Variation among host species in probability of parasitism by brown-headed cowbirds: the role of everyday host activity

Alison J. Banks
The University of Montana

Follow this and additional works at: https://scholarworks.umt.edu/etd

Let us know how access to this document benefits you.

Recommended Citation
https://scholarworks.umt.edu/etd/6575
Permission is granted by the author to reproduce this material in its entirety, provided that this material is used for scholarly purposes and is properly cited in published works and reports.

** Please check "Yes" or "No" and provide signature **

Yes, I grant permission  
No, I do not grant permission

Author's Signature [Signature]

Date 12/3/97

Any copying for commercial purposes or financial gain may be undertaken only with the author's explicit consent.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
Variation among host species in probability of parasitism by Brown-headed Cowbirds: the role of everyday host activity

by

Alison J. Banks

B. A. University of California, San Diego 1993

presented in partial fulfillment of the requirements for the degree of Master of Science Wildlife Biology University of Montana 1997

Approved by:

[Signatures]

Committee Chair

Graduate School Dean

12-19-97

Date

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.
ABSTRACT

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 thought to find nests by watching adult behavior. I tested the hypothesis that the activity of hosts during nest-building correlates to probability of parasitism among and within four sympatric hosts, American Redstarts (Setophaga ruticilla), Dusky Flycatchers (Empidonax oberholserii), Warbling Vireos (Vireo gilvus), and Yellow Warblers (Dendroica petechia). Daily probability of parasitism varied substantially among these species, from three percent for Dusky Flycatchers to over four times that for Warbling Vireos. Species were apparently similar in quality, because species did not differ in the proportion of cowbird eggs they fledged from their nests. Differences in nest placement also could not explain differences in probability of parasitism either within or among species. In contrast, behavioral differences among species correlated with parasitism rates among species and with probability of parasitism within species. Parasitism rates increased across species with increasing durations of nest-building visits, propensity for birds to perch when approaching nests, the minutes per hour during which hosts were active near their nests, and the rate of male vocalizations near nest. In addition, 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. In sum, I found that daily probability of parasitism by Brown-headed Cowbirds varied among four sympatric host species that raised cowbirds, and that parasitism probability increased with increased activity of hosts near their nests both within and among host species. These data support the hypothesis that cowbirds use host activity during nest-building to find nests.
Table of Contents

Abstract ................................................................................................................................... ii
List of Tables ........................................................................................................................ iv
List of Figures ......................................................................................................................... v
Introduction ............................................................................................................................ 1
Methods ................................................................................................................................... 5
   Nest monitoring ........................................................................................................ 5
   Probability of parasitism ................................................................................... 5
   Host quality ........................................................................................................... 7
   Nest placement ...................................................................................................... 8
   Host activity ........................................................................................................ 9
   Statistical tests ...................................................................................................... 12
Results .............................................................................................................................. 15
   Probability of parasitism ..................................................................................... 15
   Host quality ........................................................................................................... 18
   Nest placement ..................................................................................................... 18
   Host activity ........................................................................................................ 21
   Multivariate model of activity predicts parasitism ........................................... 39
Discussion ........................................................................................................................ 41
Acknowledgments ........................................................................................................... 47
Literature Cited ................................................................................................................ 48
List of Tables

Table I. Timing of cowbird egg-laying in relation to host egg-laying from nests in riparian habitat in western Montana. ............................................. 15

Table II. Mean (s.e., n=nests) days of susceptibility of host species to detection and parasitism by Brown-headed Cowbirds in riparian habitat of western Montana. Nests are susceptible to detection by cowbirds during both nest-building and after hosts begin to lay eggs, a sum of both columns. ................................................................. 17

Table III. The probability of a cowbird egg fledging did not differ among four host species breeding in riparian habitat in western Montana. ...................... 19

Table IV. Correlations among behaviors during nest-building for four Brown-headed Cowbirds host species breeding in riparian habitat in western Montana. ................................................................. 36-37

Table V. Forward stepwise logistic regression model including behavioral variables classified nests for whether or not they were parasitized by Brown-headed Cowbirds. The model used a likelihood-ratio test for variable removal and correctly classified 84% of 44 cases. ......................................................... 40
List of Figures

Figure 1. Proportions of nests parasitized by Brown-headed Cowbirds (hatched bars) differed among four host species nesting in riparian habitat in western Montana. The daily probability of parasitism (+/- s.e.; solid bars) controls for differences among species in their duration of susceptibility to parasitism, and also varied substantially among species. Numbers of nests are shown beneath the bars. . .16

Figure 2. Nest concealment did not vary as predicted among species; probability of parasitism was actually higher for more highly concealed nests. Yellow Warbler nests were more concealed than Dusky Flycatcher, American Redstart and Warbling Vireo nests (Bonferroni p<0.001, p<0.001, p=0.020) and Warbling Vireo nests were more concealed than American Redstart nests (p=0.026). Numbers of nests are shown in parentheses. . .20

Figure 3. Female activity near nests.

a). The minutes per hour (x +/- s.e.) females spent on or within 5 m of their nests differed among species and correlated with parasitism rates at r=0.813. Numbers of females are shown in parentheses. . .22

b). Female Warbling Vireos tended to concentrate their activity in fewer directions relative to their nests (higher R) than females of the other species, though differences among species were not significant. Numbers of females are shown in parentheses. . .23

c). Vocalizations per minute (x +/- s.e.) by females within 5 m of their nests differed among species but did not correlate with daily parasitism rates. Numbers of females are shown in parentheses. . .24

Figure 4. Male activity near nests.

a). Minutes per hour (x +/- s.e.) that males were active within 5 m of their nests differed among species and was highly correlated with daily parasitism rates. Numbers of males are shown in parentheses. . .26

b). Males whose nests were subsequently parasitized confined their activity to fewer directions from their nests (higher R) during the nest-building period than males whose nests were not parasitized. Numbers of males are shown in parentheses . . .27
c). Vocalizations per minute (x +/− s.e.) by males within 5 m of their nests differed among species and were highly correlated with parasitism rates across species. Numbers of males are shown in parentheses ................................... 28

d). Males whose nests were subsequently parasitized vocalized more frequently (x +/− s.e.) from within 15 m of their nests during the nest-building period than males whose nests were not parasitized. Numbers of males are shown in parentheses ................................... 29

Figure 5. Nest-building visitation activity.

