

What cues do brown-headed cowbirds use to locate red-winged blackbird host nests?

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Abstract. I examined ecological and behavioural variables influencing the susceptibility of red-winged blackbird, *Agelaius phoeniceus*, nests to brood parasitism by brown-headed cowbirds, *Molothrus ater*, in a prairie-nesting population of redwings in southern Wisconsin. I compared the following variables between parasitized and unparasitized nests: proximity of nests to trees and other prominent perches; physical characteristics of nests such as nest height and cover; and aspects of host behaviour, including vocal behaviour and aggression directed towards female cowbirds. I used these data to discriminate among four non-exclusive hypotheses for how brood parasites locate host nests: the perch-proximity, nest-exposure, nesting-cue and host-activity hypotheses. Parasitized nests were significantly closer than unparasitized nests to trees in the 2 years of the study. There was no evidence that nest height or nest cover differed significantly between parasitized and unparasitized nests, suggesting that cowbirds do not use nest exposure as a cue for locating redwing nests. The responses of both parasitized and unparasitized redwings towards a female cowbird mount decreased with increasing mount presentation distance from the nest. There were no significant differences in responses towards the mount between parasitized and unparasitized redwings, giving no support for the nesting-cue hypothesis. Female redwings whose nests were subsequently parasitized gave significantly more nest-associated (type I) vocalizations during the egg-laying period than did unparasitized females. These findings suggest that female brown-headed cowbirds in search of potential host nests use trees to search from, and that female redwing vocalizations may serve as a proximate cue for cowbirds to locate redwing nests at appropriate stages for parasitism, giving support for both the perch-proximity and host-activity hypotheses.

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There is considerable interest in assessing the effects avian brood parasites have on their hosts, and in understanding coevolutionary processes in host-parasite systems (e.g. Rothstein 1990; Rothstein & Robinson, in press; Smith et al., in press). As a consequence of the high fecundity characteristic of many parasitic species, and because parasitizing hosts at appropriate stages in the egg-laying period is necessary for high hatching success and nestling survival, brood parasites must continually search for hosts throughout the breeding season (Payne 1977; Wyllic 1981; Scott & Ankney 1983). Little is known, however, about how parasites locate host nests. Information on parasite nest-searching behaviour has been hard

to obtain, in part due to the difficulties in following the movements of individual parasites and to the scarcity of some species relative to their hosts (Wyllic 1981; Rothstein et al. 1984; Brooke & Davies 1987).

Brood parasites use both active and passive strategies for locating host nests. Some authors have observed individuals or groups of brood parasites systematically searching the vegetation, presumably for nesting birds (Norman & Robertson 1975; Carter 1986; Wiley 1988). More commonly, brood parasites have been seen cryptically observing their prospective hosts' activity (Hann 1941; Gochfeld 1979; Wiley & Wiley 1980; Alvarez 1993). For example, host nests near prominent perch sites (e.g. trees, snags) are more susceptible to parasitism than are nests further away from such perches (Anderson & Storer 1976; Freeman et al. 1990; Romig & Crawford 1995;

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Øien et al. 1996). Nests that can be seen without obstruction from perch sites are also at a greater risk than nests obscured from view (Øien et al. 1996). Despite this evidence, however, little is known about the specific cues that brood parasites use to locate nests.

The nest-exposure hypothesis predicts that brood parasites cue on visually conspicuous host nests. Nests constructed in tall vegetation or with little cover may be more visible to brood parasites than are concealed nests, and are therefore more likely to be parasitized. In ground-nesting ducks, for example, exposed nests are more susceptible to interspecific parasitism than are concealed nests (Hines & Mitchell 1984; Lokemoen 1991). In passerine species, the relationship between parasitism and nest characteristics may vary among habitat types. Parasitism of many host species by brown-headed cowbirds, *Molothrus ater*, has been shown to increase with increasing nest height in shrub or grassland habitats (Martin 1993). Parasitism of other shrub-nesting species, however, occurs regardless of the percentage of nest cover (Smith 1981; Eckerle 1994; Barber & Martin 1997). In forested habitats, the importance of nest height and nest exposure as predictors of brood parasitism is unclear (Wolf 1987; Briskie et al. 1990; Martin 1993; Brittingham & Temple 1996).

