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Factors Affecting Reed Warbler Risk of Brood Parasitism by the Common Cuckoo

ALICE L. CLARKE,[1,5] INGAR J. ØIEN,[2] MARCEL HONZA,[3] ARNE MOKSNES,[4] AND EIVIN RØSKAFT[4]
[1]*Department of Environmental Studies, Florida International University, Miami, Florida 33199, USA;*
[2]*Norwegian Ornithological Society, Seminarplassen 5, N-7540 Klæbu, Norway;*
[3]*Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Kvetná 8, 603 65 Brno, Czech Republic; and*
[4]*Norwegian University of Science and Technology, NTNU, Department of Zoology, N-7491 Trondheim, Norway*

ABSTRACT.—In this study we conducted a multiple logistic regression analysis of factors hypothesized to influence the risk of Reed Warbler (*Acrocephalus scirpaceus*) brood parasitism by the Common Cuckoo (*Cuculus canorus*) on study sites in the south-eastern part of the Czech Republic. We collected data from Common Cuckoo nesting sites surrounding two fishponds. Our logistic regression models were based on the dichotomous dependent variable, parasitism of the Reed Warbler nest, and seven independent variables. Our first model used all data available across sites and years and resulted in a final model in which the only significant contributor was the independent variable "cuckoo view," the view of host nests from the cuckoo's vantage point in a tree. A second model was developed using data limited to sites and years with the largest sample sizes and expected to yield the most reliable results. That model resulted in three significant contributors: site, cuckoo view, and neighborhood view. In both data sets, the odds of nest parasitism were shown to increase as the view of the host nest became more direct. However, a direct view of the focal nest raised the risk of parasitism to a much greater degree than did a direct view of the neighborhood of nests. Our results provide support for a nest-exposure hypothesis of brood parasitism risk. Although our models have identified nest exposure to be the best predictor of nest parasitism in this system, work remains to unravel the potentially complex relationship among Common Cuckoos, habitat structure, and Reed Warbler hosts.

In recent decades, scientists have focused particular attention on the process by which avian brood parasites search for host nests. In fact, as early as the 1920s, the ornithologist E. Chance (1922, 1940) described female Common Cuckoos (*Cuculus canorus*) using visual vantage points in trees to observe their host's nest building activity. From such vantage points, the cuckoo would later fly secretively down to the host nest and, usually within seconds, lay its egg. Subsequently published observations by Gärtner (1981, 1982) and Wyllie (1981) have supported Chance's original observations. Despite the fact that watching the activity of the hosts is frequently referred to as the only nest-finding cue employed by the cuckoo, systematic studies of its nest-searching behavior are more or less lacking (Øien 2000). Recently, Alvarez (1993), Øien et al. (1996), and Moskát and Honza (2000) have observed that hosts breeding close to trees suffered a higher risk of being parasitized by cuckoos than those breeding farther away from trees. That higher risk is hypothesized to occur because it is easier for cuckoos to spot host-nesting activity when the nests are built near trees. Furthermore, Øien et al. (1996) and Moskát and Honza (2000) recorded the degree of concealment of host nests (referred to as "cuckoo view") and found a strong, negative relationship between the degree of nest concealment and risk of parasitism.

Clotfelter (1998) recently reviewed the literature on the nest searching behavior of the North American generalist brood parasite, the Brown-headed Cowbird (*Molothrus ater*), and suggested four different hypotheses that might explain how this parasite searches for and localizes nests. He found little sup-

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[5] E-mail: clarkea@fiu.edu

TABLE 1. Total number of Reed Warbler nests found at Mlynsky South and North and Hlohovecky North in 1993 and 1994, number of nests used in the models, number and percentage of nests parasitized by Common Cuckoos, and lengths of study sites.

Study site and year	Total no. of nests	No. nests used in model	No. and % nests parasitized	Study site length (m)	Mean distance between nests
Mlynsky S 1993	49	36	11 (30.6)	1102	22
Mlynsky S 1994	77	64	15 (23.4)	1684	22
Mlynsky N 1994	120	89	16 (18.0)	1490	12
Hlohovecky N 1993	45	32	4 (12.5)	1695	38
Hlohovecky N 1994	74	45	6 (13.3)	1635	22
Total	365	266	52 (19.5)	7606	21

port for the "nest-exposure hypothesis," which assumes that visually conspicuous nests are at a higher risk of parasitism. Neither could he find any support for the "nesting-cue hypothesis," which predicts that hosts that are more aggressive towards adult parasites suffer a higher risk of parasitism. However, he found good support for the "perch-proximity hypothesis," which predicts nests close to trees to suffer a higher risk of being parasitized, and the "host-activity hypothesis," which predicts that active hosts attract brood parasites (for further references, see Clotfelter 1998). Recent studies by Larison et al. (1998) and Burhans and Thompson (1998) have similarly showed effects of habitat and microhabitat variation on risks of parasitism by Brown-headed Cowbirds among North American hosts (but see also Averill-Murray et al. 1999, Chace and Cruz 1999, and Spautz 1999).