a). Species differed in the proportion of nest approaches (x +/− s.e.) in which perches within 5 m of the nest were used, and there was a trend for perching frequency to correlate with parasitism rates. Numbers of females are shown in parentheses ................................... 31

b). Counter to predicted, females who were subsequently parasitized visited their nests (x +/− s.e.) less frequently during nest-building than females who were not parasitized, for all species combined. This difference was also significant within Warbling Vireos. Numbers of females are shown in parentheses ................................... 32

c). Duration of time on the nest per nest-building visit (x +/− s.e.) differed among species and correlated strongly with daily parasitism rates. Numbers of females are shown in parentheses ................................... 33

d). Females who were subsequently parasitized spent more time on their nests per nest-building visit (x +/− s.e.) than females who were not parasitized, for all species combined. This difference was also significant within Dusky Flycatchers. Numbers of females are shown in parentheses ................................... 34

e). Species differed in the number of vocalizations (x +/− s.e.) given by females from the nest per nest-building visit, but these differences did not correlate with parasitism rates. Numbers of females are shown in parentheses. ................................... 38
INTRODUCTION

Parasitism by Brown-headed Cowbirds (*Molothrus ater*) has significant fitness costs (e.g. Mayfield 1965, Goguen and Matthews 1996) and has contributed to population declines in some host species (Post and Wiley 1977, Franzreb 1989, Trail and Baptista 1992), while exerting minimal costs to others (Smith and Arcese 1994, Eckerle and Breitwitsch 1997). Fitness costs vary strongly among host species in part because cowbirds parasitize host species at widely differing frequencies, even among hosts breeding sympatrically (e.g. Gochfeld 1979, Briskie et al. 1990, Smith and Arcese 1994, Barber and Martin 1997). What factors contribute to the probability of parasitism among these hosts is poorly understood. Traits that increase probability of parasitism are important to identify given the fitness and demographic costs of cowbird parasitism.

Cowbirds may differentially parasitize host species based on their quality in raising cowbirds. Cowbirds less frequently parasitize species that reject cowbird eggs or that feed their young diets inappropriate for cowbirds (Scott 1977, Sealy and Bazin 1995). Yet, probability of parasitism varies even among high-quality hosts (Gochfeld 1979, Briskie et al. 1990, Barber and Martin 1997, Ward and Smith in press, Tewksbury et al. in press), suggesting that host species differ in other ways affecting the rate at which cowbirds find and parasitize their nests.

Hosts may differ in parasitism probability because of differences in host behaviors that serve as cues to nest-searching cowbirds. A variety of evidence suggests
that parental behaviors at the nest influences detection and parasitism of nests. Female Brown-headed Cowbirds spend morning hours on breeding grounds watching host behavior, especially nest-building, presumably to locate or assess the stages of nests (Friedmann 1929, Hann 1941, Norman and Robertson 1975). Similarly, over two-thirds of the nest visits made by female Shiny Cowbirds (Molothrus bonariensis) were preceded by watching hosts in nest-building and territorial defense activities (Wiley 1988; see also Kattan 1997). In contrast, studies of old nests lacking parental activity find little or no parasitism (Thompson and Gottfried 1976, 1981, Lowther 1979, Kale 1985, Grieef 1995, Jobin and Picman 1995).

While these studies suggest that host activity increases the probability of parasitism across species, this hypothesis has never been explicitly tested. The only investigation of host behavior and probability of parasitism across species has been a series of experiments assessing host nest defense in response to cowbird models. Although these studies were designed to ask whether host nest defense could decrease the risk of parasitism, most actually found a positive relationship between host defense and parasitism rates among host species (Robertson and Norman 1977, Burgham and Picman 1989, Hobson and Sealy 1989, but see Briskie et al. 1990). These results suggest that nest defensive activity might be exploited by cowbirds looking for nests (Robertson and Norman 1977). Other behaviors also may be used by nest-searching cowbirds. For example, Yellow Warblers (Dendroica petechia) that gave more "seet" calls and sat on the nest more frequently in response to cowbird models were more likely to be parasitized (Hobson and Sealy 1989; see also Uyehara and Narins 1995).
In summary, investigations of host nest defense found positive associations between responses to cowbirds and parasitism probabilities, suggesting that activity near nests may increase parasitism by cowbirds. Thus, I tested a “general activity” hypothesis: the activity of hosts near their nests increases the probability of parasitism among and within host species. First I asked if parasitism rates increased with increasing mean activity levels across species, and then I asked if, within species, parasitized pairs were more active near their nests than unparasitized pairs.

I tested the general activity hypothesis during the nest-building period because that is when cowbirds appear to locate most nests; cowbirds lay most of their eggs during host laying periods, and direct, pre-dawn flights to lay eggs suggest that nests are located previous to the day of parasitism (Friedmann 1929, Hann 1937, 1941, Norris 1944, Scott 1991, Neudorf and Sealy 1994).

I tested the hypothesis in riparian habitat in western Montana, an ideal study location because of high cowbird and host abundances and a short duration of sympatry (about 50 years; D. Hutto, pers. comm.) of cowbirds and hosts. Due to the short duration of sympatry between cowbirds and hosts, I expected higher variation in traits that increase the probability of parasitism in this location relative to areas in which cowbirds and hosts had been sympatric for longer.

I chose four Brown-headed Cowbird hosts based on similarities in their nesting biology: American Redstarts (*Setophaga ruticilla*), Dusky Flycatchers (*Empidonax oberholserii*), Warbling Vireos (*Vireo gilvus*), and Yellow Warblers. All four species built open-cup nests in the same shrub and tree species. All four were known to accept
cowbird eggs and to feed their young an insect diet suitable for cowbirds. I tested the assumption that hosts were equal in quality to cowbirds by calculating the proportion of cowbirds fledged by each species.

Nest location characteristics may also affect the probability of parasitism among nests. Cowbirds appear to search for nests from prominent perches (Gochfeld 1979, Alvarez 1993, Barber and Martin 1997), affecting the risk of parasitism at different nest heights (Briskie et al. 1990, Petit 1991, Martin 1992, 1993). Nest concealment may decrease probability of parasitism (DellaSalla 1985; but see Anderson and Storer 1976, Best 1978, Smith 1981, Buech 1982, Barber and Martin 1997), or may influence behavior of hosts around their nests (Hobson et al. 1988, Hobson and Sealy 1989). Therefore, I tested whether nest placement explained differences in behaviors or probabilities of parasitism.
METHODS

Nest monitoring

I located nests on sixteen riparian study sites (5.5 - 24 ha, \(\bar{x} = 13.1\) ha) along the Bitterroot River and its tributary streams in western Montana. River sites were dominated by Black cottonwood (\textit{Populus trichocarpa}) with lesser amounts of aspen (\textit{Populus tremuloides}), mountain alder (\textit{Alnus incana}), willow (\textit{Salix} spp.), black hawthorn (\textit{Crataegus douglasia}), and chokecherry (\textit{Prunus virginiata}). Streamside sites were dominated by aspen, alder, and willow.

