001, and 2002). bRelative to value of substrate (olive/frutal). cRelative to value of year 2000.

Explanatory variable ^a	Parameter likelihood	Parameter estimate \pm SE	Confidence interval	
			Lower	Upper
Intercept		0.758 \pm 0.762	-0.736	2.252
DROA	0.58	-0.005 \pm 0.003	-0.011	0.001
SUBS (vine) ^b	0.36	0.740 \pm 0.765	-0.760	2.240
DCAN	0.28	-0.001 \pm 0.003	-0.006	0.004
CONC	0.26	0.001 \pm 0.010	-0.019	0.021
YEAR (2001) ^c	0.19	0.537 \pm 0.647	-0.731	1.805
YEAR (2002) ^c	0.19	1.036 \pm 0.878	-0.684	2.757

quent lack of congruence between studies has been attributed to the presence of multiple predator species differing in their prey search strategies (Filliater *et al.* 1994, Matsui & Takagi 2012, Svobodova *et al.* 2012). Besides, differences in the density of a single predator species could produce changes in nest predation rates (Lahti 2001). In the study area, I found a great variety of predators (both visual and olfactory) but I lack information about their densities. The absence of a clear pattern in this study could be related to the different ways in which each predator affects nest predation rates.

In this study area, brood parasitism affects most of the Creamy-bellied Thrush nests. The model that best explained brood parasitism included nest concealment (more concealed nests were slightly more parasitized), but this variable was not enough to explain the observed variance (Table 4). As with nest predation analysis, I found no effect of any of the microhabitat characteristics I examined on parasitism rates. This result agrees with several previous studies that found that parasitism rates were not

affected by nest concealment (Smith 1981, Brittingham & Temple 1996, Burham 1997, Svagelj *et al.* 2009) or distance to perches (Brittingham & Temple 1996, Fiorini *et al.* 2009).

An alternative explanation for mechanisms and cues used by brood parasites to find host nests (not tested in this study) is that cowbirds use nest building behavior to locate nests (Bank & Martin 2001). Evidence supporting this hypothesis has been provided for Shiny Cowbirds (but see Fiorini *et al.* 2009), e.g., they synchronize egg laying with hosts almost perfectly (Lichtenstein 1998, Massoni & Reboresda 1998, Mermoz & Reboresda 1999, Astié & Reboresda 2009b). However, the host-activity hypothesis and the microhabitat-cues hypothesis are not mutually exclusive; furthermore, they could be complementary (Clotfelter 1998).

Brood parasitism and nest predation rates in this study were similar. Cowbird parasitism decreases breeding success by 20% while nest predation decreases breeding success by 100%. Predation seems to be a more important selective force. Still, I cannot discard that

TABLE 3. GLM analysis of parasitized and non-parasitized nests (binomial distribution and logit link function). Models are listed in decreasing order of importance. The null model, and models with support $w_i > 0.05$ are shown. Number of observations used = 67 nests. ^aDROA = distance to closest road, SUBS = substrate (olive/frutal or vine), CONC = concealment, DWAT = distance to closest canal, and YEAR (2000, 2001, and 2002).

Model ^a	k	AICc	Δ AICc	w_i
YEAR CONC	4	76.89	0.00	0.151
Null model	1	77.96	1.07	0.089
CONC	2	78.54	1.65	0.066
YEAR CONC DROA	5	78.73	1.84	0.060
DROA	2	78.86	1.97	0.056
YEAR CONC SUBS	5	78.88	1.99	0.056
YEAR CONC DCAN	5	79.01	2.12	0.052
CONC DROA	3	79.02	2.13	0.052

TABLE 4. Full GLM analysis (binomial distribution and logit link function) of the parasitized and not parasitized nests. ^aRelative to value of substrate (olive/frutal). ^bRelative to value of year (2000).