Brood parasites might also cue on conspicuous host behaviours, especially behaviours performed near the nest. The nesting-cue hypothesis predicts that hosts that respond more aggressively towards adult parasites are parasitized more often than are their less aggressive conspecifics (Robertson & Norman 1977; Smith 1981; Smith et al. 1984). The host-activity hypothesis predicts that brood parasites are attracted to highly vocal hosts (Gochfeld 1979; Uyehara & Narins 1995) or to host nest-building behaviour (Hann 1941; Weller 1959; Wiley & Wiley 1980). Some hosts give specific nest-associated vocalizations, which could alert brood parasites to the presence of an active nest (McDonald & Greenberg 1991). Freeman et al. (1990) found that on marshes with no trees, the timing of egg laying by brown-headed cowbirds was less synchronized with their red-winged blackbird, *Agelaius phoeniceus*, hosts than on marshes with trees present. This result suggests that perch sites are necessary for obtaining accurate information on nest status, and that host activity is a more important cue than nest exposure. Studies using artificial nests typically experience very low

parasitism rates, which has been attributed to the absence of host activity to attract brood parasites (Thompson & Gottfried 1976, 1981; Yahner & DeLong 1992). The use of decoy hosts near wood duck, *Aix sponsa*, nestboxes increased the rate of conspecific brood parasitism, giving additional support for the hypothesis that brood parasites cue on host activity near the nest (Wilson 1993).

The goal of the current study was to evaluate the cues available to brown-headed cowbirds as they search for nests of red-winged blackbirds, and the extent to which natural variation in these potential cues affects actual parasitism decisions. Brown-headed cowbirds are obligate, generalist brood parasites (Friedmann & Kiff 1985), and red-winged blackbirds are one of their most widespread and abundant hosts (Freeman et al. 1990). In this study, I evaluated the importance of the following variables in determining patterns of cowbird parasitism in a prairie-nesting population of redwings: proximity of trees and perches to redwing nests; physical characteristics such as nest height and nest cover; and aspects of redwing behaviour such as male and female vocalizations and aggressive behaviour towards female cowbird mounts. These data allowed me to test the perch-proximity, nest-exposure, nesting-cue and host-activity hypotheses in the same host-parasite system.

METHODS

Study Area and General Methods

I studied brown-headed cowbird parasitism of a prairie-nesting population of red-winged blackbirds in southern Wisconsin, U.S.A. (42°32'N, 89°08'W) in March–July of 1995 and 1996. The study area, Diehls Prairie, is an 18-ha grass and sedge meadow marked with a grid of 20 × 20-m squares (measured and positioned with a Topcon GTS-300 electronic surveying station). Diehls Prairie is adjacent to Newark Road Prairie, where red-winged blackbirds have been studied extensively by Yasukawa and colleagues (e.g. Yasukawa et al. 1987, 1992; Yasukawa 1989). Diehls Prairie supports 30–35 territorial male redwings per year, each of which usually attracts two to three females to his territory. I found 86 and 111 redwing nests in 1995 and 1996, respectively, of which 13 (15.1%) and 27 (24.3%) were parasitized. Most parasitized nests contained only

one cowbird egg; no multiple parasitism occurred in 1995, and only five of 27 (18.5%) parasitized nests contained more than one cowbird egg in 1996. I experimentally parasitized 17 of 86 (19.8%) and 8 of 111 (7.3%) nests with cowbird eggs taken from Newark Road Prairie in 1995 and 1996, respectively. In 1995, I found evidence to suggest that experimentally parasitized nests were more likely to be avoided by brown-headed cowbirds than expected by chance (unpublished data; see Ortega et al. 1994). Therefore, these nests were excluded from all comparisons of parasitized and unparasitized nests, although separate analyses showed that their inclusion would not alter any of the results.

Nearest Tree and Perch Distances

I measured the distances between redwing nests and the nearest tree (defined as any woody vegetation higher than 3 m) to the nearest cm with a 30-m measuring tape, except in cases where the nearest tree was further away than 30 m. In those cases, I calculated the distance as the hypotenuse of the right triangle formed by the grid coordinates of the nest and the nearest tree. In 1995, the distances between redwing nests and the nearest natural perch site (non-woody vegetation) or nearest fencepost were also measured. Hereafter, these will be referred to as perches to distinguish them from trees. Although perches were potentially usable by both cowbirds and redwings, I identified nearest perches by observing perch-use by territorial male redwings. I measured distances between perches and nests as well as perch heights to the nearest cm. Nearest tree distance was recorded for 13 parasitized and 55 unparasitized nests in 1995, and for 27 parasitized and 73 unparasitized nests in 1996. In addition to experimentally parasitized nests, I excluded nearest tree distances for one and three nests in 1995 and 1996, respectively, because they were not within the gridded study area and therefore distances could not be accurately measured. Nearest perch distances were measured for 13 parasitized and 56 unparasitized nests in 1995.