Clotfelter's (1998) approach can easily be applied to cuckoos. Øien et al. (1996) found support for both the nest-exposure hypothesis and the perch-proximity hypothesis. They found that nests of Reed Warblers (*Acrocephalus scirpaceus*) located close to trees, with little concealment, suffered a higher risk of being parasitized by cuckoos than concealed nests located farther from trees. Furthermore, in an experimental setting, Øien (2000) has found that well-exposed Reed Warbler nests, into which eggs are artificially placed, may suffer parasitism by cuckoos even though the nests are not actively visited by the host.

Methods.—The study was conducted in the Breclav district in the southeastern part of the Czech Republic. In that area, Reed Warblers are one of the most important hosts of cuckoos. The study area is situated near the village Lednice (47°40'N 16°34'E), ~40 km south of Brno, and 70 km north of Vienna, Austria. Most Reed Warbler nests were found in reed beds (*Phragmites australis*), with a smaller number in reedmace stands (*Typha angustifolia*) (Honza et al. 1998). We collected data from nesting sites surrounding two fishponds—Mlynsky (107 ha) and Hlohovecky (104 ha). The ponds and reed beds are surrounded by arable land, but are separated from it by a strip of mature parkland and forest. Cuckoos use trees within that forested strip for perching. Descriptions of the study area are also given by Hudec (1975), Moksnes et al. (1993), Øien et al. (1996) and Honza et al. (1998). The fieldwork related to this paper was carried out during the periods 1 June to 20 July 1993, and 15 May to 10 July 1994. Øien et al. (1996) reported on a portion of the data used in this study; however, here we expand the analysis using multiple logistic regression methods to explore the influence of a set of independent variables on nest parasitism.

We located Reed Warbler nests by systematically searching reed beds and reedmace vegetation surrounding the fishponds. We numbered each nest and marked its position with a small plastic tag on the outer edge of the reed bed towards the open water. Further, we recorded the number of eggs in each nest and, when we found nests during incubation, we floated the eggs to determine how long they had been incubated (Hays and Lecroy 1971). By that method and by direct observations, we were able to estimate laying dates for most clutches. To record clutch size, estimate breeding success of each nest, and assess nest parasitism by Common Cuckoos, all nests were checked at least two to three times and up to seven times a week. Most Reed Warblers accepted the cuckoo egg; however, rejected cuckoo eggs were easily found because egg rejection was most often accomplished by desertion of the nest. There was no difference between acceptor and rejecter nests with regard to nest-site characteristics (F test, $P = 0.764$).

We divided the Mlynsky and Hlohovecky ponds each into two observational units: the northern and southern banks. In both ponds, an area at each short end (east and west) was either inaccessible or had a very low density of reeds and, hence, few Reed Warbler nests.

The Mlynsky South reed-bed habitat was relatively narrow (2–6 m) and close to potential perch trees. The reed bed in that site was more or less continuous, only occasionally broken by 30–50 m stretches of open water. Nest density was medium, whereas rate of parasitism was higher than at other sites (Table 1). Mlynsky North, on the other hand, consisted of an unbroken reed bed. The reed bed was here quite wide (up to 50 m), with most nests situated farther away from trees—well concealed from the cuckoo. Nest density was particularly high, while the rate of parasitism was moderate relative to other sites (Table 1).

The reed beds at Hlohovecky North were much more heterogeneous than the Mlynsky sites. The Hlohovecky North reed bed was discontinuous, having long sections totally lacking reeds. Some portions, on the other hand, consisted of 30–40 m of narrow reed strips, with one or two Reed Warbler nests. Other areas were similar to Mlynsky North, with broad reed belts with poor cuckoo view. Very few of those areas were of sufficient extent for a cuckoo female to simultaneously monitor several nests. Because of low host density and low rate of parasitism, the Hlohovecky South area was not surveyed in this study.

We used multiple logistic regression techniques to model the relationship between the dichotomous dependent variable, parasitism of the Reed Warbler nest (0 = not parasitized, 1 = parasitized), and seven independent variables, described below. The logistic regression model is defined as: Probability (event) = $e_z/(1 + e_z)$, where $z = B_0 + B_1X_1 + B_2X_2 + \dots + B_nX_n$; where B_0 through B_n are coefficients estimated from the data, X_1 to X_n are the independent variables, and e is the base of the natural logarithms, ~2.718 (Hosmer and Lemeshow 1989). All modeling was conducted using SPSS 6.1 for Macintosh (Norusis 1995). Only nests that were found to be active during the season for which data on all seven independent variables were available, and for which the parasitism status was known, were included in the analyses (see Table 1).

