REPEATED PRESENTATIONS OF THE COMMON CUCKOO INCREASE NEST DEFENSE BY THE EURASIAN REED WARBLER BUT DO NOT INDUCE IT TO MAKE RECOGNITION ERRORS

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Abstract.   Previous studies have shown that Eurasian Reed Warblers (*Acrocephalus scirpaceus*) are able to distinguish the Common Cuckoo (*Cuculus canorus*) from other intruders at the nest and that mobbing is an effective defense measure against brood parasitism. Here we studied the nest-defense behavior of Eurasian Reed Warblers facing four successive exposures to a Common Cuckoo to investigate whether a previous experience of interacting with a brood parasite may play a role in shaping the host's defenses in further encounters. Nesting warblers significantly increased their aggressive behavior from the first to the second presentation of a dummy Common Cuckoo and then sustained their response at the same intensity. The intensity with which the birds tested mobbed the dummy decreased both as the season progressed and with the time of the day. Multiple encounters with the dummy, however, did not increase the warblers' propensity to make recognition errors, i.e., to reject their own eggs in the absence of a Common Cuckoo egg in the nest. We discuss possible explanations of the increased intensity of nest defense with respect to the positive-reinforcement hypothesis and known patterns of nest attendance in the Eurasian Reed Warbler.

Key words: Acrocephalus scirpaceus, Cuculus canorus, *nest defense, recognition errors, repeated visits.*

Las Presentaciones Repetidas de *Cuculus canorus* Incrementan la Defensa del Nido por Parte de *Acrocephalus scirpaceus* pero no lo Inducen a Cometer Errores de Reconocimiento

Resumen.   Estudios previos han demostrado que *Acrocephalus scirpaceus* es capaz de distinguir a *Cuculus canorus* de otros intrusos en el nido y que las conductas de acoso son una medida defensiva efectiva contra el parasitismo de nidada. Estudiamos el comportamiento de defensa del nido de *A. scirpaceus* al enfrentar cuatro exposiciones sucesivas a *C. canorus* para investigar si la experiencia previa de interacción con un parásito de nido cumple un rol en modelar las defensas del hospedador en encuentros futuros. Los individuos de *A. scirpaceus* que nidifican incrementaron significativamente su comportamiento agresivo de la primera a la segunda presentación de *C. canorus* y luego mantuvieron esa respuesta con la misma intensidad. La intensidad con la que las aves estudiadas acosaron a individuos de *C. canorus* disminuyó a medida que la estación progresó y con el momento del día. Sin embargo, encuentros múltiples con *C. canorus* no aumentaron la tendencia de *A. scirpaceus* de cometer errores de reconocimiento, es decir, a rechazar sus propios huevos en ausencia de un huevo de *C. canorus* en el nido. Discutimos las posibles explicaciones del aumento de la intensidad de la defensa del nido con respecto a la hipótesis de refuerzo positivo y de patrones conocidos de visita al nido en *A. scirpaceus*.

INTRODUCTION

Apart from incubating the clutch and provisioning the nestlings, defending the nest is another important component of parental care by which birds increase their reproductive success (Montgomerie and Weatherhead 1988). Although nest defense is selected to reduce losses to predators and brood parasites, it may be costly for the defenders in terms of increased expenditure of time and energy and of risk of injury or even death (Sordahl 1990, Komdeur and Kats 1999). Moreover, conspicuous aggressive behavior may attract other enemies and put the nest and its owners at further risk (Banks and Martin 2001, Krams et al. 2007). Therefore, the optimal level of nest defense should be determined by the balance between these costs and benefits, which is likely to vary with the type of enemy (Montgomerie and Weatherhead 1988).

Although some brood parasites prey also upon the hosts' eggs or young (Soler et al. 1995, Arcese et al. 1996, Honza et al. 2002), they generally pose a kind of threat different from that of genuine nest predators. Successful brood parasitism is often more costly to hosts than is nest predation because the prolonged period of care of unrelated parasitic young precludes hosts from renesting (Rothstein 1990). If the clutch or brood is depredated, however, the parents may still have enough time

to renest within that breeding season. Although nest predators may be dangerous both to the defending adults and their offspring (Duckworth 1991, Davies et al. 2003, Požgayová et al. 2009), brood parasites are harmful to the nest contents only. Therefore, as there is still much to lose in terms of reproduction if a host's clutch is parasitized, aggressive behavior may work as a front line of antiparasitic defense, especially in situations when egg rejection is not possible or is too costly for a host (Moksnes et al. 1991, Røskaft et al. 2002a).