Nest Characteristics

I measured nest height, lateral nest cover and overhead nest cover of redwing nests during the egg-laying period in 1996. Nest height was

measured to the nearest cm from the ground to the top rim of the nest cup. For nests built in emergent vegetation, I measured nest height from the water surface to the top of the nest cup. Lateral nest cover was estimated by taking four measurements 1 m from the nest at nest-height level. I made the four measurements approximately 90° apart beginning with magnetic north, and estimated by eye the percentage of lateral nest cover (to the nearest 10%) as the proportion of the nest cup obscured from view at this distance. I obtained a mean measure of lateral nest cover from these four measurements. Overhead nest cover, also recorded to the nearest 10%, was measured by standing directly above the nest and estimating by eye the percentage of the open cup obscured from view. For nests too tall to view in this manner, I used an adjustable mirror mounted on a 2-m pole to estimate the percentage of overhead nest cover. Nest characteristics were measured for 24 parasitized and 71 unparasitized nests in 1996. In addition to experimentally parasitized nests, nest height and nest cover were not measured for eight and nine nests, respectively, because these nests were too inaccessible to measure without disturbing them.

Host Behaviour

In 1995, I presented a female brown-headed cowbird mount at the nests of red-winged blackbirds and recorded aggressive responses by male and female redwings to compare between parasitized and unparasitized nests. I prepared three cowbird mounts by freeze-drying adult female cowbird specimens; the mount to be used in a given presentation was determined randomly. Live cowbirds courted and displayed to the freeze-dried mounts, which suggests that they were realistic representations of living cowbirds. Cowbird mounts were wired to wooden T-shaped perches approximately 0.75 m tall. I presented redwing nests with a cowbird mount for 5 min once during the morning (0500–0900 hours Central Daylight Time) on 2 consecutive days during the egg-laying period. Presentations were made when both the male and female redwing were present on the breeding territory. The cowbird mount was presented at one of three distances from the nest: within 1 m, and at 5 m and 10 m. The presentation distance was randomly determined for the two presentations. To avoid possible problems with

habituation, only responses from the first presentation at each nest were included in this analysis. During the 5-min presentation period, I recorded redwing responses in each 10-s interval (Smith et al. 1984). In each interval, I recorded the following responses by male and female redwings: the number of approaches to within 2 m of the mount (approaches); the number of vocalizations given (alarm calls); the number of dives within 1 m of the mount (passes); and the number of times physical contact was made with the mount (strikes) following Neudorf & Sealy (1992). I combined male and female responses to reflect the total response experienced by an approaching cowbird (Gill et al. 1997). Cowbird mounts were presented twice each at 34 red-winged blackbird nests, and one or both members of each pair responded aggressively in 33 of the 34 (97.1%) first presentations. No controls were used in these presentations, but numerous previous studies have established that red-winged blackbirds recognize brown-headed cowbirds as threats to the nest (Robertson & Norman 1977; Folkers & Lowther 1984; Neudorf & Sealy 1992; Gill et al. 1997). I made seven presentations within 1 m of the focal nest, 14 at 5 m and 12 at 10 m. Five experimentally parasitized nests were excluded from the comparison of aggressive responses between parasitized ($N=13$) and unparasitized ($N=15$) nests.

In 1996, I recorded male and female redwing vocalizations in the proximity of nests using lapel microphones (1.75×0.75 cm) concealed in milkweed, *Asclepias syriaca*, seed pods and connected to Sony TCM-500 tape-recorders. Microphones were placed within 50 cm of the focal nest; tape-recorders were covered with camouflaged mesh and placed 1.3 m away. I recorded 30-min segments at each focal nest once during the egg-laying period, and made all recordings during the morning (0600–0900 hours). All recordings were made after the first or second egg was laid to control for differences in vocal behaviour across the nesting cycle. These recordings were used to quantify two vocalizations: the male song-spread and the female type 1 (chit) song (Orians & Christman 1968; Beletsky & Orians 1985). I analysed tapes in real time and totaled vocalizations using hand-held counters. Recordings of male and female redwing vocal behaviour near nests were made for 34 nests in 1996. I excluded six recordings from the analysis because the focal nests were abandoned or because of poor recording quality.

Of the remaining 28 recordings, eight were from nests that were subsequently parasitized, and 20 were from unparasitized nests.

Statistical Analyses

I performed Mann-Whitney U -tests, t -tests, ANOVA and multiple regressions using SYSTAT software (Wilkinson 1990). The percentages of overhead and lateral nest cover data were not normally distributed; I used the angular transformation before analysing these data (Sokal & Rohlf 1981). Both nest height and percentage of overhead nest cover were positively related to nest initiation date; therefore, standardized residuals from regressions of nest initiation date on these dependent variables were used in comparisons of parasitized and unparasitized nests. In the comparison of aggressive responses towards cowbird mounts between parasitized and unparasitized pairs of redwings, I used standardized residuals from multiple regressions of presentation date, presentation time, clutch size and presentation distance on the four dependent variables (approaches, alarm calls, passes and strikes) to control for the confounding effects of these independent variables. Male and female redwing vocalization rates were unrelated to three independent variables (clutch size, recording time and recording date); therefore, I used the raw data in these comparisons. I considered differences significant at $P < 0.05$, and all statistical tests are two-tailed. Means are presented \pm SE.

