

Strategic Variation in Mobbing as a Front Line of Defense against Brood Parasitism

Justin A. Welbergen^{1,*} and Nicholas B. Davies¹

¹Department of Zoology
University of Cambridge
Cambridge CB2 3EJ
United Kingdom

Summary

Coevolutionary arms races, where adaptations in one party select for counter-adaptations in another and vice versa, are fundamental to interactions between organisms and their predators, pathogens, and parasites [1]. Avian brood parasites and their hosts have emerged as model systems for studying such reciprocal coevolutionary processes [2, 3]. For example, hosts have evolved changes in egg appearance and rejection of foreign eggs in response to brood parasitism from cuckoos, and cuckoos have evolved host-egg mimicry as a counter-response [4–6]. However, the host's front line of defense is protecting the nest from being parasitized in the first place [7–10], yet little is known about the effectiveness of nest defense as an antiparasite adaptation, and its coevolutionary significance remains poorly understood [10]. Here we show first that mobbing of common cuckoos *Cuculus canorus* by reed warblers *Acrocephalus scirpaceus* is an effective defense against parasitism. Second, mobbing of cuckoos is a phenotypically plastic trait that is modified strategically according to local parasitism risk. This supports the view that hosts use a “defense in-depth strategy,” with successive flexible lines of defense that coevolve with corresponding offensive lines of the parasite. This highlights the need for more holistic research into the coevolutionary consequences when multiple adaptations and counter-adaptations evolve in concert [11].

Results and Discussion

The reed warbler is one of the favorite hosts of the common cuckoo [12] with adaptations that indicate a protracted coevolutionary arms race with this brood parasite [13, 14]. Therefore, this provides an excellent system for studying nest defense as a specific adaptation against brood parasitism. We analyze data on natural parasitism from our long-term study population of reed warblers near Cambridge (UK) to determine spatial and temporal variation in local parasitism risk. We then use experiments to test whether mobbing is an effective nest defense and whether mobbing of cuckoos is phenotypically plastic and specifically so with respect to parasitism risk.

Variation in Local Parasitism Risk

From 2001 to 2008, 9.8% of 697 reed warbler nests were parasitized. To assess variation in local parasitism risk, we used five predictors of parasitism that had previously been identified in the literature: proximity to potential cuckoo look-out

perches [15, 16], laying date [17], year [17], parasitized nest density, and host density [16] (for definitions see [Experimental Procedures](#)). When entered together in a multiple logistic regression model, four of these predictors had independent significant effects on parasitism in our study population ([Figure 1](#)). Parasitism declined significantly with the distance between a nest and the nearest potential cuckoo perch ([Figure 1A](#)). Although nests were found between 0 and 563 m from the nearest potential cuckoo perch, all parasitized nests were within 28.1 m from a perch. This is in keeping with the fact that cuckoos usually locate host nests by observing host behavior from concealed perches in nearby trees [2, 15]. Parasitism also decreased significantly within breeding seasons ([Figure 1B](#)). The two nests with the earliest recorded laying date (8 May and 10 May) were both parasitized. This may reflect a decrease in nest conspicuousness to cuckoos through seasonal growth of reeds [18]. In addition, parasitism increased significantly with parasitized nest density ([Figure 1C](#)). Because individual cuckoos are territorial [19], this likely reflects localized activity of female cuckoos. Finally, parasitism decreased significantly with host density ([Figure 1D](#)), perhaps through dilution or through communal anti-brood parasite defense [10, 16]. Multiple logistic regression of the above predictors on recorded parasitism provided us with a composite prediction of local “parasitism risk” for any given nest in our population (see [Experimental Procedures](#) for details) that we use in subsequent analyses.

Does Mobbing Protect against Parasitism?

By defending their nests from cuckoos, reed warblers may reduce the probability that they will be parasitized. Reed warblers mob cuckoos with stereotyped audible and visual displays and direct physical attack [10, 20]. Mobbing by hosts is costly to cuckoos. Physical attacks can inflict direct costs, through feather loss or injury [10, 13, 19], and Molnár [21] reported an extreme case where a female cuckoo drowned after being forced into the water by host attacks. However, mobbing can also confer indirect costs, which may dissuade the cuckoo from laying. Mobbing attracts predators and other brood parasites [22, 23], which increases the risk that the cuckoo or her egg is depredated. It also alerts mates and neighboring hosts, which may join the mobbing [10, 24] and increase their nest guarding [8] and egg rejection [13]. However, determination of the effectiveness of nest defense against brood parasitism has proven difficult [25]; in fact, one study found evidence that mobbing increases parasitism [23].