The following seven independent variables, believed to be important on the basis of previous studies of that population, were used in the analysis. (1) *Distance to tree* was measured as the horizontal distance (nearest meter) between each nest and the nearest tree branch where it was possible for a cuckoo to sit watching the nest. (2) *Cuckoo view* is the degree of concealment of the nest as measured from nest looking toward the branches of the nearest tree. Categorized as follows as in Øien et al. (1996): *No Nest View* (= 0), nest very well concealed. *Indirect Nest View* (= 1), nest less well concealed, however, cuckoo could only discover the nest by watching the activity patterns of the nesting birds. *Direct Nest View* (= 2), cuckoo had an unimpeded view of the nest. (3) *Neighborhood view* was measured as median degree of concealment within a radius of 40 m of focal nest based on the nest-view parameters given above. Limited to two categories: *No Nest View* to *Indirect Nest View* = 0, and *Direct Nest View* = 1, because very few neighborhoods resulted in no nest view. (4) *Number of neighbors* was measured as number of nests within a radius of 40 m of the focal nest, independent of whether those neighboring nests were simultaneously active or not. (5) *Number of neighbors simultaneously active in breeding* represents those nests breeding within a radius of 40 m of focal nest and where egg laying occurred during the same, synchronous time period as in focal nest, that is, focal nest laying date plus four days. This assumes that a neighborhood with several simultaneously active nests is more attractive to cuckoos than one with fewer simultaneously active nests. (6) *Site* is Mlynsky North, Mlynsky South, or Hlohovecky North. (7) *Year* is 1993 or 1994.

TABLE 2. Final logistic regression model for Reed Warbler nests parasitized by Common Cuckoos at Mlynsky South and North and Hlohovecky North in 1993 and 1994. Variables are listed in the order entered into the final model.

Variable	Wald χ^2	df	P	Odds ratio
Site	1.52	1	0.22	0.78
Year	0.06	1	0.81	1.11
Cuckoo view—none	13.44	2	0.001	
Indirect	7.95	1	0.005	11.24
Direct	12.81	1	0.000	27.19
Neighborhood view	3.63	1	0.06	2.38
Distance to tree	0.46	1	0.50	1.01
Number of neighbors	0.05	1	0.83	1.02
Number active neighbors	0.57	1	0.45	1.13
Constant	19.90	1	0.000	

Results.—Sufficient data (>40 nests located) were obtained for initial consideration in the modeling analyses from the southern bank of Mlynsky pond in 1993 and 1994 and from the northern bank of Mlynsky in 1994. We obtained sufficient data from Hlohovecky pond from the northern bank only in both 1993 and 1994. Over the two year period (1993–1994), we investigated 365 nests, 72.9% of which we used in our models, 52 (19.5%) of which were parasitized (Table 1).

We first used all available data, combined from each location and year, to build a logistic regression model in which the independent variables listed above were entered into the model in three phases. In the first phase, site and year were forced into the model. In the model resulting from that step, site was significant (Wald $\chi^2 = 4.68$, $P = 0.03$).

In the second phase, the variables cuckoo view, neighborhood view, and distance to nest were forced into the model, in addition to those entered in the first phase. In the resulting model, whereas site was no longer found significant ($P = 0.16$), cuckoo view was a significant contributor to the model (reference level: Wald $\chi^2 = 13.15$, $P = 0.001$).

In the third phase, the remaining variables, number of neighbors and number of active neighbors were also entered. The final model then contained all seven independent variables (Table 2). With all variables included in the model, cuckoo view remained

TABLE 3. Final logistic regression model for Reed Warbler nests parasitized by Common Cuckoos at Mlynsky South and North in 1994. Variables are listed in the order entered into the final model.

Variable	Wald χ^2	df	P	Odds ratio
Site	6.88	1	0.01	6.09
Cuckoo view—none	12.05	2	0.002	
Indirect	8.43	1	0.004	13.38
Direct	12.03	1	0.000	32.70
Neighborhood view	7.33	1	0.007	7.67
Distance to tree	0.12	1	0.73	0.99
Number of neighbors	0.95	1	0.33	1.18
Number active neighbors	0.36	1	0.55	0.89
Constant	21.01	1	0.000	

significant (Wald $\chi^2 = 13.44$, $P = 0.001$) and neighborhood view was marginally significant (Wald $\chi^2 = 3.63$, $P = 0.06$). No other variables were significant contributors to the model. The goodness-of-fit of the model, as measured by a decreasing −2 log likelihood parameter step (−2 log likelihood = 257.61, 212.37, and 210.35, respectively) increased at each. In an additional step, the interaction of the two significant variables, cuckoo view and neighborhood view, was added. The interaction did not produce a significant effect (Wald $\chi^2 = 0.54$, $P = 0.46$) and therefore the model shown in Table 2 does not reflect that additional phase of modeling.

