

# Host activity and the risk of nest parasitism by brown-headed cowbirds

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Proportions of nests parasitized by brown-headed cowbirds (*Molothrus ater*) vary greatly among host species, but factors underlying this variation remain poorly understood. Cowbirds are believed to find nests by watching host behavior. We tested the hypothesis that the activity of hosts during nest building correlates with the probability of parasitism among and within four sympatric hosts: dusky flycatchers (*Empidonax oberholseri*), warbling vireos (*Vireo gilvus*), yellow warblers (*Dendroica petechia*), and American redstarts (*Setophaga ruticilla*). Daily probability of parasitism varied substantially among these species, from 3% for dusky flycatchers to more than four times that for warbling vireos. The four species did not differ in the proportion of cowbirds fledged from their nests. Differences in nest placement did not explain differences in probability of parasitism among or within species. Parasitism frequencies increased among species that made longer nest-building visits, had a greater propensity to perch during nest approach, spent more time near their nests, and had males that vocalized more often near nests. Within species, females that visited their nests less often, spent more time on the nest per visit, and males that sang more and were active in a smaller area around their nests were more likely to be parasitized by cowbirds. These data support the hypothesis that cowbirds use the activity of hosts during nest building to locate nests. **Key words:** American redstart (*Setophaga ruticilla*), brood parasitism, brown-headed cowbird (*Molothrus ater*), dusky flycatcher (*Empidonax oberholseri*), host behaviors, host quality, nest building, nest concealment, nest visitation, perching frequency, vocalization rates, warbling vireo (*Vireo gilvus*), yellow warbler (*Dendroica petechia*). [*Behav Ecol* 12:31–40 (2001)]

Parasitism by brown-headed cowbirds (*Molothrus ater*) often has significant fitness costs (Payne, 1977; Rothstein, 1990) and has contributed to population declines in some host species, while exerting minimal costs to others (Lorenzana and Sealy, 1999). Fitness costs vary greatly among host species in part because cowbirds parasitize host species at widely divergent frequencies, even among hosts breeding in the same habitat (e.g., Barber and Martin, 1997; Briskie et al., 1990; Gochfeld, 1979; Smith and Arcese, 1994). The causes for variation in probability of parasitism among coexisting host species are poorly understood.

Cowbirds may parasitize suitable hosts more frequently than species that reject cowbird eggs (Scott, 1977; Sealy and Bazin, 1995) or more frequently than species that feed their young diets inappropriate for cowbirds (Kozlovic et al., 1996; Middleton, 1991). Yet parasitism frequencies vary even among coexisting high-quality hosts (Barber and Martin, 1997; Briskie et al., 1990; Gochfeld, 1979; Tewksbury et al., 1998), suggesting that host quality cannot adequately explain variation in parasitism frequencies among species.

The probability of parasitism may vary among hosts because differences in their behaviors assist cowbirds in locating nests. A variety of evidence suggests that parental behaviors at the nest influence detection and parasitism of nests. Female brown-headed cowbirds and shiny cowbirds (*M. bonariensis*) typically spend morning hours on breeding grounds watching host behavior, especially nest building (Friedmann, 1929; Hann, 1941; Kattan, 1997; Norman and Robertson, 1975; Wiley, 1988). Old nests, without parental activity are rarely parasitized (Grief, 1995; Jobin and Picman, 1995; Kale, 1985; Lowther, 1979; Thompson and Gottfried, 1976, 1981). Positive associations between nest-defense behavior and parasitism fre-

quency among species have been noted (Hobson and Sealy, 1989b; Robertson and Norman, 1977; but see Briskie et al., 1990), although evidence of cowbirds exploiting nest-defense behavior has been equivocal (Gill et al., 1997; Sealy et al., 1998). Other behaviors of hosts also may be used by nest-searching cowbirds. Within species, the behaviors of parasitized and unparasitized individuals have been found to differ; for instance, parasitized willow flycatchers (*Empidonax traillii*) vocalized more frequently than unparasitized conspecifics (Uyehara and Narins, 1995; see also Smith, 1981).

Following these studies, we tested a “general activity” hypothesis that host activity near nests increases the probability of parasitism among and within host species. First, we tested whether parasitism frequencies increased with increasing mean levels of activity across species. Second, we tested whether parasitism was more likely for pairs that were more active near their nests, within species.

We studied the four most abundant brown-headed cowbird hosts in riparian habitat in western Montana: dusky flycatchers (*Empidonax oberholseri*), warbling vireos (*Vireo gilvus*), yellow warblers (*Dendroica petechia*), and American redstarts (*Setophaga ruticilla*; see Tewksbury et al., 1998, for a description of the host community). These species build open-cup nests in the same shrub and tree species, usually accept cowbird eggs and feed their young diets suitable for fledging cowbirds (Ortega, 1998). We tested our hypothesis during nest building because that is when cowbirds appear to locate most nests: cowbirds lay most eggs during host-laying periods (Banks, 1997; Nolan, 1978; Sealy, 1995), and they fly directly to nests before dawn, which suggests that nests are located before laying (Friedmann, 1929; Hann, 1937, 1941; Neudorf and Sealy, 1994; Norris, 1944; Scott, 1991).

We also considered other factors that might influence parasitism frequencies. We tested whether differences in the proportion of cowbirds fledged by host species, as an index of host quality, could explain variation in parasitism frequencies. We tested whether probability of parasitism varied with nest heights because cowbirds appear to search for nests from prominent perches (Barber and Martin, 1997; Gochfeld,

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1979), affecting the risk of parasitism at different nest heights (Briskie et al., 1990; Martin, 1992, 1993; Petit, 1991). We measured nest concealment because it may decrease the probability of parasitism (DellaSala, 1985; but see Anderson and Storer, 1976; Barber and Martin, 1997; Best, 1978; Buech, 1982; Smith, 1981), or it may influence the behavior of birds around their nests (Hobson et al., 1988; Hobson and Sealy, 1989b; Ricklefs, 1977). The timing of nesting within the breeding season may also affect the probability of parasitism (e.g., Briskie et al., 1990; Finch, 1983; Mariani et al., 1993; Petit, 1991).