We examined the effectiveness of mobbing as a nest defense against cuckoos by placing a model cuckoo at 191 reed warbler nests. Models were placed at clutch completion, after any parasitism. This was necessary because any tests done at an earlier stage that elicited mobbing may have affected actual parasitism. We then recorded mobbing responses for 5 min, to test whether nests with birds that mobbed were less likely to be parasitized than predicted from their local parasitism risk. Our previous work on reed warblers has shown that mandible snaps and rasp calls can be used as reliable measures of mobbing (*sensu* [20]) because they are associated with a close approach of a target by

*Correspondence: jaw44@cam.ac.uk

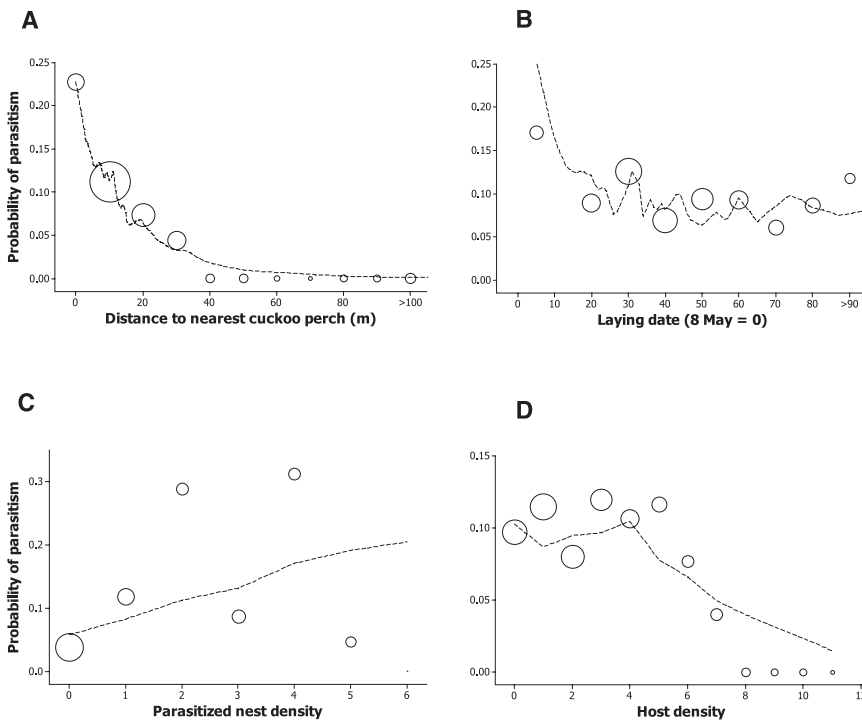


Figure 1. Local Brood Parasitism Risk Varies in Space and Time

Probability of parasitism in the Wicken Fen Area versus: (A) the distance (m) to the nearest cuckoo perch; (B) laying date (8 May = 0); (C) parasitized nest density (number of parasitized nests within 250 m); and (D) host density (number of active nests within 100 m). Symbol areas are proportional to sample size ($N_{total} = 697$). In each graph, continuous lines are the smoothed fits of a multiple logistic regression on parasitism probability (Model: Log-likelihood -200.6 ; test that all slopes equal to zero: $G_5 = 44.46$, $p < 0.001$; Goodness of fit test: Pearson $\chi^2_{690} = 637.93$, $p > 0.922$; 72.0% concordant, 27.2% discordant), which included perch distance (coefficient: -0.065 ; $Z = -3.16$; $p = 0.002$), laying date (coefficient: -0.023 ; $Z = -2.37$; $p = 0.018$), parasitized nest density (coefficient: 0.315 ; $Z = -3.94$; $p < 0.001$), host density (coefficient: -0.193 ; $Z = -2.60$; $p = 0.009$), and year (coefficient: -0.021 ; $Z = -0.37$; $p = 0.711$) as predictor variables.

multiple individuals and are accompanied by threat postures, swoops, and direct attacks [10]. We found remarkable variation between nests in the number of host mobbing signals (rasp calls and mandible snaps), and the responses were surprisingly dichotomous (Figure 2): at 52% of the nests there were no mobbing signals at all (0 mobbing signals/5 min), whereas at 31% of the nests, birds mobbed strongly (>200 mobbing signals/5 min).