Explanatory variable ^a	Parameter likelihood	Parameter estimate \pm SE	Confidence interval	
			Lower	Upper
Intercept		0.977 \pm 0.905	-1.011	2.820
CONC	0.61	0.020 \pm 0.012	-0.004	0.043
YEAR (2001) ^b	0.50	-1.630 \pm 0.942	-3.476	0.216
YEAR (2002) ^b	0.50	-1.956 \pm 1.143	-4.197	0.285
DROAD	0.34	0.004 \pm 0.004	-0.005	0.012
SUBS (vine) _a	0.27	-0.190 \pm 1.007	-2.165	1.784
DWAT	0.26	0.001 \pm 0.004	-0.006	0.009

microhabitat characteristics that minimize predation were different from microhabitat characteristics that minimize parasitism, in which case selection forces could be in conflict and no pattern would emerge. Likewise, it is possible that other characteristics, not recorded in this work, could be playing a main role in nest predation and parasitism rates.

This study, in concordance with several previous studies, fails to support the hypothesis that nest-site selection affect nest predation or brood parasitism rates. Future work should include a wider variety of microhabitat and nest variables, as well as an estimation of

predators diversity and abundance and information about parental activity. Besides, increase database could bring a better idea of the importance of the variables in the models that best explained the likelihood of nest predation and brood parasitism.

ACKNOWLEDGMENTS

I thank Nicolás García, Paulo E. Llambías, and Florencia Fernandez Campón for helpful comments on this manuscript and for statistical advice and Valentina Ferretti, and two

anonymous reviewers for comments on the manuscript. AAA is a Research Fellow of CONICET. This study was supported by grants of Agencia Nacional de Promoción Científica y Tecnológica and CONICET.

REFERENCES

- Astié, A. A. 2004. Interacciones entre el parásito de cría *Molothrus bonariensis* y uno de sus hospedadores, *Turdus amaurochalinus*. Tesis Doctoral, Univ. de Buenos Aires, Buenos Aires, Argentina.
- Astié, A. A., & N. Luchesi. 2012. Reproductive success of the Creamy-bellied Thrush in a southern temperate zone. *Wilson J. Ornithol.* 124: 136–141.
- Astié, A. A., & J. C. Reboreda. 2005. Creamy-bellied Thrush defenses against Shiny Cowbird brood parasitism. *Condor* 107: 788–796.
- Astié, A. A., & J. C. Reboreda. 2006. Cost of egg punctures and parasitism by Shiny Cowbirds (*Molothrus bonariensis*) at Creamy-bellied Thrush (*Turdus amaurochalinus*) nests. *Auk* 123: 23–32.
- Astié, A. A., & J. C. Reboreda. 2009a. Function of egg punctures by Shiny Cowbirds in parasitized and non-parasitized Creamy-bellied Thrush nests. *J. Field Ornithol.* 80: 336–343.
- Astié, A. A., & J. C. Reboreda. 2009b. Shiny Cowbird parasitism of a low quality host: effect of host traits on a parasites reproductive success. *J. Field Ornithol.* 80: 224–233.