RESULTS

Nearest Tree and Perch Distances

Parasitized nests were significantly more likely to be located near trees than were unparasitized nests (1995: $t_{66} = -2.52$, $P = 0.014$; 1996: $t_{98} = 3.17$, $P = 0.002$; Fig. 1). Perches were not significantly nearer to parasitized than to unparasitized nests ($t_{67} = 1.22$, $P = 0.23$; Fig. 1). The height of the nearest perches also did not differ significantly between parasitized and unparasitized nests ($X_{\text{parasit}} = 1.92 \pm 0.29$ m, $\bar{X}_{\text{unparasit}} = 2.13 \pm 0.25$ m; $t_{67} = 0.37$, $P = 0.60$).

Nest Characteristics

Nest height did not differ between parasitized ($\bar{X}_{\text{parasit}} = 40.61 \pm 3.82$ cm) and unparasitized

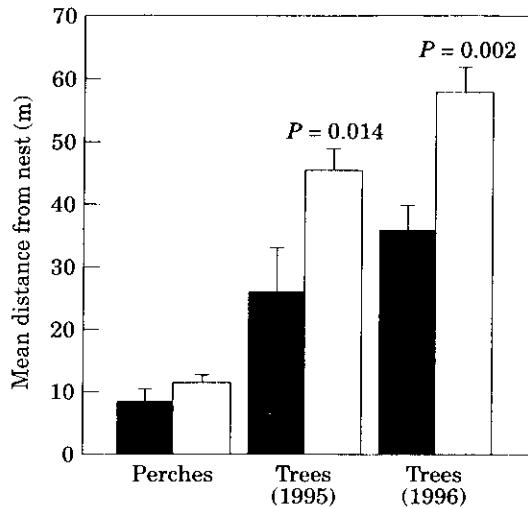


Figure 1. Comparison of nearest-perch and nearest-tree distances from parasitized (■) and unparasitized (□) red-winged blackbird nests. Nearest-perch distances were measured at 13 parasitized and 56 unparasitized nests in 1995. Nearest-tree distances were measured at 13 parasitized and 55 unparasitized nests in 1995 and at 27 parasitized and 73 unparasitized nests in 1996. Bars represent mean \pm SE distances; *P*-values are the results of two-tailed *t*-tests.

($\bar{X}_{\text{unparasit}} = 34.18 \pm 1.72$ cm) nests after controlling for nest initiation date ($X_{\text{parasit}} = 3.10 \pm 3.28$ cm, $X_{\text{unparasit}} = -1.05 \pm 1.31$ cm; $t_{93} = 1.41$, $P = 0.16$). Lateral ($\bar{X}_{\text{parasit}} = 79.50 \pm 4.58\%$, $X_{\text{unparasit}} = 83.87 \pm 1.87\%$) and overhead nest cover ($\bar{X}_{\text{parasit}} = 49.48 \pm 6.59\%$, $\bar{X}_{\text{unparasit}} = 42.50 \pm 3.28\%$) estimates were also similar between parasitized and unparasitized nests. After controlling for nest initiation date, differences were still not significant (lateral nest cover: $X_{\text{parasit}} = -0.034 \pm 0.081\%$, $\bar{X}_{\text{unparasit}} = 0.012 \pm 0.037\%$; $t_{93} = -0.58$, $P = 0.57$; overhead nest cover: $X_{\text{parasit}} = 0.048 \pm 0.082\%$, $X_{\text{unparasit}} = -0.016 \pm 0.043\%$; $t_{92} = 0.71$, $P = 0.48$).

Host Behaviour

Redwings responded more strongly towards the cowbird mount as the distance between the mount and the nest decreased (Fig. 2). One-way ANOVA results showed that approaches ($F_{1,31} = 9.12$, $P = 0.005$), alarm calls ($F_{1,31} = 17.41$, $P < 0.001$) and strikes ($F_{1,31} = 9.45$, $P = 0.004$) were all significantly more frequent when the mount was placed within 1 m of the nest than when it was placed either 5 or