As expected, actual parasitism of the 191 experimental nests increased with local parasitism risk; however, there was a significant interaction with mobbing propensity, with mobbers increasingly less likely to be parasitized than nonmobbers at higher-risk locales (multiple logistic regression: parasitism versus local parasitism risk $Z = 3.69$, $p = 0.001$; interaction predicted parasitism risk versus mobbing propensity: $Z = -2.56$, $p = 0.010$; Figure 3).

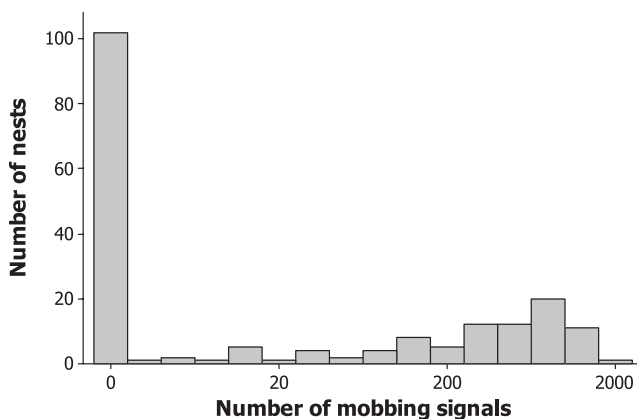


Figure 2. Mobbing Intensity Varies Strongly between Nests
Histogram of the number (log scale) of mandible snaps and rasp calls [10] recorded during 5 min presentations of model cuckoos at reed warbler nests ($N = 191$).

Mobbing had no effect at low-risk locales; indeed, there was a hint that it might attract parasitism (Figure 3). This suggests that at high-risk sites, where cuckoos can more easily locate nests from look-out perches, mobbing is the best strategy, whereas at low-risk sites the best strategy may be to refrain from conspicuous defense and remain hidden.

We considered the possibility that mobbers had a lower recorded parasitism at higher-risk sites simply because they were more likely to have ejected cuckoo eggs before we inspected their nest. However, ejection of cuckoo eggs

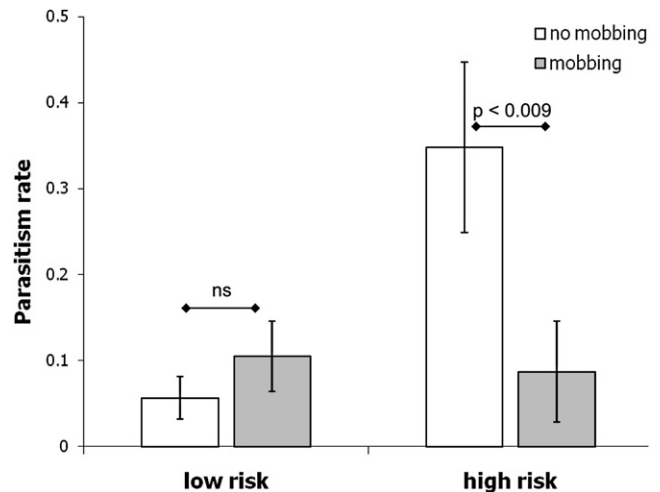


Figure 3. Nests with Owners that Mob Are Parasitized Less than Expected
The figure shows actual parasitism \pm SE according to whether reed warblers mobbed (dark bars) or did not mob (light bars) a model cuckoo placed at nests ($N_{total} = 191$) that had a parasitism risk lower or higher than average (10%). p values refer to results from post-hoc χ^2 tests (for more detailed analysis, see text).

is rare from naturally parasitized nests (9.5% [13]) and unlikely to have been missed by us because the average time from laying of the parasitic egg to ejection is about 3 days [13]. Furthermore, because the female cuckoo almost always removes one host egg (or more) before it lays [13, 19], we would have detected any “missed parasitisms” as reductions in the host’s clutch. However, clutch size did not differ between mobbers and nonmobbers overall (4.0 ± 0.07 versus 4.1 ± 0.07 , respectively; Student’s *t* test, $t = 0.78$, $df = 168$, $p = 0.434$), nor within higher-risk locales (4.0 ± 0.18 versus 4.2 ± 0.08 , respectively; $t = 0.86$, $df = 31$, $p = 0.398$). Therefore, there was no evidence that we had underestimated parasitism among mobbers.