I monitored nests according to BBIRD protocols (Martin et al. 1996, as described at http://pica.wru.umt.edu/bbird) every two or four days. I checked active nests with poles and mirrors during egg-laying and once several days into incubation to detect late parasitism. I checked nests deserted after nest-building or during egg-laying for cowbird eggs.

Probability of parasitism

I calculated the proportion of nests parasitized for each species ("cohort parasitism fraction," Pease and Grzybowski 1995). Proportions of nests parasitized did not differ between 1995 and 1996 for all species, so data from both years were combined.

I took into account host responses to parasitism which could bias (lower) estimates of proportions of nests parasitized. I included only nests found prior to egg laying to adequately detect early nest desertions in response to parasitism (Pease and
Grzybowski 1995). Yellow Warblers bury cowbird eggs in their nests (Friedmann 1929, Sealy 1995), so I collected and examined Yellow Warbler nests for cowbird eggs at the end of nesting. I also considered the possibility that hosts might eject cowbird eggs from nests. Yellow Warblers did not reject experimentally introduced cowbird eggs (Rothstein 1975, Sealy 1995), nor did Dusky Flycatchers at three nests (A. Banks, unpub. data). American Redstarts remain untested. Only the eastern (*Vireo gilvus gilvus*) of two Warbling Vireo subspecies or species (Sibley and Monroe 1990) is known to reject cowbird eggs (Sealy 1996), and which species or subspecies is represented in this study is not clear. Due to geographical range and high observed parasitism frequencies (Sealy 1996), I expected the western form (*V. g. swainsonii*) to exist on my sites. However, cowbird eggs were rejected at two of five experimentally parasitized vireo nests (A. Banks, unpub. data), suggesting that my sites may have both subspecies, or that ejection is not restricted to the eastern form as previously thought. This also means that I may have underestimated the proportion of Warbling Vireo nests parasitized. However, Warbling Vireos were already the most frequently parasitized species, so this bias would only increase differences among species in their probabilities of parasitism, and I therefore did not consider it problematic for these analyses.

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, egg-laying and incubation periods. To control for this variation among species, I estimated for each species a daily parasitism probability = \( \frac{\sum \text{cowbird eggs laid}}{\sum \text{days that nests were susceptible to parasitism}} \). This is equivalent to the "instantaneous parasitism rate" of
Pease and Grzybowski (1995). To calculate susceptibility days, I made the following assumptions: a.) Cowbirds can successfully lay eggs a day before hosts initiate egg-laying; this is supported by nests in which I knew hosts laid eggs after cowbirds laid eggs. b.) Cowbirds require 11 days of incubation, based on a minimum observed period of 10 and a mean observed period of 12 days (Lowther 1993). c.) Cowbirds can hatch up to two days after the first host young hatches, based on asynchronous hatching spanning up to three days in Yellow Warblers (Schrantz 1943) and Dusky Flycatchers (Sedgwick 1993b). Thus, for nests which survived through hatching, susceptibility days = 1+ (date of first hatch - date of first host egg laid) - 11 + 2. For nests which failed before hatching, I used mean incubation period lengths for each species derived from nests on our sites. For nests which failed during egg-laying, susceptibility days = 1+ (failure date - date of first host egg laid). I compared the daily parasitism rates with a chi-square statistic using standard errors for proportions (Johnson 1979, Hensler and Nichols 1981, Zar 1984) using the program CONTRAST (Sauer and Williams 1990, described in Sauer and Williams 1989).

Host quality

To test the assumption that probability of parasitism was unrelated to differences among hosts in host quality, I measured the proportion of cowbird eggs raised to fledging by each of the host species. I present data for singly parasitized nests, as each represents an independent parasitism-nest event; the relative proportions of cowbird eggs fledging per host species did not differ from calculations made from singly and doubly parasitized nests or from all parasitized nests.
after a Bonferroni correction for multiple tests (Holm 1979, Rice 1989). In addition, when nest concealment is included in analysis of covariance models for behaviors, it never explains a significant amount of variation (p > 0.335).

Host activity

To quantify host activity near nests, two field assistants and I watched nests for an average of 70 minutes per nest (st. dev. = 7.81; range 43-115 mins.) from camouflage cloth blinds at 5 to 15 m from nests, depending on the density of vegetation. Watches were initiated between 6:00 and 12:00 hours between May 28 and July 21, 1995 and 1996. Over 100 nest watches were completed of all species combined, though some watches were excluded because of rain or because nest building was complete. Hosts occasionally reacted to our presence near nests with chipping and flights near the blind, which subsided after several minutes. To minimize recording behaviors that were affected by our presence, behavioral observations were initiated after 10 minutes in the blind. Observations of all behaviors of focal adults, cowbirds, and intruding birds or squirrels were tape recorded and later transcribed.

For American Redstarts and Yellow Warblers, only females built nests; males were never observed with nesting material or weaving nests. For Dusky Flycatchers and Warbling Vireos I identified males and females based on singing and nest-building behaviors. I assumed that nest-building Dusky Flycatchers were females, because two birds were never observed at nests and research with color-banded birds indicated that males did not build nests (Pereyra 1990 in Sedgwick 1993a). For Warbling Vireos I assumed the same, as males usually sang during watches, nest-building birds often
visited nests while males were singing, two birds were never observed at nests, and
previous research indicated that nest building was accomplished only by females
(Howes-Jones 1985a). Warbling Vireo females did sing on two occasions, but their
songs were different from male songs. Without color-marked birds, I could not be
certain that I correctly identified sexes, but behaviors associated with nest visitation and
non-vocal activity around nests should be similar in detectability for males and females
of monomorphic species. Therefore these assumptions should create minimal bias in
this study.