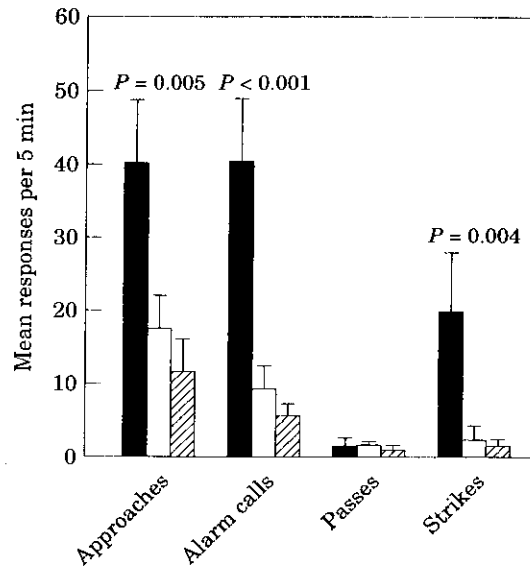


Figure 2. Combined aggressive responses by male and female red-winged blackbirds towards a female brown-headed cowbird mount during a 5-min period. Aggressive responses include approaches to within 2 m of the mount, alarm calls, passes within 1 m of the mount and strikes. Seven nests were presented with the mount within 1 m of the nest (■), 14 nests were presented with the mount 5 m from the nest (□), and 12 nests were presented with the mount 10 m from the nest (▨). Bars represent mean \pm SE responses; *P*-values are the results of one-way ANOVA.

10 m from the nest. The number of passes made towards the mount did not differ among the three presentation distances (Fig. 2).

Parasitized and unparasitized pairs of redwings responded similarly to the cowbird mount (approaches/5 min: $X_{\text{parasit}} = 21.38 \pm 5.29$, $\bar{X}_{\text{unparasit}} = 18.27 \pm 5.21$; alarm calls/5 min: $X_{\text{parasit}} = 10.92 \pm 4.32$, $\bar{X}_{\text{unparasit}} = 16.07 \pm 5.27$; passes/5 min: $X_{\text{parasit}} = 1.54 \pm 0.51$, $X_{\text{unparasit}} = 1.87 \pm 0.65$; strikes/5 min: $X_{\text{parasit}} = 4.0 \pm 2.34$, $X_{\text{unparasit}} = 6.2 \pm 3.85$). After controlling for presentation distance, clutch size, presentation time and presentation date, there were no significant differences between parasitized and unparasitized redwings in the residual number of approaches ($X_{\text{parasit}} = 1.74 \pm 5.09$, $X_{\text{unparasit}} = 0.78 \pm 3.38$; $t_{26} = 0.16$, $P = 0.87$), alarm calls ($X_{\text{parasit}} = -3.57 \pm 4.04$, $\bar{X}_{\text{unparasit}} = 3.72 \pm 2.74$; $t_{26} = -1.53$, $P = 0.14$), passes ($X_{\text{parasit}} = 0.065 \pm 0.45$, $X_{\text{unparasit}} = 0.40 \pm 0.65$; $t_{26} = -0.41$, $P = 0.69$) or strikes ($X_{\text{parasit}} = -2.12 \pm 2.15$; $X_{\text{unparasit}} = 1.83 \pm 2.88$; $t_{26} = -1.07$,

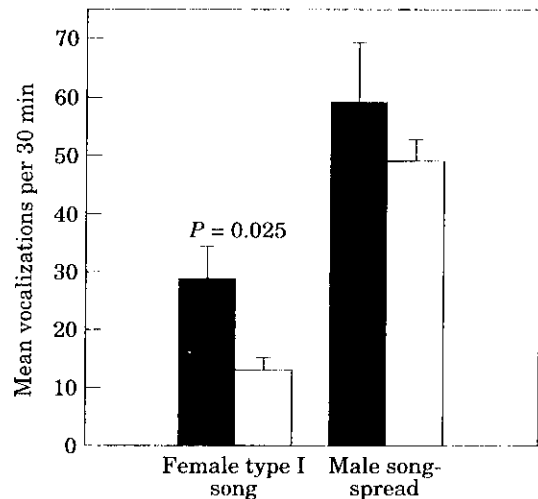


Figure 3. Differences in the mean number of vocalizations given by male and female red-winged blackbirds ($N=8$ parasitized pairs and $N=20$ unparasitized pairs) in 30-min recordings made during the egg-laying stage. Bars represent mean \pm SE vocalization rates; P -value represents the result of a two-tailed Mann-Whitney U -test. ■: Parasitized nests; □: unparasitized nests.

$P=0.29$) made in 5 min towards the cowbird mount.

There was no evidence that the number of song-spreads performed by a male redwing influenced the probability that a nest on his territory would be parasitized (Mann-Whitney U -test, $U=60.0$, $P=0.31$; Fig. 3). Female redwings whose nests were subsequently parasitized, however, gave significantly more type I songs than did females whose nests were not parasitized (Fig. 3; $U=36.0$, $P=0.025$). None of the other variables (clutch size, recording time and recording date) was a significant predictor of either male or female vocalization rates; therefore, differences in these variables do not explain the significant difference in type I song rate between females with parasitized and unparasitized nests.