## METHODS

### Study sites

We located and observed nests on 16 study sites in the Bitterroot Valley in western Montana, USA (see Tewksbury et al., 1998). Riparian habitats were dominated by black cottonwood (*Populus trichocarpa*) or aspen (*Populus tremuloides*), with fewer numbers of mountain alder (*Alnus incana*), willow (*Salix* species), black hawthorne (*Crataegus douglasia*), and chokecherry (*Prunus virginiana*).

### Nest monitoring

We monitored nests according to BBIRD protocols (Martin et al., 1996) every 2–4 days. We checked active nests with mirrors on poles during laying and once several days into incubation to detect late parasitism. We checked for cowbird eggs in all nests deserted after nest building or during laying and collected all yellow warbler nests after nesting to detect buried cowbird eggs (Friedmann, 1929; Sealy, 1995).

### Probability of parasitism

The proportion of nests parasitized for each species did not differ among years (Tewksbury et al., 1998), so we combined data from 1995 and 1996. To better estimate the frequency of early nest desertions, we report parasitism frequency from only nests found before egg laying (Pease and Grzybowski, 1995). Egg ejection by hosts could also bias the data. Yellow warblers seldom eject cowbird eggs (Sealy, 1995); dusky flycatchers did not eject experimentally introduced cowbird eggs at three nests (Banks AJ, unpublished data). American redstarts remain untested. The eastern subspecies of warbling vireos rejects cowbird eggs (Sealy, 1996); which species or subspecies is represented in this study is not clear. Due to geographical range and high observed parasitism frequency (Sealy, 1996), we expected the western form (*V. g. swainsonii*) to be present on our sites. However, cowbird eggs were rejected at two of five experimentally parasitized vireo nests (Banks AJ, unpublished data), suggesting that our sites may have both subspecies or that ejection occurs at a low frequency in one or both types. Thus, we may have underestimated the proportion of warbling vireo nests parasitized. However, warbling vireos were the most frequently parasitized species in our study, so this bias could only increase the observed differences in probability of parasitism among species.

Species can differ in the duration of time they are susceptible to detection and parasitism by cowbirds due to variation in lengths of nest building, laying, and incubation. To control for this variation, we estimated for each species a daily parasitism probability ( $=$  cowbird eggs laid/days that nests were susceptible to parasitism; “instantaneous parasitism rate;” Pease and Grzybowski, 1995). To calculate duration of nest-building periods, we used only nests found with nest cups less than half complete, estimated as either the first or second day

of building, and for which the first day of egg laying was known. To calculate susceptibility days, we assumed that (1) cowbirds may lay eggs a day before hosts initiate their clutches (we observed nests in which hosts began laying after cowbirds laid); (2) cowbirds require 12 days of incubation (Lowther, 1993; McMaster and Sealy, 1998); (3) cowbirds hatch up to 2 days after the first host young hatches, based on asynchronous hatching of up to 3 days in yellow warblers (Hébert and Sealy, 1992; Schrantz, 1943) and dusky flycatchers (Sedgwick, 1993b).

### Host quality

As an index of relative host quality, we calculated the proportion of cowbird eggs raised to fledging by each host species. Estimates of host quality would be strengthened by data on postfledging survival of cowbirds raised by each species, but such data were unavailable.

### Nest placement

To determine whether nest placement explained variation in probability of parasitism, we measured nest heights and an index of concealment. We measured heights of nests with clinometers or a pole and measuring tape. As an index of nest concealment, we measured foliage density around nests, using a  $0.5 \times 0.5$  m board gridded into 100 squares. While one observer held the board at the nest site with a pole, a second person at 5 m away observed the proportion of the board covered by foliage, noting how many quarters of squares were covered by foliage. Nests were scored in the four cardinal directions.

### Host activity

To quantify host activity, we watched nests during the building phase for an average of 70 min (SD = 7.81; range 43–115 min) from camouflaged blinds at 5–15 m from nests, depending on the density of vegetation. Ninety watches were initiated between 0600 and 1200 h between 28 May and 21 July 1995 and 1996. Observations were initiated after 10 min in the blind to minimize influence of our arrival on behavior; tape recorded, and later transcribed. In 1996, we rated nests on the day of observation as being in early (cup less than half complete), middle (cup more than half complete) or late building stage (cup complete, lining). We watched 2 nests in early, 17 nests in middle, and 21 nests in late building. Study species did not differ in the proportions of nests observed in early–middle versus late stages ( $\chi^2 = 1.79$ ,  $p = .618$ ,  $n = 42$ ).

#### Activity in area around nests

We analyzed the time spent by hosts near their nests on the premise that hosts that concentrate their activity in a smaller area around nests may call attention to the location of their nests. We estimated the location of perches as horizontal and vertical distance (m) from nests and recorded the duration of time (s) hosts spent at each perch. We generally present behaviors within 5 m of nests, except for using 15 m to compare parasitized and unparasitized males because only 24% of males were observed within 5 m of their nests.

We recorded the locations and types of all host vocalizations from near their nests. Female vocalizations included dusky flycatcher “whits,” and solicitation calls (Sedgwick, 1993a); “chips” by American redstarts, yellow warblers, and warbling vireos; yellow warbler “seets” (Hobson and Sealy, 1989b); and warbling vireo “buzz” and “breech” calls. Two female warbling vireos also sang (easily distinguishable from male song). Male vocalizations were 81% songs, but some chips, buzzes,

breeches, and solicitation calls were also recorded. Occasionally, a combination of distance from the nest and ambient noise prevented us from hearing all vocalizations that we observed in focal birds. In these situations, we excluded the watch from analyses of vocalization rates; sample sizes are generally lower for vocalization rates than for other behavioral measures.

We measured directional use because hosts that are active in fewer directions relative to their nests may draw more attention to their nest sites by concentrating their movements within smaller areas relative to their nests. We recorded the activity of hosts relative to their nests in eight directions (N, NE, E, etc.), noting a direction for each perch used and one direction per minute for perches used for longer than 1 min.