To characterize activity levels, I analyzed the activity of male and female hosts
near their nests: time spent by hosts near nests, vocalizations given when near nests,
and the variety of directions from nests in which hosts were active. I analyzed the time
spent by hosts near their nests because hosts that concentrate their activity into a
smaller area surrounding nests may call attention to the location of their nests and
increase their probability of being parasitized. I estimated the location of perches as
horizontal and vertical meters from nests and recorded the duration of time hosts spent
at each perch in seconds. Although I recorded activity out to 15 m from nests,
behaviors closer to nests are likely to be more important to a nest-searching cowbird,
so I generally present behaviors within 5 m of nests. However, to compare the
behavior of parasitized and unparasitized males near their nests, I analyzed activity
within 15 m. because so few males (24% of 82) were observed within 5 m of their
nests. I also recorded the location of all vocalizations given near nests, because
vocalizations might enhance the detectability of hosts around their nests.
Hosts which are active in fewer directions relative to their nests may concentrate their movements within a smaller area near their nests, thereby drawing more attention to their nest sites. I therefore 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 a minute. I quantified the variety of directions used by hosts with a unit of concentration from angular statistics, \( R = \sqrt{\left(\sum \cos(a)/n\right)^2 + \left(\sum \sin(a)/n\right)^2} \) (Zar 1984). An \( R = 1 \) indicated use of one direction exclusively, while \( R = 0 \) indicated use of directions without preference. I compared mean \( R \) values across species and \( R \) values for parasitized and unparasitized individuals within species. \( R \) is inversely related to sample size (number of observations of directions), so analyses of variance include sample size as a covariate.

I also analyzed activity associated with nest-building visits: perch use during nest approach, nest visitation rate, duration of nest visits, and vocalizations from the nest per visit. I 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. Because many approaches were made directly without perches, a mean duration of time spent perching during nest approach was not representative. Therefore I calculated "the proportion of nest approaches with perches," which was the proportion of nest visits during which nest-building females perched within 5 m. of their nests on the way to their nests. I analyzed only females with at least five observed approaches and proportions were derived for each female, then means for each species. The data were arc-sine square-root transformed to
achieve normality. I missed some approaches to nests, but knew that they occurred because I detected a bird just getting on a nest, while on her nest, or when leaving the nest. If approaches without perches were more likely to be missed than approaches with perches, then the proportion of nest approaches with perches would be overestimated. I therefore also estimated the proportion of nest approaches with perches assuming all missed approaches were direct; results did not differ.

I measured the rate of nest visitation because birds who 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 $r=-.397$, $p=0.033$, $df=28$), so I included time as a covariate in the analysis of covariance. I 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 (e.g. nest-building, incubating, provisioning, or foraging). I also counted host vocalizations from the nest per nest-building visit, as vocalizations may assist cowbirds in locating hosts on nests.

**Statistical tests**

To test for differences in behaviors and nest placement characteristics among species and between parasitized and unparasitized pairs within species, I used analysis of covariance (ANCOVA) models. I ran two sets of models, the first asking if species explained a significant amount of variation in behaviors or nest placement; the second asking if a significant amount of variance was explained by species or by whether the pair was parasitized or not. I used two sets of models because there were many nests for which parasitism was never ascertained and this allowed me to use a larger data set.
for species comparisons. ANCOVA models contained a single behavior or nest placement characteristic as the response variable and species, or species and parasitism, as the fixed main effect(s). Models with both species and parasitism included species by parasitism interaction terms which were insignificant unless reported. I entered the relative abundance of cowbirds per site as a covariate into all models, because variation in the abundance of cowbirds across study sites might affect proportions of nests parasitized. Relative abundances were derived from ten minute 50 meter fixed-radius point counts conducted by censusers on the project with which I collaborated (Tewksbury 1997). Cowbird abundance did not explain a significant amount of variation in the response variables unless otherwise reported. Variation in behaviors due to time of day, time of season, and observer were also insignificant unless noted.

For vocalization data that occurred in positively skewed distributions (many zeros and few very large observations), I used ranked tests. Because a non-parametric equivalent to an ANCOVA with multiple effects is unavailable, I tested separately for differences among species with Kruskal-Wallis tests and then between parasitized and unparasitized individuals with Mann-Whitney U tests. I present Mann-Whitney U tests for species lumped together; I also looked for differences within each species and I present those results whenever they are significant.

To test for correlations between behavioral means and daily parasitism probabilities across species, I used a Pearson correlation. To control for variation due to covariates, I used estimated marginal means for variables which had significant covariates in their ANCOVAs.
To determine the relative importance of behavioral and non-behavioral variables in predicting parasitism, I used a forward stepwise logistic regression model with a likelihood ratio for variable removal. All species were lumped for this analysis (n=44); sample sizes were insufficient to generate separate models for each species. To correct for species differences, I obtained residuals for all variables from one factor ANOVAs with species as the main effect. I then entered these residuals into the logistic regression model. Because I did not have nest concealment data for all nests, I first ran a model including nest height and concealment on the subset of nests with those data (n=34). Since neither nest height nor concealment were significant in the model (p > 0.165), I ran a second model with behavioral variables from the larger data set (n=44), and this is the model I present.
RESULTS

Probability of parasitism

Most nests were parasitized during host egg-laying periods (Table I).

Proportions of nests parasitized differed among species (loglinear likelihood ratio $\chi^2=19.340$, $p=0.0002$, df=3), from 27% for Dusky Flycatchers to 68% for Warbling Vireos (Fig 1). Species differed in the number of days they were susceptible to being parasitized (Table II; ANOVA $F=15.637$, $p<0.001$), indicating that a daily parasitism rate was more appropriate for comparing parasitism probability among species. Daily parasitism rates differed substantially among species ($\chi^2=41.787$, $p<0.0001$, df=3); on a daily basis, Warbling Vireos had over 4 times a greater probability of being parasitized than Dusky Flycatchers (Fig 1).