Eurasian Reed Warblers (*Acrocephalus scirpaceus*) often suffer from brood parasitism by the Common Cuckoo (*Cuculus canorus*), which can depress their fitness substantially (Øien et al. 1998). Selection pressure on the Eurasian Reed Warbler to reduce the risk of parasitism should therefore be strong. Indeed, several studies have shown that the reed warbler has developed an ability to recognize the cuckoo as a specific threat (Duckworth 1991, Davies et al. 2003, Welbergen and Davies 2008, Campobello and Sealy 2010) and adjust its antiparasitic behavior strategically according to the local risk of parasitism (Davies et al. 1996, Lindholm 2000, Lindholm and Thomas 2000). Moreover, Welbergen and Davies (2009) showed the reed warbler's mobbing of the cuckoo to be an effective defense. As the cuckoo may visit hosts' nests repeatedly before it parasitizes them (Moksnes et al. 2000, Honza et al. 2002), reed warblers also spend a significant amount of time near their nests to watch out for the parasite (Davies et al. 2003). Being on alert may enable them to drive out the cuckoo and thus escape parasitism. Additionally, direct encounters with the brood parasite may help hosts to determine whether they are likely to be parasitized or not and promote rejection of parasitic eggs (Davies and Brooke 1988, Mosknes et al. 2000, Davies et al. 2003).

The sight of a cuckoo at a host's nest has been also supposed to increase the probability that the host will erroneously damage or reject its own eggs in absence of any parasitism (Røskaft et al. 2002b, Stokke et al. 2002). The occurrence of these recognition errors is a fundamental assumption of the theory of co-evolutionary equilibrium (Rothstein 1990, Davies et al. 1996), yet their documentation has proven extremely difficult. According to this hypothesis, rejection of parasitic eggs may not spread in a host population because it incurs some costs that make it even less adaptive than accepting them. Until now, no experimental study has demonstrated that the presence of a brood parasite itself induces a host to eject its own eggs erroneously. However, as hosts may make egg-rejection decisions according to the frequency of their interactions with the brood parasite (Davies et al. 1996, Øien et al. 1999), multiple encounters could make recognition errors more likely than a single sighting of a parasite.

Taking into account the conditional nature of hosts' antiparasitic responses (Øien et al. 1999), we investigated whether experience of interacting with a brood parasite plays a role in shaping a host's defensive behavior in further encounters. More specifically, by simulating repeated visits of a cuckoo to the same reed warbler nests, we explored the patterns of

intensity of a host's nest defense and the incidence of possible recognition errors. If hosts are to defend their nests strategically with respect to the local parasitism pressure, they should be able to assess the risk of parasitism and modulate their behavior accordingly. To our knowledge, no similar study has ever been conducted in the wild.

METHODS

FIELD WORK AND EXPERIMENTAL DESIGN

We conducted the study from 15 May through 30 June 2008 around ponds between Hodonín (48° 51′ N 17° 07′ E) and Mutěnice (48° 54′ N 17° 02′ E), Czech Republic. The study population of reed warblers numbered about 100–120 breeding pairs and experienced a rate of cuckoo parasitism of ~14% (calculated from 98 nests checked daily during laying and early incubation).

We systematically searched for reed warbler nests in vegetation around the ponds, and thus the experimental nests represent a random sample of the study population. We found the vast majority of nests while they were being built, and we checked them daily to record the date of clutch initiation and to detect possible cuckoo parasitism. Then, on the day when the second egg was laid, we exposed a taxidermic mount of a cuckoo attached to a wooden pole 0.5–1 m from the focal nest, leveled with it facing the nest rim. After setting the mount in place, the experimenter (MČ) retreated to a minimum distance of 10 m to hide in reedbeds or bushes, then observed and recorded the warblers' responses, measured with a stopwatch. He repeated the presentation in the same manner daily over the following 3 days. Each experiment thus consisted of four successive trials at one nest. We performed all the experiments randomly between 06:30 and 20:30 CET so that the subsequent trials at the same nest were not repeated at the same time of the day. To reduce pseudoreplication, we used two different dummy cuckoos in a random order at each nest. Once the experiment was finished, we checked the nest on each of the two following days to record possible later egg losses. After that, we checked the nests at intervals of about 2 to 3 days until the chicks hatched.