#### *Activity associated with nest-building visits*

In addition to activity near nests, we also analyzed activity directly associated with nest-building visits: perch use during nest approach, nest visitation rate, duration of nest visits, and vocalizations from the nest per visit. All visits to nests were attributed to females. We observed only females building nests for yellow warblers and American redstarts; for dusky flycatchers and warbling vireos, we assumed that the nest-building individuals were female, based on previous studies (Howes-Jones, 1985a; Sedgwick, 1993a). We analyzed the propensity of females to perch on the way to their nests during nest building because perching more frequently during nest approaches could assist cowbirds in tracking hosts to nests. Many approaches were made directly without perching, so we calculated the proportion of nest visits during which host females perched within 5 m of their nests on the way to their nests. We analyzed only females with at least five observed approaches; proportions were derived for each female, then means were derived for each species. The data were arcsine square-root transformed to improve fit to normality. We measured nest visitation rate because birds that visit their nests more frequently may draw attention to their nests. Nest visitation rate was inversely correlated with time of day for dusky flycatchers (Pearson  $r = -.397$ ,  $p = .033$ ,  $df = 28$ ), so time was included as a covariate in analysis of covariance. We measured the duration of nest-building visits because longer visits may give cowbirds more time to locate hosts and to ascertain what the host is doing at the nest (e.g., nest building, incubating, provisioning).

#### **Statistical tests**

We compared the daily parasitism rates with a chi-square statistic using standard errors for proportions (Sauer and Williams, 1989) using the program CONTRAST (Hines and Sauer, 1989).

We quantified the variety of directions used by hosts with a unit of concentration from angular statistics,  $R = \sqrt{[\cos(a_i/n)]^2 + [\sin(a_i/n)]^2}$  (Zar, 1984).  $R$  was inversely related to sample size (number of observations of directions), so analyses of variance included sample size as a covariate.

To test for differences in behaviors and nest placement characteristics among species and between parasitized and unparasitized pairs within species, we ran two sets of ANCOVA models. The first set of ANCOVA models asked if behaviors or nest placement varied significantly among species. When species explained a significant amount of variation, we then used a Pearson correlation to test for correlations between the behavioral or nest placement means and daily parasitism rates across species. We used estimated marginal means for variables that varied significantly with covariates in the ANCOVA models. The second set of ANCOVA models asked if behaviors or nest placement varied significantly by whether a

**Table 1**

**Brown-headed cowbird parasitism frequency (proportion of nests parasitized), parasitism intensity (number of cowbird eggs per parasitized nest), and proportion of cowbird eggs fledged for focal host species in Bitterroot Valley, Montana, USA, 1995–1996**

Host species	Frequency ( <i>n</i> )	Intensity ( <i>n</i> )	Fledged ( <i>n</i> )
Warbling vireo	.68 (28)	1.29 (45)	.48 (44)
Yellow warbler	.64 (66)	1.23 (81)	.38 (76)
American redstart	.43 (37)	1.12 (26)	.42 (24)
Dusky flycatcher	.27 (49)	1.10 (20)	.42 (19)

Parasitism frequency was calculated for all nests found on or before the first day of egg laying.

pair was parasitized when blocked by species. These models included species-by-parasitism interaction terms, which were insignificant unless reported. Because variation in the abundance of cowbirds among study sites might affect proportions of nests parasitized, we entered as covariates the relative abundances of cowbirds per site, from 10-min, 50-m fixed-radius point counts (Tewksbury, 1997). Variation in behaviors due to time of day, time of season, cowbird abundance, nest concealment, and observer were insignificant unless noted.

We used ranked tests for vocalization data that occurred in positively skewed distributions. We tested separately for differences among species with Kruskal-Wallis tests and then between parasitized and unparasitized individuals with Mann-Whitney  $U$  tests. We present Mann-Whitney  $U$  tests for species lumped together; we also tested for differences within each species and present those results whenever significant.

To determine whether host behaviors might vary with nest concealment, behavioral variables were tested for correlations with foliage density at nests for each species separately using a Bonferroni correction for multiple tests (Holm, 1979; Rice, 1989).

To determine the relative importance of behavioral and nonbehavioral variables in predicting parasitism, we used a forward stepwise logistic regression model with a likelihood ratio for variable removal. All species were lumped, as sample sizes were insufficient to generate separate models for each species. To correct for species differences, we entered residuals for all variables from one-factor ANOVAs with species as the main effect. Because we did not have nest concealment data for the highest nests, we first ran a model including nest height and concealment for the subset of nests with those data ( $n = 34$ ). Because neither nest height nor concealment were significant ( $p > .165$ ), we present a model from the larger data set ( $n = 44$ ) with behavioral variables only.

## **RESULTS**

### **Probability of parasitism**

Proportions of nests parasitized differed among species (log-linear likelihood ratio  $\chi^2 = 19.340$ ,  $p = .0002$ ,  $df = 3$ ), from 27% for dusky flycatchers to 68% for warbling vireos (Table 1). The mean number of cowbird eggs per parasitized nest did not differ significantly among focal species, but showed the same trend as parasitism frequencies ( $F = 1.578$ ,  $p = .197$ ,  $df = 3$ , 168; Table 1). Species differed in the number of days of susceptibility to parasitism (Table 2), so daily parasitism rates were more appropriate for comparing parasitism probabilities among species. Daily parasitism rates differed substantially among species ( $\chi^2 = 41.787$ ,  $p < .0001$ ,  $df = 3$ ); warbling vireos had more than four times greater probability of being parasitized than dusky flycatchers (Figure 1).

Table 2

Mean number of days (SE,  $n$  = nests) that hosts spent building nests and that nests were susceptible to parasitism by brown-headed cowbirds

Host species	Nest-building	Susceptible to parasitism
Dusky flycatcher	9.12 (0.50, 8)	5.89 (0.68, 47)
American redstart	5.68 (0.31, 8)	3.90 (0.07, 21)
Yellow warbler	7.25 (1.06, 6)	2.57 (0.28, 109)
Warbling vireo	5.41 (0.60, 6)	4.01 (0.04, 71)
ANOVA $F$ ( $p$ )	8.165 (.001)	15.637 (<.001)

ANOVA values indicate differences among species; see Methods for calculation of duration of nest-building and susceptibility periods.