At parasitized nests, reed warblers may have been more likely to have seen a real cuckoo prior to our test, and this experience may have affected the birds’ responses to the model cuckoo. However, repeated tests at 65 nests showed that there was a strong correlation between the number of mobbing signals during the first and second presentation of model cuckoos at the same nest (Spearman’s $\rho = 0.508$, $p < 0.001$). There was no difference in the number of mobbing signals nor in the propensity of birds to mob during the first versus the second presentation (Wilcoxon matched-pairs signed-ranks test, $p = 0.243$; McNemar’s test, $p = 0.383$, respectively). This shows that mobbing responses are highly repeatable and unlikely to have been influenced by whether or not birds were previously exposed to a real cuckoo at their nest.

Does Mobbing Vary with Local Parasitism Risk?

Although nest defense can benefit hosts, it can also be costly. Resemblance between common cuckoos and sparrowhawks *Accipiter nisus* [26] may necessitate dangerous enemy inspection. In addition, nest defense may attract predators [22] and brood parasites [23] and takes time and effort [27]. Such costs would select for phenotypic plasticity of nest defense in populations where local parasitism varies in space and time [28] and where the relative benefit of mobbing varies with parasitism risk (Figure 3). Previous studies have shown that species vulnerable to cuckoo parasitism are more likely to attack a cuckoo model near their nest than are species unsuitable as hosts [7, 9]. Furthermore, some host populations show greater aggression to brood parasite models in sympatry than in allopatry with brood parasites [9]. However, the question of whether this variation reflects genetic differences or phenotypic plasticity remains unresolved.

To test whether reed warbler nest defense varies strategically in our population, we determined whether propensity to mob cuckoos varied with local parasitism risk. As predicted, mobbing propensity showed a clear positive relationship with parasitism risk (logistic regression: $Z = 3.02$, $p = 0.003$; Figure 4A). Previous studies have shown phenotypic plasticity in egg rejection by hosts in concert with temporal changes in local parasitism [17, 29]. Our results show that the front line of defense, namely mobbing, also varies strategically according to local parasitism risk.

It is unlikely that this reflects variation in local predation risk from sparrowhawks, rather than variation in local parasitism risk from cuckoos. Although some passerine birds will mob dangerous predators, such as sparrowhawks [30], nesting adult reed warblers do not do so. Instead, their reaction to a sparrowhawk near their nest is to retreat to a safe distance and remain silent and hidden [10, 31]. This difference in response to sparrowhawks and cuckoos makes adaptive