<table>
<thead>
<tr>
<th>Table I. Timing of cowbird egg-laying in relation to host egg-laying from nests* in riparian habitat in western Montana.</th>
</tr>
</thead>
<tbody>
<tr>
<td>cowbird egg timing</td>
</tr>
<tr>
<td>---------------------</td>
</tr>
<tr>
<td>before first host egg</td>
</tr>
<tr>
<td>during host egg-laying</td>
</tr>
<tr>
<td>during incubation</td>
</tr>
</tbody>
</table>

a. Data were combined from Yellow Warbler (12), Dusky Flycatcher (7), and American Redstart (3) nests; data were unavailable for Warbling Vireo nests.
Figure 1. Proportions of nests parasitized by Brown-headed Cowbirds (hatched bars) differed among four host species nesting in riparian habitat in western Montana. The daily probability of parasitism (+/- s.e.; solid bars) controls for differences among species in their duration of susceptibility to parasitism, and also varied substantially among species. Numbers of nests are shown beneath the bars.
### Table II. Mean (s.e., n=nests) days of susceptibility of host species to detection and parasitism by Brown-headed Cowbirds in riparian habitat of western Montana. Nests are susceptible to detection by cowbirds during both nest-building and after hosts begin to lay eggs, a sum of both columns.

<table>
<thead>
<tr>
<th>Host species</th>
<th>nest-building susceptible to parasitism^b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dusky Flycatcher</td>
<td>9.12 (0.50, 8)</td>
</tr>
<tr>
<td>American Redstart</td>
<td>5.68 (0.31, 8)</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>7.25 (1.06, 6)</td>
</tr>
<tr>
<td>Warbling Vireo</td>
<td>5.41 (0.60, 6)</td>
</tr>
<tr>
<td></td>
<td>6.89 (0.68, 47)</td>
</tr>
<tr>
<td></td>
<td>4.90 (0.07, 21)</td>
</tr>
<tr>
<td></td>
<td>3.57 (0.28, 109)</td>
</tr>
<tr>
<td></td>
<td>5.01 (0.04, 71)</td>
</tr>
</tbody>
</table>

a. Species differed (ANOVA F=8.165, p=0.001) in the mean duration of nest-building, defined as ending on the first day of egg-laying. Includes nests found on first or second day of building, with known egg-laying dates.

b. Species differed in the length of time nests were susceptible to parasitism (ANOVA F=15.637, p<0.001). Days of susceptibility to parasitism were egg-laying days plus incubation days depending on the length of the incubation period of the host. See methods for calculation of susceptibility days.
**Host quality**

Species did not differ in the proportion of cowbird eggs they fledged from their nests ($\chi^2 = 3.323, p = .344$), suggesting that nests of all four species were of similar quality to cowbirds searching for nests in which to lay their eggs (Table III).

**Nest placement**

Nest heights did not differ among species (ANCOVA: species $F = 1.856, p = .142, df = 3, 104$), nor between parasitized and unparasitized pairs within species (ANCOVA: parasitism $F = 0.828, p = 0.441, df = 1, 71$). Nest concealment (foliage density at nests) differed among host species (ANCOVA $F = 5.761, p = 0.001, df = 3, 106$), but not as predicted relative to parasitism risk (Fig 2); probability of parasitism was actually higher for species with more highly concealed nests ($r = 0.849, p = 0.151, n = 4$). Within species, parasitized and unparasitized nests did not differ in concealment (ANCOVA $F = 0.295, p = 0.746, df = 1, 74$).
**Table III.** The probability of a cowbird egg fledging did not differ among four host species breeding in riparian habitat in western Montana.

<table>
<thead>
<tr>
<th>proportion fledged</th>
<th>n¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dusky Flycatcher</td>
<td>0.47</td>
</tr>
<tr>
<td>American Redstart</td>
<td>0.39</td>
</tr>
<tr>
<td>Yellow Warbler</td>
<td>0.30</td>
</tr>
<tr>
<td>Warbling Vireo</td>
<td>0.47</td>
</tr>
</tbody>
</table>

a. n = number of cowbird eggs, one per nest.
Figure 2. Nest concealment (x +/- s.e.) did not vary as predicted among species; probability of parasitism was actually higher for more highly concealed nests. Yellow Warbler nests were more concealed than Dusky Flycatcher, American Redstart and Warbling Vireo nests (Bonferroni p<0.001, p<0.001, p=0.020) and Warbling Vireo nests were more concealed than American Redstart nests (p=0.026). Numbers of nests are shown in parentheses.
Host activity

Female activity near nests. As predicted, the time females were active on and within 5 m of their nests showed a trend for correlating with probability of parasitism. Species differed in the time females were active on and near their nests (ANCOVA $F=3.927, p=0.012$ df=3, 73), and these differences tended to correlate with daily parasitism rates (Fig 3a; $r=0.813, p=0.187, n=4$). Parasitized females also tended to spend more time on and within 5 m of their nests than unparasitized females (ANCOVA parasitism $F=3.164, p=0.084$, df=1,46). When excluding time on the nest, the time that females were active near their nests did not differ among species (ANCOVA $F=0.179, p=0.911$, df=3,73), or between parasitized and unparasitized females within species (ANCOVA $F=0.086, p=0.771$, df=1,37).

The range of directions from the nest in which females were active differed marginally among species (ANCOVA $F=2.504, p=0.065$, df=3,79), and probability of parasitism tended to increase with higher directional preference (Fig 3b). Directional use did not differ between parasitized and unparasitized females within species (ANCOVA $F=0.244, p=0.625$, df=1,36). In general, females were active in more directions relative to nests than were males (ANCOVA $F=11.048, p=0.001$, df=1,162; $\bar{x}$, s.e.: female $R=0.41, 0.03$, male $R=0.54, 0.03$).

Vocalizations per minute by females near their nests (Fig 3c) differed
Figure 3. Female activity near nests. a). The minutes per hour (\( \bar{x} +/- s.e. \)) females spent on or within 5 m of their nests differed among species and correlated with parasitism rates at \( r=0.813 \). Numbers of females are shown in parentheses.
Figure 3. Female activity near nests. As predicted, female Warbling Vireos tended to concentrate their activity in fewer directions relative to their nests (higher R) than females of the other species, though differences among species were not significant. Numbers of females are shown in parentheses.
Figure 3. Female activity near nests. c). Vocalizations per minute (x +/- s.e.) by females within 5 m of their nests differed among species but did not correlate with daily parasitism rates. Numbers of females are shown in parentheses.
among species (Kruskal-Wallis $\chi^2=16.374$, $p=0.001$, $n=75$), but did not correlate with daily parasitism rates ($r=-0.445$, $p=0.555$, $n=4$). This was due to Dusky Flycatchers vocalizing more than predicted; among the other three species parasitism probability increased with female vocalizations. Vocalization rates did not differ between parasitized and unparasitized females (Mann-Whitney $U=173$, $p=0.560$, $n=43$).