### Host quality

The four study species did not differ in the proportion of cowbird eggs fledged from their nests (Pearson  $r^2 = 1.051$ ,  $p = .789$ ), suggesting that nests of all four species were of similar quality to cowbirds (Table 1).

### Nest placement

Nest heights differed among species (ANOVA,  $F = 3.001$ ,  $p = .033$ ,  $df = 3$ , 103; Table 3), and parasitism probability tended to increase with average nest height among species (Pearson  $r = 0.73$ ;  $p = .27$ ,  $df = 3$ ). However, the heights of parasitized and unparasitized nests within species did not differ (ANCOVA; parasitism,  $F = 0.200$ ,  $p = .656$ ,  $df = 1$ , 101). Nest concealment differed among host species (ANOVA,  $F = 14.680$ ,  $p < .001$ ,  $df = 3$ , 100; Table 3), but not as predicted relative to parasitism risk. Yellow warbler nests were more concealed than dusky flycatcher, American redstart, and warbling vireo nests (Bonferroni  $p < .001$ ,  $p < .001$ , and  $p = .020$ , respectively) and warbling vireo nests were more concealed than American redstart nests ( $p = .026$ ). Within species, parasitized and unparasitized nests did not differ in concealment (ANCOVA,  $F = 0.125$ ,  $p = .724$ ,  $df = 1$ , 100). No behaviors were significantly correlated with nest concealment. In addition, nest concealment never explained a significant amount of variation when included as a covariate in analysis of covariance models for behaviors ( $p > .335$ ).

### Nest timing

The mean dates of clutch initiation did not differ among host species ( $F = 2.133$ ,  $p = .096$ ;  $df = 3$ , 342); the mean clutch initiation date for all species was June 17.

### Host activity

#### Female activity in area around nests

Species differed in the time females were active on and near their nests (ANCOVA,  $F = 3.927$ ,  $p = .012$ ,  $df = 3$ , 73); more active species tended to be more frequently parasitized ( $r = 0.813$ ,  $p = .187$ ,  $n = 4$ ; Figure 2a). This relationship was repeated within species: parasitized females tended to spend more time around their nests than unparasitized females (ANCOVA; parasitism,  $F = 3.164$ ,  $p = .084$ ,  $df = 1$ , 46).

Vocalizations per minute by females near their nests differed among species (Kruskal-Wallis  $\chi^2 = 16.374$ ,  $p = .001$ ,  $n = 75$ ), but did not vary with parasitism rates (Figure 2b). Dusky flycatchers vocalized most frequently; among the other three species the probability of parasitism increased with female vocalizations. Vocalization rates did not differ between

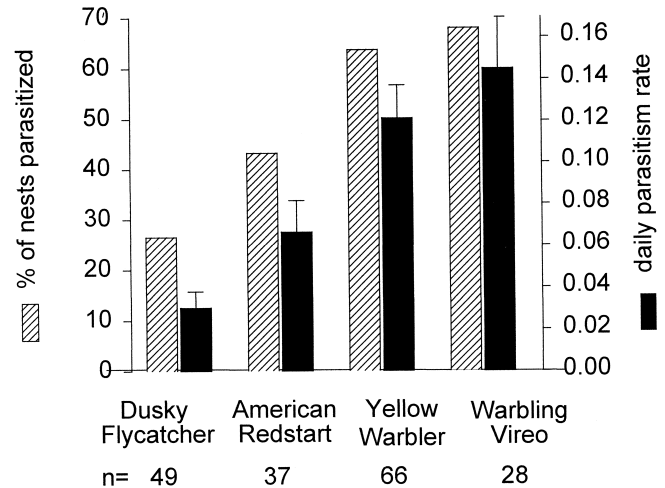


Figure 1

Proportions of nests parasitized by brown-headed cowbirds (hatched bars) for four host species in riparian habitat in western Montana, USA. Daily probability of parasitism (solid bars,  $\pm$  SE) controls for differences among species in duration of susceptibility to parasitism (see Methods). Numbers of nests are beneath the bars.

parasitized and unparasitized females of each species (Mann-Whitney  $U = 173$ ,  $p = .560$ ,  $n = 43$ ).

The range of directions that females used around the nest did not differ significantly among species (ANCOVA,  $F = 2.504$ ,  $p = .065$ ,  $df = 3$ , 79), although parasitism tended to increase with higher directional preference among three of the species (Figure 2c). The range of directions used also did not differ between parasitized and unparasitized females of each species (ANCOVA,  $F = 0.244$ ,  $p = .625$ ,  $df = 1$ , 36).

#### Male activity in area around nests

The minutes per hour that males were active within 5 m of their nests differed among species (ANCOVA,  $F = 2.796$ ,  $p = .046$ ,  $df = 3$ , 73) and was highly correlated with daily parasitism rates ( $r = .999$ ,  $p = .001$ ,  $n = 4$ ; Figure 3a). Parasitized and unparasitized males did not differ in the amount of time they were active near their nests (ANCOVA,  $F = 0.090$ ,  $p = .766$ ,  $df = 1$ , 37).

Vocalization rates by males near their nests differed among species (Kruskal-Wallis  $\chi^2 = 12.134$ ,  $p = .007$ ,  $n = 75$ ) and were highly correlated with parasitism frequencies ( $r = .973$ ,  $p = .027$ ,  $n = 4$ ; Figure 3b). In addition, parasitized males vocalized more than unparasitized males (Mann-Whitney  $U = 97$ ,  $p = .023$ ,  $n = 40$ ; Figure 3c).