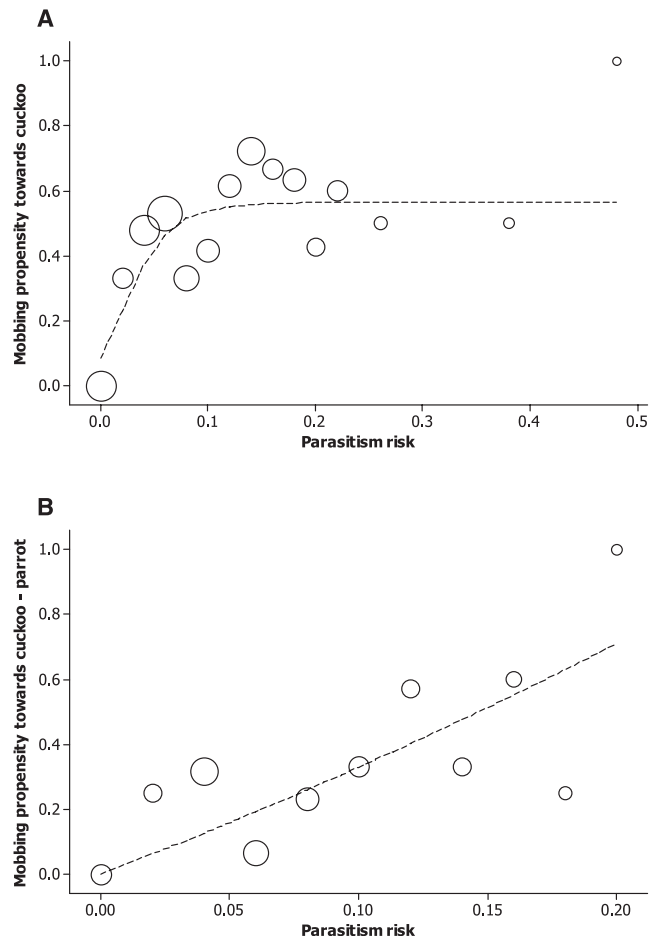


Figure 4. Local Parasitism Risk Predicts the Propensity of Reed Warblers to Mob and the Plasticity of the Response Is Specific to Cuckoos

(A) The propensity of birds to mob a model cuckoo versus the risk that their nest is parasitized. Continuous line is the result of a logistic regression on the dichotomous mobbing data with parasitism risk as a covariate. Symbol area is proportional to sample size ($N_{total} = 191$).

(B) The difference between the propensity of a reed warbler pair to mob a model cuckoo and their propensity to mob a model parrot versus parasitism risk. Continuous line is the result of an ordinal logistic regression on the trichotomous mobbing data (mobbing to cuckoo only = 1; to parrot only = -1; identical response = 0) with parasitism risk as a covariate. Symbol area is proportional to sample size ($N_{cuckoo} = N_{parrot} = 97$ nests).

sense given that sparrowhawks are specialized predators of adult birds whereas cuckoos are a threat only to the nest [10, 28]. Sparrowhawks, like cuckoos, usually stalk their victims from perches [30], so if the variation in mobbing had reflected local predation from sparrowhawks, we would have expected less mobbing nearer perches, the opposite result to what we found.

In theory it is possible that different genotypes sort by parasitism risk, with mobber genotypes choosing higher-risk sites; however, it is unlikely that there is genetic differentiation on such fine local and temporal scales, for example where parasitism risk declines 5-fold from 0 to 20 m from a cuckoo perch (Figure 1A). Furthermore, previous studies have already shown that mobbing by reed warblers is phenotypically plastic with regards to the danger a cuckoo poses to the nest. For example, individual reed warbler pairs are more likely to mob cuckoos than other enemies, and their response is affected

by the distance of the cuckoo mount to the nest and the timing of its presentation during the nesting cycle [10, 31]. Analogous plasticity has also been recorded in the context of predator mobbing [32, 33], with individual American robins, *Turdus migratorius*, varying their nest defense according to variation in predation risk [34].

Is Variation in Mobbing Specific to the Enemy?

If the strategic variation in mobbing is the result of sorting of bold and shy genotypes by parasitism risk, we would expect the variation in mobbing propensity to be a generalized response to intruders rather than a specific response to cuckoos. To examine this, we presented reed warblers (N = 97 nests) with both a wooden cuckoo model and a novel intruder, a wooden model of a generalized parrot (dark-green upperparts, pale-green underparts). We then related the paired differences in mobbing propensity toward the two wooden models to parasitism risk. Reed warblers mobbed parrots less than cuckoo models (23.3% versus 43.6%, respectively; McNemar's test, $p < 0.001$), but importantly, they were increasingly likely to mob a cuckoo relative to a parrot model as parasitism risk increased (ordinal logistic regression: $Z = 2.47$, $p = 0.013$; Figure 4B). Indeed, mobbing propensity increased with parasitism risk in response to presentations of cuckoo models only (binary logistic regressions, cuckoos: $Z = 2.86$, $p = 0.004$; parrots: $Z = 1.06$, $p = 0.228$). Thus, the plasticity of nest defense with parasitism risk was specific to cuckoo models and not a general aggressive response to intruders. This is further evidence that mobbing is a phenotypically plastic trait that is adaptive in the context of brood parasitism [10]. Further work is needed to test whether such plasticity arises because reed warblers assess parasitism risk by observing cuckoos directly, or by some other temporal or spatial correlate of brood parasitism.