DISCUSSION

Proximity to trees appears to be an important predictor of cowbird parasitism in this population of red-winged blackbirds, which supports results from studies of several host-parasite systems and gives support for the perch-proximity hypothesis (Anderson & Storer 1976; Freeman et al. 1990;

Romig & Crawford 1995; Øien et al. 1996). Observations of cowbirds perching in trees on both Diehls Prairie and Newark Road Prairie give additional support for the conclusion that they use trees to monitor their redwing hosts (personal observation). Mean distances from trees to both parasitized and unparasitized nests were approximately 10 m greater in 1996 than in 1995, which is probably the result of the increased nesting density in 1996, when more females nested in the interior of the study area. Unlike the nearest-tree data, I found no evidence that cowbird parasitism was related to nearest-perch distance. Perches were no closer to parasitized nests than to unparasitized nests. It is likely that perches were used rarely by cowbirds because they were used so frequently by male redwings. When artificial perches were added to redwing territories lacking perches, male redwings frequently used these perches but cowbirds never did (Yasukawa et al. 1992; K. Yasukawa, personal communication).

Nest cover and nest height have been shown to be important factors affecting brood parasitism in ground- and canopy-nesting birds, with more exposed nests usually suffering higher rates of parasitism (Hines & Mitchell 1984; Wolf 1987; Briskie et al. 1990; Lokemoen 1991; Martin 1993). Wiley & Wiley (1980) observed shiny cowbirds, *M. bonariensis*, hovering over marshes occupied by yellow-hooded blackbirds, *A. icterocephalus*, which they interpreted as cowbird nest-searching behaviour. If brown-headed cowbirds search for redwing nests in a manner similar to their congeners, then higher or more exposed nests are more likely to be parasitized. Martin (1993), whose study of grassland- and shrub-nesting birds included red-winged blackbirds, found evidence that nest height was a significant predictor of cowbird parasitism. I found no evidence, however, that any measure of nest conspicuousness influenced cowbird parasitism in my population of red-winged blackbirds, giving no support for the nest-exposure hypothesis.

Host species that are too small to repel brood parasites physically should benefit by adopting cryptic, inconspicuous behaviour near their nests (McLean 1987). In host species that are large enough to deter parasites, such as red-winged blackbirds, selection may favour aggression towards the parasite. Such behaviour would be maladaptive, however, if parasites are able to use host aggression to locate host nests (Robertson &

Norman 1977). For example, older female song sparrows, *Melospiza melodia*, were more frequently parasitized by brown-headed cowbirds than were younger females and this difference was due to higher aggression by older females towards cowbirds (Smith 1981; Smith et al. 1984). In the current study and others, red-winged blackbirds responded aggressively to the threat of cowbirds (Robertson & Norman 1977; Folkers & Lowther 1984; Neudorf & Sealy 1992; Gill et al. 1997). Results show that their responses decrease significantly at 5 m from the nest, suggesting that there is some threshold distance beyond which aggression toward parasites is not adaptive. The observation that redwings whose nests were subsequently parasitized were no more aggressive than unparasitized redwings, however, gives no support for the nesting-cue hypothesis. These results complement those of Gill et al. (1997) who tested the nesting-cue hypothesis in six species of cowbird hosts, including red-winged blackbirds.

Consistent with the host-activity hypothesis, female redwings whose nests were subsequently parasitized gave the nest-associated type I (chit) song significantly more frequently than did females whose nests escaped parasitism. The type I song is most often given as females depart from and return to the nest (Beletsky & Orians 1985; Yasukawa 1989). Thus, cowbirds may use this vocalization to locate nests, much as humans do. This finding is counterintuitive since one of the putative functions of the type I song is to coordinate male vigilance and nest defence when the female is away from the nest (Yasukawa 1989), although the importance of male vigilance in deterring brood parasitism is unknown. The rate at which the type I song is given also varies across the nesting cycle (Beletsky & Orians 1985; Yasukawa et al. 1987), so cowbirds may be able to obtain information regarding nest stage (i.e. egg laying, incubation or nestling) by observing arriving and departing female redwings. Cowbirds did not appear to cue on male singing behaviour in the current study as has been reported by previous authors (Gochfeld 1979; Uychara & Narins 1995; A. Banks, personal communication). A difference between these studies and the current one is that male redwing song-spreads are performed throughout the male's territory (Orians & Christman 1968). Therefore, song-spreads would not convey specific information to cowbirds as to the location of the host female or the location

of the nest (Gochfeld 1979; Uychara & Narins 1995).