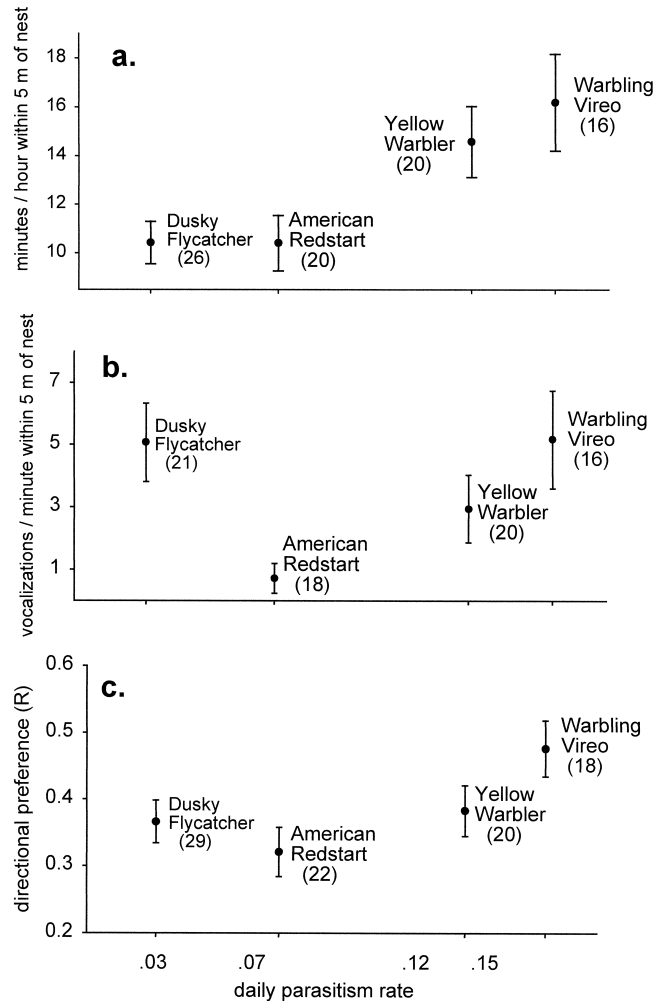
The variety of directions from the nest in which males were active did not differ among species (ANCOVA,  $F = 1.836$ ,  $p = .148$ ,  $df = 3$ , 71). However, within species, males that used

Table 3

Nest concealment and heights for focal species of brown-headed cowbird hosts in Bitterroot Valley, Montana, USA, 1995–1996

Host species	Concealment (SE, $n$ )	Height (SE, $n$ )
Dusky flycatcher	44.3 (3.9, 38)	3.64 (.28, 40)
American redstart	39.7 (3.3, 45)	3.10 (.28, 42)
Yellow warbler	73.8 (6.0, 14)	3.88 (.35, 26)
Warbling vireo	55.5 (5.3, 18)	4.39 (.34, 27)

Nest concealment is mean foliage density at nests from four directions (see Methods).



**Figure 2**

Female activity ( $\pm$  SE) near nests during the nest-building period (numbers of females in parentheses). (a) The minutes per hour females spent on or within 5 m of their nests. (b) Vocalizations per minute by females within 5 m of their nests. (c) The degree to which females concentrated their activity in few directions from their nests (see Methods for an explanation of  $R$ ).

fewer directions had a higher probability of parasitism than males using a greater variety of directions (ANCOVA,  $F = 8.323$ ,  $p = .007$ ,  $df = 1,35$ ; Figure 3d).

#### Activity associated with nest-building visits

Species differed in the proportion of nest visits during which females used perches on the way to the nest (ANCOVA,  $F = 4.136$ ,  $p = .009$ ,  $df = 3, 71$ ), although probability of parasitism was not correlated to perching frequency across species (Figure 4a). Moreover, parasitized and unparasitized females did not differ in perching frequency within species (ANCOVA,  $F = 0.607$ ,  $p = .441$ ,  $df = 1,37$ ).

Rate of nest visitation during nest building did not differ among species (ANCOVA,  $F = 0.028$ ,  $p = .994$ ,  $df = 3, 61$ ). Within species, nest visitation varied inversely with parasitism: females whose nests were subsequently parasitized visited less frequently than unparasitized females (ANCOVA,  $F = 4.732$ ,  $p = .036$ ,  $df = 1, 36$ ).

The mean duration of nest-building visits increased with probability of parasitism both across and within species. Duration of nest-building visits differed among species (ANCOVA,  $F = 4.153$ ,  $p = .009$ ,  $df = 3, 61$ ) and correlated strongly

with daily parasitism rates ( $r = .974$ ,  $p = .026$ ,  $n = 4$ ; Figure 4a). In addition, females with longer nest-building visits were more likely to be parasitized than females with shorter visits (ANCOVA,  $F = 11.786$ ,  $p = .001$ ,  $df = 1, 37$ ; Figure 4b). The mean duration of nest-building visits was negatively correlated with nest visitation rate for three species (Pearson  $r = -.59$ ,  $-.47$ ,  $-.44$  for yellow warblers, American redstarts, and warbling vireos, respectively), although was not significant after correction for multiple tests.

The rates at which females vocalized from their nests during nest-building trips differed among species (Kruskal-Wallis  $\chi^2 = 13.581$ ,  $p = .004$ ,  $df = 3$ ) but did not correlate with parasitism rates ( $r = -.551$ ,  $p = .449$ ,  $n = 4$ ) due to high rates of vocalizations by dusky flycatchers. Parasitized and unparasitized females did not differ in the number of vocalizations per nest visit when species were combined (Mann-Whitney  $U = 196.5$ ,  $p = .642$ ,  $n = 43$ ). However, warbling vireos that were subsequently parasitized vocalized more than conspecifics that were not parasitized (Mann-Whitney  $U = .000$ ,  $p = .017$ ,  $n = 7$ ).

#### Multivariate model of activity

The logistic regression model of brown-headed cowbird parasitism contained 3 of 10 behavioral variables entered: male directional preference, nest visit duration, and male vocalizations within 15 m of nests (Table 4). The model correctly classified 84% of 44 cases ( $\chi^2 = 18.622$ ,  $p = .0003$ ).