Nest Defense and Cuckoo-Hawk Mimicry

We suggest that the plasticity of mobbing responses is analogous to the conditionality of egg rejection on parasitism risk. It pays hosts to vary egg rejection with parasitism risk if they make recognition errors and sometimes mistake their own eggs for mimetic parasitic eggs [35]. Cuckoo-sparrowhawk resemblance in size, shape, and plumage and in swift, direct flight may introduce recognition errors that make discrimination between cuckoos and potentially lethal sparrowhawks more costly for a host. Indeed, great tits *Parus major* and blue tits *P. caeruleus*, which are unsuitable as hosts, and so have no history of coevolution with cuckoos, are as wary of cuckoos as of sparrowhawks [26]. This suggests that aggression toward adult cuckoos by some host species [7, 10, 31, 36] is an evolved response to cuckoo parasitism. Given that mobbing by hosts is costly for cuckoos, this favors cuckoo adaptations that reduce the probability that a cuckoo is mobbed. Comparative analyses show that cuckoo-hawk resemblance likely evolved after the evolution of brood parasitism [37], which suggests that it may have evolved in response to host aggression. Thus, just as egg mimicry by cuckoos has coevolved with egg discrimination by hosts [4], so perhaps Batesian mimicry of hawks by cuckoos has coevolved with enemy discrimination by hosts.

Conclusions

Our study shows that in a world where brood parasitism varies along temporal and spatial dimensions, and where the parasite

resembles a deadly predator, hosts vary their nest defense strategically according to the likelihood that they will be parasitized. Nest defense has important implications for our understanding of brood parasite-host coevolution because it can affect the intensity of selection for later defenses, such as egg discrimination and chick discrimination, and therefore their subsequent evolutionary trajectories. The emerging view is that hosts use a “defense in-depth strategy,” whereby they deploy sequential lines of defense in a coevolutionary arms race with corresponding offensive lines of the parasite [11, 38]. This highlights the need for more holistic research into the coevolutionary consequences when various adaptations and counter-adaptations evolve in concert.

Experimental Procedures

Study Site

From April to July each year in 2001–2008, we studied reed warblers at one continuous study site, comprising Wicken Fen (52°18'29"N, 0°16'50"E) and adjacent fenlands along the Burwell and Reach Lodes, Cambridgeshire, UK. Nests were located along reed fringes of lodes (waterways through the fens), where pairs defended 11–35 m linear territories along one bank [8]. The study area included 360–500 pairs of reed warblers and 5–14 female cuckoos each year [17].

Predictors of Parasitism

Linear reed stretches were marked at 20 m intervals, and nest locations were determined to within ± 1 m relative to the markers. We monitored nests regularly during laying and incubation and searched the stretches exhaustively for new nests 2–3 times per week throughout each season. During 2006–2008, nests were also located to within ± 3 m (95% confidence) with to a WAAS-enabled Garmin Etrex GPS. Laying dates (first egg) were determined directly or by calculating backward from later stages (date – clutch size + 1 day) or from hatching day (date – 11 days + clutch size). The frequency of parasitized nests during our study period was 68/697 = 9.8% (9/107 in 2001; 7/106 in 2002; 7/55 in 2003; 5/57 in 2004; 5/20 in 2005; 4/118 in 2006; 11/106 in 2007; 20/128 in 2008). Reed warblers occasionally reject cuckoo eggs (~9.5% [13]), and therefore parasitism frequencies are underestimates. Sample sizes varied between years because not all stretches of reeds were studied in every breeding season.

Nest locations were entered in Google Earth Plus v4.2, and the nearest potential cuckoo perches were traced with polygons. Cuckoo perches were conservatively defined as any tree, bush, or hedge, easily identified from high-resolution aerial images (Google Earth server, August 2008). Cuckoo perches below dyke level, without line of sight to reeds, were excluded. Google Earth kml files with nest locations and tree polygons were exported to ArcMap 9.1 with Kml2shp v2.0 and to Microsoft Excel with KMLCSV Converter v2.0. Perch distance (nearest cuckoo perch) was calculated in ArcMap as the distance from each nest to the nearest linked perch polygon. Distances between all nests were calculated in Microsoft Excel with Pythagoras' theorem on the UTM coordinates of nests.