Many studies have presented evidence that brood parasites use prominent perch sites to search for potential hosts, and that host behaviour or host-nest characteristics may provide important cues in locating nests. The current study is one of the first to test these different hypotheses in the same host-parasite system. The results presented here suggest that in open habitats, conspicuous host behaviours such as the type I song are more important determinants of cowbird parasitism of redwings than are characteristics of the nest itself. Future studies should examine the relative importance of host behaviour and nest characteristics in other habitats, such as woodlands, where perches are theoretically unlimited. The fact that nest-associated vocalizations similar to the type I song in red-winged blackbirds are found in other cowbird host species (McDonald & Greenberg 1991) suggests that host behaviour may be more important than we realize in determining patterns of brood parasitism in a variety of species.

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REFERENCES

- Alvarez, F. 1993. Proximity of trees facilitates parasitism by cuckoos, *Cuculus canorus* on rufous warblers *Cercotrichas galactotes*. *Ibis*, **135**, 331.

- Anderson, W. L. & Storer, R. W. 1976. Factors influencing Kirtland's warbler nesting success. *Jack-pine Warbler*, **54**, 105-115.
- Barber, D. R. & Martin, T. E. 1997. Influence of alternate host densities on brown-headed cowbird parasitism rates in black-capped vireos. *Condor*, **99**, 595-604.
- Beletsky, L. D. & Orians, G. H. 1985. Nest-associated vocalizations of female red-winged blackbirds, *Agelaius phoeniceus*. *Z. Tierpsychol.*, **69**, 329-339.
- Briskie, J. V., Sealy, S. G. & Hobson, K. A. 1990. Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behav. Ecol. Sociobiol.*, **27**, 403-410.
- Brittingham, M. C. & Temple, S. A. 1996. Vegetation around parasitized and non-parasitized nests within deciduous forest. *J. Field Ornithol.*, **67**, 406-413.
- Brooke, M. de L. & Davies, N. B. 1987. Recent changes in host usage by cuckoos *Cuculus canorus* in Britain. *J. Anim. Ecol.*, **56**, 873-883.
- Carter, M. D. 1986. The parasitic behavior of the bronzed cowbird in south Texas. *Condor*, **88**, 11-25.
- Eckerle, K. P. 1994. Northern cardinal response to brood parasitism by brown-headed cowbirds. M.Sc. thesis, University of Dayton.
- Folkers, K. L. & Lowther, P. E. 1984. Responses of nesting red-winged blackbirds and yellow warblers to brown-headed cowbirds. *J. Field Ornithol.*, **56**, 175-177.
- Frecman, S., Gori, D. F. & Rohwer, S. 1990. Red-winged blackbirds and brown-headed cowbirds: some aspects of a host parasite relationship. *Condor*, **92**, 336-340.
- Friedmann, H. & Kiff, L. F. 1985. The parasitic cowbirds and their hosts. *Proc. West. Found. Zool.*, **2**, 226-304.
- Gill, S. A., Grief, P. M., Staib, L. M. & Sealy, S. G. 1997. Does nest defence deter or facilitate cowbird parasitism? A test of the nesting-cue hypothesis. *Ethology*, **103**, 56-71.
- Gochfeld, M. 1979. Brood parasite and host coevolution: interactions between shiny cowbirds and two species of meadowlarks. *Am. Nat.*, **113**, 855-870.
- Hann, H. W. 1941. The cowbird at the nest. *Wilson Bull.*, **53**, 211-221.
- Hines, J. E. & Mitchell, G. J. 1984. Parasitic laying in nests of gadwalls. *Can. J. Zool.*, **62**, 627-630.
- Lokemoen, J. T. 1991. Brood parasitism among waterfowl nesting on islands and peninsulas in North Dakota. *Condor*, **93**, 340-345.
- McDonald, M. V. & Greenberg, R. 1991. Nest departure calls in female songbirds. *Condor*, **93**, 365-373.
- McLean, I. 1987. Response to a dangerous enemy: should a brood parasite be mobbed? *Ethology*, **75**, 235-245.
- Martin, T. E. 1993. Nest predation among vegetation layers and habitat types: revising the dogmas. *Am. Nat.*, **141**, 897-913.
- Neudorf, D. L. & Sealy, S. G. 1992. Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? *Behaviour*, **123**, 84-105.
- Norman, R. F. & Robertson, R. J. 1975. Nest-searching behavior in the brown-headed cowbird. *Auk*, **92**, 610-611.
- Øien, I. J., Honza, M., Moksnes, A. & Røskoft, E. 1996. The risk of parasitism in relation to the distance from reed warbler nests to cuckoo perches. *J. Anim. Ecol.*, **65**, 147-153.
- Orians, G. H. & Christman, G. M. 1968. A comparative study of the behavior of red-winged, tricolored, and yellow-headed blackbirds. *Univ. Calif. Publ. Zool.*, **84**, 1-81.
- Ortega, C. P., Ortega, J. C. & Cruz, A. 1994. Use of artificial brown-headed cowbird eggs as a potential management tool in deterring parasitism. *J. Wildl. Mgmt.*, **58**, 488-492.
- Payne, R. B. 1977. The ecology of brood parasitism in birds. *A. Rev. Ecol. Syst.*, **8**, 1-28.
- Robertson, R. J. & Norman, R. F. 1977. The function and evolution of aggressive host behavior towards the brown-headed cowbird (*Molothrus ater*). *Can. J. Zool.*, **55**, 508-518.
- Romig, G. P. & Crawford, R. D. 1995. Clay-colored sparrows in North Dakota parasitized by brown-headed cowbirds. *Prairie Nat.*, **27**, 193-203.
- Rothstein, S. I. 1990. A model system for coevolution: avian brood parasitism. *A. Rev. Ecol. Syst.*, **21**, 481-508.
- Rothstein, S. I. & Robinson, S. K. In press. *Parasitic Birds and Their Hosts*. New York: Oxford University Press.
- Rothstein, S. I., Verner, J. & Stevens, E. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird. *Ecology*, **65**, 77-88.
- Scott, D. M. & Ankney, C. D. 1983. The laying cycle of brown-headed cowbirds: passerine chickens? *Auk*, **100**, 583-592.
- Smith, J. M. N. 1981. Cowbird parasitism, host fitness, and age of the host female in an island song sparrow population. *Condor*, **83**, 152-161.
- Smith, J. M. N., Arcese, P. & McLean, I. 1984. Age, experience, and enemy recognition by wild song sparrows. *Behav. Ecol. Sociobiol.*, **14**, 101-106.
- Smith, J. M. N., Cook, T., Robinson, S. K., Rothstein, S. I. & Sealy, S. G. In press. *Ecology and Management of Cowbirds*. Austin, Texas: University of Texas Press.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry*. 2nd edn. New York: W.H. Freeman.
- Thompson, C. F. & Gottfried, B. M. 1976. How do cowbirds find and select nests to parasitize? *Wilson Bull.*, **88**, 673-675.
- Thompson, C. F. & Gottfried, B. M. 1981. Nest discovery and selection by brown-headed cowbirds. *Condor*, **83**, 268-269.
- Uyehara, J. C. & Narins, P. M. 1995. Nest defense by willow flycatchers to brood-parasitic intruders. *Condor*, **97**, 361-368.
- Weller, M. W. 1959. Parasitic egg-laying in the redhead (*Aythya americana*) and other North American Anatidae. *Ecol. Monogr.*, **29**, 333-365.
- Wiley, J. W. 1988. Host selection by the shiny cowbird. *Condor*, **90**, 289-303.