**Male activity near nests.** The minutes per hour that males were active within 5 m of their nests differed among species (ANCOVA $F=2.796$, $p=0.046$, $df=3,73$) and was highly correlated with daily parasitism rates (Fig 4a; $r=0.999$, $p=0.001$, $n=4$). Parasitized and unparasitized males did not differ in the time they were active near their nests (within 5 m: ANCOVA $F=0.090$, $p=0.766$, $df=1,37$; within 15 m: ANCOVA $F=0.168$, $p=0.684$, $df=1,37$).

The variety of directions from the nest in which males were active did not differ among species (ANCOVA $F=1.836$, $p=0.148$, $df=3,71$). As predicted, however, males that were active in fewer directions relative to nests had a higher probability of parasitism than males active in a greater variety of directions (Fig 4b; ANCOVA $F=8.323$, $p=0.007$, $df=1,35$).

Vocalization rates by males near their nests differed among species (Kruskal-Wallis $\chi^2=12.134$, $p=0.007$, $n=75$) and were highly correlated with parasitism rates across species (Fig 4c; $r=0.973$, $p=0.027$, $n=4$). In addition, parasitized males vocalized more than unparasitized males (Fig 4d;
Figure 4. Male activity near nests. a). Minutes per hour (x +/- s.e.) that males were active within 5 m of their nests differed among species and was highly correlated with daily parasitism rates. Numbers of males are shown in parentheses.
Figure 4. Male activity near nests. Males whose nests were subsequently parasitized confined their activity to fewer directions from their nests (higher R) during the nest-building period than males whose nests were not parasitized. Bars represent mean R's +/- s.e. Numbers of males are shown in parentheses (parasitized, unparasitized).
Figure 4. Male activity near nests. c). Vocalizations per minute (x +/- s.e.) by males within 5 m of their nests differed among species and were highly correlated with parasitism rates across species. Numbers of males are shown in parentheses.
Figure 4. Male activity near nests. Males whose nests were subsequently parasitized vocalized more frequently (x ± s.e.) from within 15 m of their nests during the nest-building period than males whose nests were not parasitized. Numbers of males are shown in parentheses (parasitized, unparasitized).
Nest-building visitation activity. Species differed in the proportion of nest visits during which females used perches within 5 m of the nest during nest approach (Fig 5a; ANCOVA F=4.136, p=0.009, df=3,71). Parasitism probability tended to increase with perching frequency across species (r=0.612, p=0.388, n=4) as expected, but parasitized and unparasitized females did not differ in perching frequency (ANCOVA F=0.607 p=0.441, df=1,37).

Rate of nest visitation by nest-building females did not differ among species (ANCOVA F=0.028, p=0.994, df=3,61). For all species combined, females whose nests were subsequently parasitized visited their nests less frequently than females who were not parasitized (Fig 5b; ANCOVA F=4.732, p=0.036, df=1, 36), which is opposite to predictions. This difference was also significant within Warbling Vireos (ANCOVA F=8.615, p=0.032, df=1,5).

In contrast, the mean duration of nest-building visits increased as predicted with parasitism probability both across and within species. Duration of nest-building visits differed among species (ANCOVA F=4.153, p=0.009, df=3, 61) and correlated strongly with daily parasitism rates (Fig 5c; r=0.974, p=0.026, n=4). In addition, females who spent more time on their nests per nest-building visit were more likely to be parasitized than females who visited for shorter durations, across all species (Fig 5d;
Figure 5. Nest-building visitation activity. a). Species differed in the proportion of nest approaches (± s.e.) in which perches within 5 m of the nest were used; there was a trend for perching frequency to correlate with parasitism rates. Numbers of females are shown in parentheses.
Figure 5. Nest-building visitation activity. b). Counter to predicted, females who were subsequently parasitized visited their nests ($\bar{x} +/-$ s.e.) less frequently during nest-building than females who were not parasitized, for all species combined. This difference was also significant within Warbling Vireos. Numbers of females are shown in parentheses (parasitized, unparasitized).
Figure 5. Nest-building visitation activity. c). Duration of time on the nest per nest-building visit ($\bar{x} \pm$ s.e.) differed among species and correlated strongly with daily parasitism rates. Numbers of females are shown in parentheses.
Figure 5. Nest-building visitation activity. d). Females who were subsequently parasitized spent more time on their nests per nest-building visit ($\bar{x} \pm$ s.e.) than females who were not parasitized, for all species combined. This difference was also significant within Dusky Flycatchers. Numbers of females are shown in parentheses, (parasitized, unparasitized).
ANCOVA $F = 11.786, \ p = 0.001, \ df = 1,37$). This difference was also significant within Dusky Flycatchers (ANCOVA $F = 6.329, \ p = 0.024, \ df = 1,15$).

Nest visitation rate and duration of nest visits were negatively correlated for two species (Table IV), suggesting why both traits were not correlated positively with parasitism as predicted. Visit duration was more strongly related to parasitism than nest visitation rate, suggesting that the unexpected pattern for nest visitation rate was an indirect consequence of its inverse correlation with visit duration.

Species differed in the propensity of nest-building females to vocalize from the nest per nest-building visit (Fig 5d; Kruskal-Wallis $\chi^2 = 13.581, \ p = 0.004, \ df = 3$), but these differences in vocalizations did not correlate with parasitism rates ($r = -0.551, \ p = 0.449, \ n = 4$), again due to higher than expected 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 $U = 196.5, \ p = 0.642, \ n = 43$), but Warbling Vireos that were subsequently parasitized vocalized more than conspecifics that were not parasitized (Mann-Whitney $U = .000, \ p = 0.017, \ n = 7$). Vocalizations from the nest were correlated with duration of nest visits, however, for Warbling Vireos (Table IV).
Table IV. Correlations among behaviors* during nest-building for four Brown-headed Cowbirds host species breeding in riparian habitat in western Montana.