Laying date was defined as the number of days since May 8th, i.e., the earliest first egg date. Host density was defined as the number of active nests within 100 m from a focal nest. Nests were considered active when they had a laying date within 1 week of the focal nest. This underestimates breeding density. However, because the time between nest failure and first egg of the subsequent re-nest is at least 1 week, our measure ensures only distances between nests of unique neighbors are considered. Parasitized nest density was the number of nests parasitized during a single breeding season within 250 m from a focal nest. Individual cuckoos are territorial and their approximately 8-week laying period coincides with the reed warbler breeding period (May to mid-July) [19], so parasitized nest density is a proxy for local cuckoo activity.

Assessing Mobbing Propensity

We recorded reed warbler mobbing responses to three taxidermic mounts of cuckoos and two virtually identical balsa wood cuckoo models [10]. Responses to taxidermic mounts were strongly correlated with those to balsa cuckoo models (Spearman's $\rho = 0.606$, $N = 17$, $p = 0.012$; see [10]) and are similar to responses to live cuckoos [31]. There were no differences in responses to different mount specimens [10].

Models were presented at 191 different nests with an incubating pair during 2006 (N = 66), 2007 (N = 61), and 2008 (N = 64). Within seasons, each experiment was conducted with a different pair, recognized by individually color-ringed individuals, or spatial segregation. A small proportion of pairs may have had repeated exposures between seasons. However, each season we sampled less than 20% of pairs in our study population, with annual survival rates of $32.9\% \pm 16.0\%$ for males and $52.0\% \pm 22.4\%$ for females [39]. Our results are qualitatively similar and remain significant if we limit our sample to only 2007, and the data from 2006 and 2008 show the same trends. Therefore, it is unlikely that pseudo-replication has unduly influenced our results.

To examine whether repeated exposure to cuckoos affected responses, we presented a cuckoo model twice at 65 nests. To test whether any variation in response was specific to cuckoos, we presented both a balsa wood cuckoo and a same-sized balsa wood model of a generalized parrot (dark-green upperparts, pale-green underparts) at 97 nests. When multiple models were presented at the same or neighboring nests, they were in random order and at least 2 hr apart, sufficient for birds to settle down to baseline activity levels before the next presentation [10].

To ensure a maximum response, the models were placed in direct contact with the nest, as responses decrease model distance from the nest [10]. Audible responses include song, snapping of mandibles, and calls; visible responses include threat postures, swoops, and direct attack [10]. The calls come in three types, readily distinguished by duration and structure: "kreks" are short and "rasps" and "churrs" are longer but the latter have more tremolo and amplitude tapers off toward the end of the calls [10]. "Rasps" and "bill snaps" are correlated with a close approach of multiple individuals, threat postures, and direct attack [10], and therefore they are good indicators of mobbing behavior (sensu [20]). Mobbing was considered to have occurred when the sum of rasps and snaps exceeded 20, rather than 0. Results are qualitatively similar and significant with either criterion, but the former reduces the risk of false positives from cracking of drying reeds (which sound like bill snaps) and the difficulty of distinguishing some churrs from rasps [10].

For each trial, we recorded bill snaps and rasps within 5 min after arrival of the first bird to within 1 m from the model. Previous observations of color-ringed birds showed that those first to arrive were invariably nest owners [8]. Observations were conducted from approximately 15 m away, where bird positions and activities within 10 m from the mount could be observed without disturbance. If no bird was observed less than 1 m from the focal nest within 15 min, the experiment was terminated.

Statistical Analysis

We used Minitab for Windows (v14.0, Minitab Inc.). All tests were two-tailed and significance set at $\alpha = 0.05$. We used multiple logistic regression models with a logit-link function and an iterative-reweighted least-squares algorithm to obtain maximum likelihood estimates of parameters [40]. For all models, confidence that all slopes were not equal to zero was high ($p < 0.001$) and there was no evidence of insufficient fit (Pearson, $p > 0.453$).

To estimate local parasitism risk, we used a multiple logistic regression on the data set of all the nests (N = 697) and entered perch distance, laying date (May 8th = 0), parasitized nest density, host density, and year (2001 = 1) into the model as predictor variables. Parasitism risk was defined as the probability that a nest was parasitized, as predicted by the model. In determining whether mobbing affected actual parasitism for a given parasitism risk at our sample of 191 experimental nests, we avoided circularity by estimating parasitism risk at these nests by using the parameter estimates from a multiple logistic regression on the data of nonexperimental nests only (N = 697 - 191 = 506).

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