- Banks, J., & T. E. Martin. 2001. Host activity and the risk of nest parasitism by Brown-headed Cowbirds. *Behav. Ecol.* 12: 31–40.
- Bergin, T. M., L. B. Best, & K. E. Freemark. 1997. An experimental study of predation on artificial nests in roadsides adjacent to agricultural habitats in Iowa. *Wilson Bull.* 109: 437–448.
- Best, L. B., & D. F. Stauffer. 1980. Factors affecting nesting success in riparian bird communities. *Condor* 82: 149–158.
- Brittingham, M. C., & S. A. Temple. 1996. Vegetation around parasitized and non-parasitized nests within deciduous forests. *J. Field Ornithol.* 67: 406–413.
- Brzezinski, M., M. Natorff, A. Zalewski, & M. Zmihorski. 2012. Numerical and behavioral responses of waterfowl to the invasive American mink: a conservation paradox. *Biol. Conserv.* 147: 68–78.
- Burhan, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* 99: 866–872.
- Burnham, K. P., & D. R. Anderson. 2002. Model selection and multimodel inference: a practical information theoretic approach. Springer-Verlag, New York, New York, USA.
- Carter, M. D. 1986. The parasitic behavior of the Bronzed Cowbird in south Texas. *Condor* 88: 11–25.
- Clotfelter, E. D. 1998. What cues do Brown-headed Cowbirds use to locate Red-winged Blackbird host nests? *Anim. Behav.* 55: 1181–1189.
- Colombelli-Négrel, D., & S. Kleindorfer. 2009. Nest height, nest concealment, and predator type predict nest predation in Superb Fairywrens (*Malurus cyaneus*). *Ecol. Res.* 24: 921–928.
- Cresswell, W. 1997. Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* 53: 93–103.
- Crino, O. L., B. Klaassen Van Oorschot, E. E. Johnson, J. L. Malisch, & C. W. Breuner. 2011. Proximity to a high traffic road: glucocorticoid and life history consequences for nestling White-crowned Sparrows. *Gen. Comp. Endocr.* 173: 323–332.
- Filliater, T. S., R. Breitwisch, & P. M. Nealen. 1994. Predation on Northern Cardinal nests: does choice of nest site matter? *Condor* 96: 761–768.
- Fiorini, V. D., D. T. Tuero, & J. C. Reboreda. 2009. Host behaviour and nest-site characteristics affect the likelihood of brood parasitism by Shiny Cowbirds on Chalk-browed Mockingbirds. *Behaviour* 146: 1387–1403.
- Fox, J. 2007. Polycor: polychoric and polyserial correlations. R package version 0.7-5. Available at <http://www.CRAN.R-project.org/package=polycor> [Accessed 5 October 2013].
- Freeman, S., D. F. Gori, & S. Rohwer. 1990. Red-winged Blackbirds and Brown-headed Cowbirds: some aspects of a host-parasite relationship. *Condor* 92: 336–340.
- Gates, J. E., & L. W. Gysel. 1978. Avian nest dis-