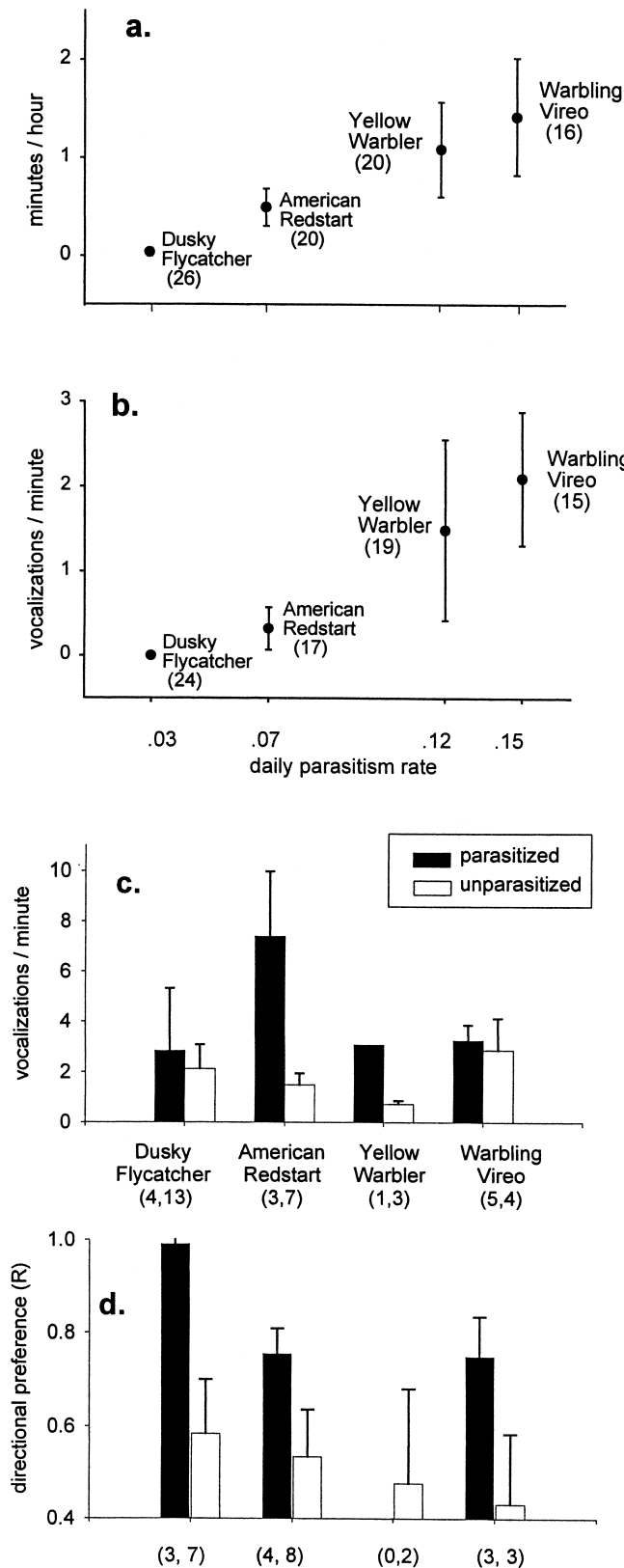
#### DISCUSSION

This study addressed the question of why sympatric host species differ in frequencies of parasitism by brown-headed cowbirds. Daily parasitism rates varied fourfold among the four host species in this study and were correlated with several measures of host activity near their nests during nest building. Because our behavioral analysis was limited to only four hosts within an assemblage of 12 species, the statistical power of patterns across species was low, but we still found strong patterns that were reinforced by analyses within species. Our study confirms the suggestions of previous investigators that the activity of hosts near their nests increases the probability of parasitism by cowbirds (e.g., Friedmann, 1929; Gochfeld, 1979; Grief, 1995; Hann, 1941; Norman and Robertson, 1975; Scott, 1977).

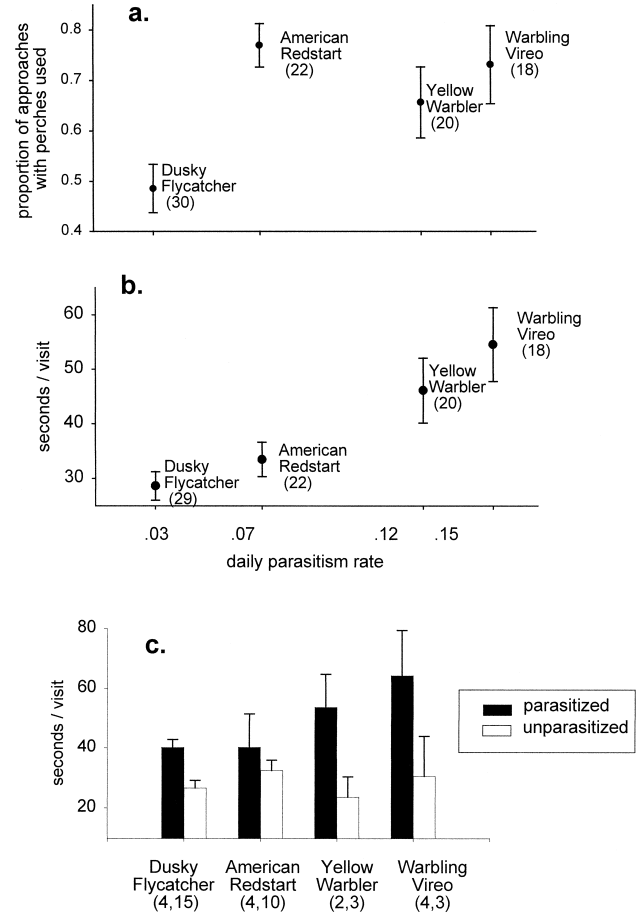
#### Host behavior

##### Activity in area around nests

The minutes per hour that males and females were active within 5 m of their nests was strongly positively correlated with parasitism frequencies among species in this study. These results support a general activity hypothesis, but they do not support a nest-guarding hypothesis in which time near the nest aids hosts in detecting brood parasites and facilitates nest defense (Møller, 1989; Slack, 1976). Clotfelter and Yasukawa (1999) found evidence that nocturnal presence on the nest reduced probability of parasitism for red-winged blackbirds (*Agelaius phoeniceus*). However, other investigations found no relationship between time near or on the nest in early morning hours and parasitism frequency (Burgham and Picman, 1989; Neudorf and Sealy, 1994). In addition, the results of studies relating nest defense to parasitism probability across species have been equivocal (Gill et al., 1997; Sealy et al., 1998). The efficacy of time near the nest in reducing cowbird parasitism may be complicated by body size, as smaller-bodied hosts may be unable to exclude brown-headed cowbirds from their nests (Hann, 1937; Neudorf and Sealy, 1994). However,