We then produced a second model using only the data from Mlynsky South 1994 and Mlynsky North 1994. We chose those data sets because they had the largest sample sizes and would be likely to produce the most reliable results in the modeling process. The Mlynsky 1994 model (Table 3) was developed in the same way as the combined model described above. At the first phase, site was the only variable entered into the model and it did not prove to be significant (Wald $\chi^2 = 0.68$, $P = 0.41$). Second, cuckoo view, neighborhood view, and distance to nest were added to site in the model. At this point in the modeling process, three variables—site, cuckoo view, and neighborhood view—were significant (Wald $\chi^2 = 7.75$, $P = 0.01$; Wald $\chi^2 = 11.75$, $P = 0.003$; and Wald $\chi^2 = 6.98$, $P = 0.01$ respectively). In a third step, number of neighbors and number of active neighbors were added, resulting in a model in which site, cuckoo view, and neighborhood view remained significant (Table 3). The −2 log likelihood parameter declined at each step (−2 log likelihood = 153.54, 108.26, and 107.27 respectively). Adding in the interaction of the significant variables, cuckoo view and neighborhood view, did not produce a significant interaction (Wald $\chi^2 = 1.90$, $P = 0.17$) and therefore the model shown in Table 3 does not reflect that final phase of modeling.

In both datasets, the odds of nest parasitism, as expressed by the odds ratios (Tables 2 and 3), were shown to increase as the view became more direct. However, a direct view of the focal nest raised the risk of parasitism to a much greater degree than a direct view of the neighborhood of nests.

Discussion.—Øien et al. (1996), reporting on Common Cuckoo parasitism of Reed Warblers in a data set representing a minor overlap with the data used in our current analysis, found that the distance from nests to trees had a significant influence on the risk of being parasitized, independent of the cuckoo view. Their analytical technique was a two-way analysis of variance. Our models, using logistic regression analyses, did not show distance to tree to be a predictor of Reed Warbler parasitism. Although our results do not exclude distance to tree as an important factor in determining parasitism, that variable, arguably the most direct measure of the perch-proximity hypothesis, did not improve our models significantly beyond that accomplished by the variables cuckoo view and neighborhood view. Neighborhood view was not assessed by Øien et al. (1996).

Though we do not have direct measures of host-activity behavior, we used number of neighbors and number of active neighbors as proxy measures of that activity. The variables, number of neighbors and number of active neighbors, did not prove important to either of our models and, therefore, we found no support for Clotfelter's host-activity hypothesis in the Common Cuckoo and Reed Warbler parasite–host system.

When all sites were included in our model, cuckoo view was the only explanatory variable for risk of parasitism of Reed Warbler nests by Common Cuckoos. Site, cuckoo view, and neighborhood view were predictors of nest parasitism in the restricted model of Mlynsky 1994. Our results, therefore, provide support for Clotfelter's (1998) nest-exposure hypothesis.

Given the apparent significance of the cuckoo's view of nests, differences between sites in available cuckoo perching positions are expected to influence risk of parasitism and site differences did prove significant within the more limited Mlynsky 1994 model. Yearly changes in reed-vegetation density and reed-bed width would also influence potential risk through influencing nest exposure. Reed Warblers, therefore, may be expected to be phenotypically plastic in choice of nest site, as they are in their response to more direct parasitism pressure (Øien et al. 1996, 1999).

Though represented in our study as a single variable, cuckoo view, nest exposure is actually a composite of vegetative factors and a range of responses of both the parasite and the host species to given conditions. Whereas our models have identified nest exposure as the best predictor of nest parasitism in this system, work remains to unravel the potentially complex relationship among Common Cuckoos, habitat structure, and Reed Warbler hosts. Habitat structure, mediating between parasite and host, is increasingly influenced by human actions (e.g. manipulation of wetlands, introduced species, removal of large trees) in this and other parasite–host systems. Whether rapid, human-induced environmental change favors one player over another remains to be determined. Mapping seasonal and yearly distribution of perching trees, reed-bed vegetation, and Reed Warbler nests would provide a starting point for spatially explicit modeling of that dynamic relationship.

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