- persion and fledgling success in field forest ecotones. *Ecology* 59: 871–883.
- Hauber, M. E., & S. A. Russo. 2000. Perch proximity correlates with higher rates of cowbird parasitism of ground nesting Song Sparrows. *Wilson Bull.* 112: 150–153.
- Huhta, E. 1995. Effects of spatial scale and vegetation cover on predation of artificial ground nests. *Wildl. Biol.* 1: 73–80.
- King, J. R. 1973. Reproductive relationships of the Rufous-collared Sparrow and the Shiny Cowbird. *Auk* 90: 19–34.
- Lahti, D. C. 2001. The edge effect on nest predation hypothesis after twenty years. *Biol. Conserv.* 99: 365–374.
- Larison, B., S. A. Laymon, P. L. Williams, & T. B. Smith. 1998. Song Sparrows vs. cowbird brood parasites: impacts of forest structure and nest-site selection. *Condor* 100: 93–101.
- Latif, Q. S., S. K. Heath, & J. T. Rotenberry. 2012. How avian nest site selection responds to predation risk: testing an adaptive peak hypothesis. *J. Anim. Ecol.* 81: 127–138.
- Lichtenstein, G. 1998. Parasitism by Shiny Cowbird of Rufous-bellied Thrushes. *Condor* 100: 680–687.
- Mankin, P. C., & R. E. Warner. 1992. Vulnerability of ground nests to predation on an agricultural habitat island in east-central Illinois. *Am. Midl. Nat.* 128: 281–291.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitats: revising the dogmas. *Am. Nat.* 141: 897–913.
- Martin, T. E., P. R. Martin, C. R. Olson, B. J. Heidinger, & J. J. Fontaine. 2000. Parental care and clutch sizes in North and South America birds. *Science* 287: 1482–1485.
- Marvil, R. E., & A. Cruz. 1989. Impact of Brown-headed Cowbird parasitism on the reproductive success of the Solitary Vireo. *Auk* 106: 476–480.
- Massoni, V., & J. C. Reboreda. 1998. Costs of brood parasitism and the lack of defenses on the Yellow-winged Blackbird - Shiny Cowbird system. *Behav. Ecol. Sociobiol.* 42: 273–280.
- Matsui, S., & M. Takagi. 2012. Predation risk of eggs and nestlings relative to nest-site characteristics of the Bull-headed Shrike *Lanius bucephalus*. *Ibis* 154: 621–625.
- McLaren, M. C., & S. G. Sealy. 2003. Factors influencing susceptibility of host nests to brood parasitism. *Ethol. Ecol. Evol.* 15: 343–353.
- McMaster, D. G., & S. G. Sealy. 1997. Host-egg removal by Brown-headed Cowbirds: a test of the host incubation limit hypothesis. *Auk* 114: 212–220.
- Mermoz, M. E., & J. C. Reboreda. 1999. Egg-laying behaviour by Shiny Cowbirds parasitizing Brown-and-yellow Marshbirds. *Anim. Behav.* 58: 873–882.
- Pasitschniak-Arts, M., R. G. Clark, & F. Messier. 1998. Duck nesting success in a fragmented prairie landscape: is edge effect important? *Biol. Conserv.* 85: 55–62.
- Pescador, M., & S. Peris. 2007. Influence of roads on bird nest predation: An experimental study in the Iberian Peninsula. *Landscape Urban Plann.* 82: 66–71.
- Petit, L. 1991. Adaptive tolerance of cowbird parasitism by Prothonotary Warblers: a consequence of nest-site limitation. *Anim. Behav.* 41: 425–432.
- Post, W., & J. W. Wiley. 1977. Reproductive interactions of the Shiny Cowbird and the Yellow-shouldered Blackbird. *Condor* 79: 176–184.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rodewald, A. D. 2009. Urban-associated habitat alteration promotes brood parasitism of Acadian Flycatchers. *J. Field Ornithol.* 80: 234–241.
- Rothstein, S. L., & S. K. Robinson. 1998. The evolution and ecology of avian brood parasitism. Pp 356 *in* Rothstein, S. L., & S. K. Robinson (eds). *Parasitic birds and their hosts: studies in coevolution*. Oxford Univ. Press, New York, New York, USA.
- Saunders, C. A., P. Arcese, & K. D. O'Connor. 2003. Nest site characteristics in the Song Sparrow and parasitism by Brown-headed Cowbirds. *Wilson Bull.* 115: 24–28.
- Sealy, S. G. 1992. Removal of Yellow Warbler eggs in association with Cowbirds parasitism. *Condor* 94: 40–54.
- Sheldon, R. D., K. Chaney, & G. A. Tyler. 2007. Factors affecting nest survival of Northern Lapwings *Vanellus vanellus* in arable farmland:

- an agri-environment scheme prescription can enhance nest survival. *Bird Study* 54: 168–175.
- Smith, J. N. M. 1981. Cowbird parasitism, host fitness and age of the host female in an island Song Sparrow population. *Condor* 83: 152–161.
- Svageľ, W. S., G. J. Fernández, & M. E. Mermoz. 2009. Effects of nest-site characteristics and parental activity on cowbird parasitism and nest predation in Brown-and-yellow Marshbirds. *J. Field Ornithol.* 80: 13–22.
- Svobodová, J., J. Kreisinger, M. Sálek, M. Koubová, & T. Albrecht. 2011. Testing mechanistic explanations for mammalian predator responses to habitat edges. *Eur. J. Wildl. Res.* 57: 467–474.
- Svobodová, J., M. Koubová, L. Mrstný, T. Albrecht, & J. Kreisinger. 2012. Temporal variation in nest predation risk along habitat edges between grassland and secondary forest in central Europe. *Eur. J. Wildl. Res.* 58: 315–323.