**Figure 3** Male activity ( $\pm$  SE) near nests during the nest-building period (numbers of males in parentheses). (a) The minutes per hour that males were active within 5 m of their nests. (b) Vocalizations per minute by males within 5 m of their nests. (c) Vocalization rates within 15 m of nests for males whose nests were and were not subsequently parasitized. (d) The degree to which males



**Figure 4** Activity associated with nest-building visits ( $\pm$  SE; numbers of females in parentheses). (a) The proportion of nest approaches in which females perched. (b) The duration of time spent on the nest per nest-building visit. (c) The duration of time spent on the nest per nest-building visit, for females who were and were not subsequently parasitized.

our study is the first to find that time near the nest may actually be a liability with respect to parasitism.

Male vocalizations appeared to be particularly important in determining parasitism probability across species (Figure 3b). Male warbling vireos, the most frequently parasitized species, vocalized nearly twice a minute near their nests, whereas dusky flycatcher males were never heard within 5 m of their nests. This pattern is reinforced later in the nesting period, when warbling vireo males sing from their nests during incubation. Although no published studies compare vocalization rates among brown-headed cowbird hosts, Gochfeld (1979) found that shiny cowbirds preferentially approached singing males of their preferred host in Argentina (see also Payne, 1973).

Within species, a relationship between parasitism and vocalizations was reinforced; males who were subsequently parasitized vocalized more during the nest-building period than males who were not parasitized. Uyehara and Narins (1995)

←

concentrated their activity in few directions from their nests, for males whose nests were and were not subsequently parasitized (see Methods for an explanation of  $R$ ).

**Table 4**  
**Variables used in forward stepwise logistic regression model to classify nests for parasitism by brown-headed cowbirds**

Variables used	$\beta$	$p$
Male directional preference	6.040	.013
Nest visit duration	.047	.059
Male vocalizations within 15 m	.025	.066
Constant	1.131	.030

Nests of dusky flycatcher ( $n = 14$ ), American redstart ( $n = 14$ ), yellow warbler ( $n = 4$ ), and warbling vireo ( $n = 7$ ) were combined. To control for variation in behavior due to species, variables were residuals from one-factor ANOVAs with species as main effect. Variables available but not selected in the final model: nest visitation rate; female vocalizations from nest per visit; proportion of nest approaches with perches taken; female time near nest; female directional preference; female vocalizations near nest; male vocalizations within 5 m of nests.

also found a higher median rate of vocalizations in parasitized relative to unparasitized pairs of willow flycatchers (*Empidonax traillii*), although they did not distinguish between male and female vocalizations. In our study, parasitized males were active in fewer directions from their nests than unparasitized males. These results suggest that male singing in consistent locations close to nests increases the probability of parasitism. Indeed, in the logistic regression model built from all behaviors, male directional preference and vocalizations were the two most important factors for classifying nests as parasitized or not parasitized. These data strongly suggest that cowbirds use male song during the nest-building phase to locate nests: perhaps cowbirds use male singing to locate active territories and then track females to find nests.

Male vocalizations might be used as nest-location cues by cowbirds for several reasons. First, behaviors most constrained by other factors may be those most easily exploited by cowbirds. Song is critical for male reproductive success and is believed to function in territorial defense (Krebs, 1977; McDonald, 1989; Smith, 1979), defense of mates from extrapair copulations (Hobson and Sealy, 1989a; Møller, 1988), solicitation of extrapair copulations (Møller, 1991), and stimulation of females to lay (Logan et al., 1990). Thus, for males, the benefits of singing may outweigh the potential cost of lowered reproductive success due to cowbird parasitism. This presents an interesting challenge to sexual selection theory that would generally predict a positive correlation among male song rate, mate acquisition, and fitness (Catchpole and Slater, 1995); indeed, if parasitism becomes too costly, females should select males that sing less near their nests. Second, singing may be exploited by cowbirds because singing rates often peak in paired males during nest building or egg laying (Logan, 1983; Møller, 1991; Slagsvold, 1977), precisely when cowbirds need to locate nests. Finally, singing rates and song types may serve as spatial cues for species in which males sing more frequently near their nests. For example, during nest building, warbling vireo males sing more when closer to their nests and less as they move away (Howes-Jones, 1985b). Yellow warblers sing different song types at various distances from their nests (Weary et al., 1994). Thus, cowbirds may exploit male vocalizations to locate nest sites because males must sing and because when, where, and what they sing may provide good cues to nests. Experimental manipulation of song rates near nests should provide a promising area for further research. Playback of dusky flycatcher songs near nests during nest building caused desertion (Banks AJ, unpublished data), but trials later in the nesting cycle or with other species may be more successful.

In contrast to males, female calling rate was not as clearly correlated with the probability of parasitism across species. This contrasts with the finding of a correlation between the rate of female nest-arrival calls and parasitism among seven host species in Manitoba (Duerksen, 1996). In our study, females of the least parasitized species, dusky flycatchers, vocalized at a high rate both on and around their nests during nest building, although among the remaining species parasitism increased with vocalizations.