<table>
<thead>
<tr>
<th>Behaviors</th>
<th>Dusky Flycatcher</th>
<th>American Redstart</th>
<th>Yellow Warbler</th>
<th>Warbling Vireo</th>
</tr>
</thead>
<tbody>
<tr>
<td>(female time near nest) x</td>
<td>.54* (21)</td>
<td>.24 (18)</td>
<td>.16 (20)</td>
<td>.19 (16)</td>
</tr>
<tr>
<td>(female vocalizations near nest)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(female time near nest) x</td>
<td>-.47* (23)</td>
<td>-.11 (20)</td>
<td>-.41 (20)</td>
<td>.05 (17)</td>
</tr>
<tr>
<td>(female directional preference)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(female vocalizations near nest) x</td>
<td>-.43* (23)</td>
<td>.27 (20)</td>
<td>-.19(20)</td>
<td>.12 (17)</td>
</tr>
<tr>
<td>(female directional preference)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(male time near nest (5 m)) x</td>
<td>c.</td>
<td>.73** (17)</td>
<td>.34 (19)</td>
<td>.71** (15)</td>
</tr>
<tr>
<td>(male vocalizations near nest)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(male time near nest) x</td>
<td>-.16 (11)</td>
<td>-.28 (14)</td>
<td>-.52* (15)</td>
<td>-.19 (15)</td>
</tr>
<tr>
<td>(male directional preference)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(male vocalizations near nest)</td>
<td>c.</td>
<td>-.38 (14)</td>
<td>-.38 (15)</td>
<td>-.58* (15)</td>
</tr>
<tr>
<td>(male directional preference)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(male time within 15 m) x</td>
<td>.75** (24)</td>
<td>.82** (17)</td>
<td>.85** (19)</td>
<td>.67** (15)</td>
</tr>
<tr>
<td>(male vocalizations within 15 m)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table IV. continued.

<table>
<thead>
<tr>
<th>Behaviors</th>
<th>Dusky Flycatcher</th>
<th>American Redstart</th>
<th>Yellow Warbler</th>
<th>Warbling Vireo</th>
</tr>
</thead>
<tbody>
<tr>
<td>(nest visits per hour) x (duration of nest visits)</td>
<td>.05 (26)</td>
<td>-.47* (20)</td>
<td>-.59* (20)</td>
<td>-.44 (16)</td>
</tr>
<tr>
<td>(duration of nest visits) x (vocalizations per nest visit)</td>
<td>.12 (26)</td>
<td>-.009 (20)</td>
<td>.38 (20)</td>
<td>.53* (16)</td>
</tr>
<tr>
<td>(vocalizations per nest visit) x (% of approaches with perches used)</td>
<td>.16 (26)</td>
<td>.26 (20)</td>
<td>-.45* (20)</td>
<td>-.07 (16)</td>
</tr>
</tbody>
</table>

a. Only pairs of behaviors which were correlated at $p < .05$ in at least one species are presented in this table.

b. Numbers of individuals varies among correlations because individuals were excluded for some variables for reasons such as conditions being poor for hearing vocalizations, infrequent visitation, etc.

c. No Dusky Flycatcher males vocalized within 5 m of their nests.

* **significant at $p < .05$, and $p < .01$, respectively, without correcting for multiple tests. No correlations were significant after a sequential Bonferroni correction for multiple tests.
Figure 5. Nest-building visitation activity. e). Species differed in the number of vocalizations ($\bar{x} +/-$ s.e.) given by females from the nest per nest-building visit, but these differences did not correlate with parasitism rates. Numbers of females are shown in parentheses.
Multivariate model of activity predicts parasitism

The final logistic regression model of Brown-headed Cowbird parasitism correctly classified 84% of 44 cases, significantly better than by chance (model $\chi^2 = 18.622, p = 0.0003$). The logistic regression model contained three variables, of which only the first explained a statistically significant amount of variation on its own: male directional preference, mean duration of nest visits, and male vocalizations within 15 m of nests (Table V).
Table V. Forward stepwise logistic regression model including behavioral variables classifies nests for whether or not they are parasitized by Brown-headed Cowbirds. The model used a likelihood-ratio test for variable removal and correctly classified 84% of 44 cases.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Beta</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>male directional preference</td>
<td>6.040</td>
<td>.013</td>
</tr>
<tr>
<td>nest visit duration</td>
<td>.047</td>
<td>.059</td>
</tr>
<tr>
<td>male vocalizations within 15 m</td>
<td>.025</td>
<td>.066</td>
</tr>
<tr>
<td>constant</td>
<td>-1.131</td>
<td>.030</td>
</tr>
</tbody>
</table>

Variables in the original model but not retained 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

a. Nest height and concealment were entered into a model with a subset of data (n=34) and were not significant in the model (p > .165).

b. Dusky Flycatchers (n=14), American Redstarts (14), Yellow Warblers (4), and Warbling Vireos (7) were combined in the model.

c. Variables are residuals from one factor ANOVAs with species as the main effect, to control for variation in behaviors due to species.
DISCUSSION

Although many researchers have suggested that host activity near nests increases probability of parasitism by cowbirds (e.g. Friedmann 1929, Hann 1941, Norman and Robertson 1975, Scott 1977, Gochfeld 1979), the hypothesis has not been explicitly tested. I found support for my general activity hypothesis that host activity near nests increases probability of parasitism. Specifically, I found that the time males and females were active near their nests, the vocalizations and directional preference of males near their nests, and the duration of time females spent on the nest per nest-building visit correlated strongly with probability of parasitism.

I found strong support for the prediction that pairs who were more active in the area immediately surrounding their nests would call more attention to their nest sites and increase their probability of parasitism. The minutes per hour that males and females were active within 5 m of their nests correlated strongly with parasitism rates among species. I also predicted that vocalizations by birds near their nests would further increase their detectability to cowbirds and attract more attention to their nests (Gochfeld 1979, Uyehara and Narins 1995).

Male vocalizations appeared to be particularly important in determining parasitism probability. Parasitism probability correlated strongly with male vocalizations across species: Warbling Vireos, the most highly parasitized species, vocalized most frequently, while Dusky Flycatcher males were never heard within 5 m of their nests. Within species, this pattern was reinforced; vocalization rates were
higher for males who were subsequently parasitized than for males who were not
parasitized. In concert with the finding that parasitized males used fewer directions
from their nests, these results suggest that male singing in consistent locations at close
proximity to nests increases probability of parasitism. Indeed, in the logistic regression
model built from all behaviors, male directional preference and vocalizations near nests
were the two factors most important in classifying nests as parasitized or not
parasitized. These data strongly suggest that cowbirds use male song during nest-
building to locate nests.

Like the males, parasitized female Warbling Vireos vocalized more frequently
on the nest during their nest-building visits than did their unparasitized conspecifics
(also see Uyehara and Narins 1995). However, the pattern of higher female
vocalizations among parasitized females did not hold within the other species. In
addition, in contrast to males and contrary to my prediction, females of the least
parasitized species, Dusky Flycatchers, vocalized more than expected both from near
nests and from their nests during nest-building visits.