- Wiley, R. H. & Wiley, M. S. 1980. Spacing and timing in the nesting ecology of a tropical blackbird: comparison of populations in different environments. *Ecol. Monogr.*, **50**, 153-178.
- Wilkinson, L. 1990. *SYSTAT: The System for Statistics*. Evanston, Illinois: SYSTAT.
- Wilson, S. F. 1993. Use of wood duck decoys in a study of brood parasitism. *J. Field Ornithol.*, **64**, 337-340.
- Wolf, L. 1987. Host-parasite interactions of brown-headed cowbirds and dark-eyed juncos in Virginia. *Wilson Bull.*, **99**, 338-350.
- Wyllie, I. 1981. *The Cuckoo*. London: Batsford.
- Yahner, R. H. & DeLong, C. A. 1992. Avian predation and parasitism on artificial nests and eggs in two fragmented landscapes. *Wilson Bull.*, **104**, 162-168.
- Yasukawa, K. 1989. The costs and benefits of a vocal signal: the nest-associated 'chit' of the female red-winged blackbird, *Agelaius phoeniceus*. *Anim. Behav.*, **38**, 866-874.
- Yasukawa, K., Boley, R. A. & Simon, S. E. 1987. Seasonal changes in the vocal behaviour of female red-winged blackbirds, *Agelaius phoeniceus*. *Anim. Behav.*, **35**, 1416-1423.
- Yasukawa, K., Whittenberger, L. K. & Nielsen, T. A. 1992. Anti-predator vigilance in the red-winged blackbird, *Agelaius phoeniceus*: do males act as sentinels? *Anim. Behav.*, **43**, 961-969.