The stronger relationship between male vocalizations and probability of parasitism, in comparison to female vocalizations, may best be explained by our focus on vocalization rate alone. The significance of a vocalization to a nest-searching cowbird must vary not only by its rate but also by the distance at which it can be heard. Although we lack information on how host vocalizations vary in detectability to cowbirds, we perceived a great difference in the relative audibility of vocalizations among species and between sexes. We found that the “whit” calls made so frequently by nest-building dusky flycatchers were unusually low in volume. During behavioral observations, we commonly watched female dusky flycatchers vocalize only 5–10 m away, but we could not hear them. These soft calls may not be very costly in terms of increased probability of detection by cowbirds. Thus, it is possible that male vocalizations correlated more strongly than female calls with probability of parasitism because they were more audible to cowbirds. A similar explanation could explain differences in detectability among host species if the vocalizations of more frequently parasitized species were generally louder than less parasitized species. We found a trend for the mean transmission distance of songs to be correlated with parasitism frequency among our four study species, but our sample sizes were small (Banks AJ, unpublished data). Similar to work investigating the attenuation distances of vocalizations in different habitats (e.g., Cosens and Falls, 1984), future studies should measure rates and transmission distances of vocalizations given by cowbird hosts near their nests in relation to probability of parasitism.

#### *Activity associated with nest visits*

Perching during nest approaches also may have facilitated nest detection by cowbirds. Species that perched more frequently during nest approach tended to have a higher probability of parasitism in our study. No data are available from other studies regarding perch use by hosts in relation to parasitism, but perching on the way to the nest appeared to facilitate predator detection and protection of the nest for northern mockingbirds (*Mimus polyglottos*) during the nestling phase (Breitwisch et al., 1989). In contrast, our results were consistent with a general activity hypothesis and the prediction that hosts perching near their nests during nest approach assists cowbirds in locating nests.

The probability of parasitism was also strongly correlated with the duration of nest visits, both across and within species; females who spent longer on their nests per nest-building visit were more likely to be parasitized than females who spent less time on their nests per visit. These results suggest that the duration of time a female spends at her nest during each trip increases her probability of parasitism, perhaps by facilitating detection of nests or assessment of her activity at the nest (e.g., building, incubating, provisioning) by cowbirds. These results do not support a hypothesis in which females who make longer nest visits build their nests in fewer days and thereby reduce their chances of discovery by cowbirds. Indeed, we found no relationship between the average durations of the nest-building period and parasitism frequencies among host species.

We also predicted that more frequent nest visitation would

call attention to nest sites. However, we found no significant variation in frequency of nest visitation among species, and within-species nest visitation rates were higher for unparasitized females. No other published study has examined nest visitation rate in relation to parasitism probability, although higher nest visitation rates can increase risk of nest predation (Martin et al., 2000).

Nest visitation rate and nest visit duration were negatively correlated, which is why both behaviors did not correlate positively with parasitism probability as predicted. In our study, the duration of nest visits was a stronger predictor of parasitism probability than visitation rate in the logistic regression model, although low sample sizes constrain our ability to make firm conclusions. In general, however, our results highlight the importance of measuring various behaviors to represent activity levels near nests (see also Lorenzana and Sealy, 1999). Future studies should include other behavioral measures in addition to visitation rate to characterize activity at and around nests.

### Host quality

Cowbirds did not parasitize host species in proportion to the ability of host species to fledge cowbirds. We found that all four study species fledged similar proportions of cowbirds from their nests, with a trend for yellow warblers to fledge fewer cowbird eggs due to egg burial (Sealy, 1995). We may have overestimated the proportion of cowbird eggs fledged by warbling vireos; since we experimentally found egg ejection in this population, cowbird eggs may have been ejected from nests before we detected them. However, because warbling vireos were the most frequently parasitized species, an overestimate of their fledging proportion would only strengthen the evidence that cowbirds were not selecting among hosts for differences in parental ability (e.g., Soler et al., 1995). Other workers have found similar results: in Manitoba, an apparently higher quality host, the least flycatcher (*Empidonax minimus*), was parasitized less frequently than the yellow warbler, which rejected cowbird eggs (Briskie et al., 1990). Scott and Lemon (1996) found equal parasitism frequencies among three host species, even though one species fledged significantly fewer cowbirds. Thus, differential parasitism among species cannot be explained by differences in rearing cowbirds in the nest, although variation among host species in raising cowbirds to independence needs further research.

### Nest placement

The two most heavily parasitized species built the highest nests, suggesting that in our study area nest height was associated with parasitism risk. However, nest height did not differ between parasitized and unparasitized nests within species (see also Curson, 1996; Grief, 1995; Smith, 1981). Briskie et al. (1990) found that nest height was related to probability of parasitism within and among species in riparian habitat in Manitoba, but in their study, lower nests were more likely to be parasitized. Thus, nest height may affect the vulnerability of nests to parasitism by cowbirds, but it rarely explains which nests are parasitized within species, and it is difficult to generalize among studies.

Nest concealment also did not explain differences in parasitism frequencies among species; the two most highly parasitized species built the most highly concealed nests. Concealment also did not differ between parasitized and unparasitized nests within species. These results are consistent with most previous studies (Anderson and Storer, 1976; Barber and Martin, 1997; Best, 1978; Buech, 1982; Smith, 1981; Whitfield, 1990).

### Conclusion

We found that the probability of parasitism was correlated with behaviors of male and female hosts both on and around their nests, and these behaviors formed an effective predictive model of parasitism for four host species of the brown-headed cowbird. This study identified two behaviors, male vocalizations and the duration of nest-building visits, that simultaneously explained variation in the probability of parasitism among individuals within species and that were correlated with parasitism frequencies among species. Thus, a similar mechanism potentially explains which individuals are parasitized within species while also explaining large-scale patterns of parasitism frequencies among species. These results strongly suggest that cowbirds use everyday, nondefensive host behaviors to locate nests. To make stronger inferences, of course, these results need to be replicated within other suites of sympatric host species. Future research should include detailed behavioral analyses of hosts in relation to the probability of parasitism in various habitat types, as well as experimental manipulation of activity levels, if experiments can be conducted without detrimentally affecting nesting success.

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