Why male vocalizations so clearly correlated with probability of parasitism but
female vocalizations did not may best be explained by how I characterized
vocalizations. For this study, I assumed that the behaviors of different species,
vocalizations in this case, were of equal importance to cowbirds searching for nests.
However, this may not have been a good assumption. I measured only rates of
vocalizations, while the value of a vocalization to a nest-searching cowbird is likely to
depend not only on its rate but also on its volume or the average distance at which it
can be heard. Dusky Flycatcher "whit" calls, which are uttered so frequently by females during nest-building, are unusually low in volume. During many behavioral watches I was watching a female Dusky Flycatcher vocalize while I was unable to hear her at a distance of only five to ten meters away. Thus, the answer to why male vocalization rates correlate more strongly with probability of parasitism than female calls may be related to their volume and relative audibility to cowbirds. Measuring the transmission distance of calls of different sexes and species and investigating the relationship between vocalization rates, volumes, and parasitism probability should be a promising topic for future research.

Male vocalizations might be exploited as nest-location cues by cowbirds for several other reasons. The behaviors which may be most easily exploited by cowbirds may be those most constrained by other factors. Song is critical for male reproductive success, thought to function in territorial defense (Krebs 1977, Smith 1979, McDonald 1989), defense of mates from extra-pair copulations (Moller 1988, Hobson and Sealy 1989b), solicitation of extra-pair copulations (Moller 1991), and stimulation of females to lay (Logan et al 1990). Thus, to a particular male, the benefits of singing may outweigh the potential cost of lower reproductive success due to cowbird parasitism. This has interesting implications for sexual selection; if females experience high enough costs associated with brood parasitism, they may select males that sing less near their nests. Secondly, although in some species unpaired males sing more than paired males (e.g. Catchpole 1973), singing rates generally peak during nest-building or egg-laying for paired males (Slagsvold 1977, Logan 1983, Moller 1991). Thus, singing
rates may serve as temporal cues indicating when specific nests are active in the pre-
egg-laying or egg-laying phase, precisely when cowbirds need to locate nests. Finally,
singing rates may serve as spatial cues as well, as singing rates increase as males move
closer to their nests, at least for some species. Warbling Vireo males, as they
accompanied their mates during nest building, increased their rates of singing near their
nests and decreased their song rates as they moved away from their nests (Howes-Jones
1985b). Nest-centered singing was thought to encourage copulations with the female
where she was most receptive, near the nest, while not encouraging courtship in areas
where inter-territorial conflicts or extra-pair copulations could occur. In sum, cowbirds
may exploit male vocalizations because males are constrained to sing and because
singing rates may provide particularly good temporal and spatial cues to nests.
Experimental manipulation of singing rates (although playbacks near Dusky Flycatcher
nests caused nest desertion; unpub. data) should provide important insights into the
effects of male vocalizations on probability of parasitism.

In addition to activity of hosts near nests, I found that activity associated with
nest-building visitation also correlated with parasitism probability, both across and
within species. I found support for the prediction that perching near nests during nest
approach assists cowbirds in locating nests; species that perched more frequently
during nest approach tended to have a higher probability of parasitism. In addition,
parasitized Warbling Vireos perched more than unparasitized Warbling Vireos,
although the data were not consistent across all species.

I found strong support for the prediction that longer nest visits would increase
probability of parasitism by facilitating detection of nests and assessment of host activity at the nest (e.g. building, incubating, provisioning) by cowbirds. Across species, the duration of nest visits and probability of parasitism were strongly correlated. This was repeated within species; females who were subsequently parasitized spent longer on their nests per nest-building visit than females who were not parasitized. These results suggest that the duration of time a female spends at her nest during each trip may increase her likelihood of being parasitized.

I also predicted that more frequent nest visitation would call attention to nest sites. However, I found no variation in frequency of nest visitation among species, and within species nest visitation rates were actually higher among unparasitized females. These results contrast strongly to those for the duration of nest visits. A significant negative inter-correlation between nest visitation rate and nest visit duration explain why both behaviors did not correlate positively with parasitism probability. Nest visit duration was used in the logistic regression model to classify nests as parasitized or not parasitized, and the model did not either variable if nest visit duration was excluded from use. Nest visit duration therefore seems to be the stronger predictor of parasitism, and lower visitation rates by parasitized individuals are probably artifacts of longer nest visits. The finding that duration of female activity at the nest per nest visit appeared to influence the risk of parasitism while nest visitation rate did not has important implications for studies which attempt to characterize activity at nests merely by measuring nest visitation rate.

In contrast to the behavioral data, nest height and concealment did not differ
between parasitized and unparasitized nests and did not explain differences in parasitism rates among species; in fact, probability of parasitism was actually higher for species with more concealed nests. Probability of parasitism also did not vary with differences in host quality; species fledged equal proportions of cowbirds from their nests.

To conclude, I found that probability of parasitism correlated with several behaviors of hosts at and around their nests. When combined, these behaviors formed an effective predictive model of parasitism. Both male vocalization rates and the duration of nest-building visits by females related strongly to probability of parasitism across species, and also were higher for pairs that were subsequently parasitized than for pairs who were not parasitized within species. This study is powerful because it identifies specific behaviors which explain variation in probability of parasitism among individuals within species, behaviors which simultaneously vary among species in correlation with parasitism rates. Thus it provides linkage between a mechanistic hypothesis and evolutionary differences among species. These results strongly suggest that cowbirds use everyday, non-defensive host behaviors to locate nests. Future research should investigate these patterns of host activity in relation to probability of parasitism in wider array of host species.
ACKNOWLEDGMENTS

I thank Jamie Luke and Kathleen Lynch for excellent assistance with behavioral observations. I thank Joshua Tewksbury for being a tremendously supportive and creative collaborator and for allowing me to work with nests found and monitored by the Bitterroot Riparian Bird Project crew (funded by U.S.F.S. Intermountain Research Station). Many crew members were helpful in assisting in behavioral watches, nest checks, and in lending logistical support. This paper benefitted from the comments of my advisor, Thomas E. Martin, committee members Erick Greene, I. Joe Ball, and L. Scott Mills, and Alex Badyaev, Courtney Conway, Cameron Ghalambor, J. Wajid Jenkins, Wesley Hochachka, and Paul Martin.
LITERATURE CITED