Altogether, we tested 31 nests for the warblers' responses to repeated presentations of dummy cuckoos. We excluded from the analysis nests at which the number of trials was incomplete (for example, because of nest predation or clutch abandonment before the end of the experiment), resulting in 26 nests at which we ran 104 trials. To assess possible egg-recognition errors in response to repeated exposures of the dummy, we also tracked a control group of 17 nests that we checked daily during the same period as the experimental group but at which we did not present a dummy cuckoo. None of the nests in either group was naturally parasitized by the cuckoo.

VARIABLES AND STATISTICAL ANALYSES

Each trial started when the warblers approached within 5 m of their nest. We then observed their behavior for 10 min or

until a warbler made a direct contact attack on the dummy (7% of trials only), after which case we withdrew the dummy to avoid its being damaged. During this interval we recorded all distances, activities, and vocalizations of the focal birds. From the protocol, we then extracted the time elapsed from the presentation of the dummy to the first arrival of the warblers (latency to reaction, in sec), minimum distance from the dummy (in m), proportion of time spent within 1 m, proportion of time spent singing, and proportion of time spent alarm calling. We calculated the last three variables as proportions of the total time the birds were responsive. We distinguished between various types of alarm calls (sensu Welbergen and Davies 2008). However, since some types, such as high-intensity alarm calls represented by an accelerating "churr-churrrr churrrr" or "dze dze dze dze" and associated bill-snapping occurred very rarely, we regarded all the types of vocalization except for singing as alarm calls. Because we were not able to distinguish males and females in all cases, we summed the time variables of both parents (if both responded) and recorded the shorter of the two latencies and minimum distances.

To reduce the number of behavioral variables recorded during experiments; we performed a principal component analysis (PCA) of the following variables: latency to the first arrival, minimum distance from the dummy, relative proportion of time spent within 1 m of the mount, and proportion of time singing and alarm calling. For further analyses, we selected and present only principal components complying with Kaiser's criterion (eigenvalue >1). The first principal component (PC1) explained 39% of variability (loadings: latency 0.099, minimum distance –0.616, proportion of time spent within 1 m 0.883, proportion of time spent singing –0.243, proportion of time spent alarm calling 0.850). High and positive loadings of PC1 with the proportion of time spent within 1 m of the mount and proportion of time spent alarm calling, and negative loadings with minimum distance, expressed the warblers' propensity to mob or aggression. The second principal component (PC2) explained 21% of variability (loadings: latency 0.702, minimum distance 0.074, proportion of time spent within 1 m –0.196, proportion of time spent singing –0.716, proportion of time spent alarm calling –0.030). Thus PC2 corresponded with long latencies and low proportions of time spent singing.

To explore the effect of experimental procedure on the intensity of the reed warbler's nest defense, we fitted two linear mixed-effects models with PC1 and PC2 scores as response variables; trial number (1–4), date of the season (1 = 1 May), and time of the day were fixed factors; the individual nest was a random factor. Model selection was based on the information-theoretic approach with Akaike's information criterion (AIC; Burnham and Anderson 2002), which explicitly penalizes superfluous parameters in the model by adding $2K$ to the deviance, where K is the number of parameters, including the intercept. We used the AIC values corrected for small sample sizes (AIC_c) and ranked them according to Δ_i values (where $\Delta_i = AIC_{c(i)} - AIC_{c(\min)}$). To assess the likelihood of each model

relative to others, we calculated Akaike weights (w_i) from Δ_i values (Burnham and Anderson 2002). The most parsimonious models had the lowest AIC_c, highest w_i, and included only parameters that significantly improved the fit of the model. To test the effect of nest identity, we compared the most parsimonious linear mixed-effect model to an equivalent linear model without nest identity.

To evaluate the incidence of recognition errors, we used Fisher's exact test to compare the proportion of nests at which eggs were lost in the experimental group to that in the control group.

Statistical analyses were performed in R 2.9.2 (R Development Core Team 2009) and STATISTICA 6.0 (StatSoft 2001).

RESULTS

The most parsimonious linear mixed-effects model explaining the pattern of reed warbler aggression (PC1) across the four consecutive trials included the trial number, date, and nest's identity (Table 1). The model showed that PC1 scores varied through the experiment (from trial 1 to trial 4; Friedman

TABLE 1. Selection of linear mixed-effects models explaining the Eurasian Reed Warbler's nest-defense behavior toward repeated presentations of a mounted Common Cuckoo. For each principal component, models are listed with the best-fitting model at the top and sorted by Akaike's information criterion adjusted for small sample size (ΔAIC_c). Also shown for each model are the number of parameters (K) and model weight (w_i), which indicates the relative likelihood of each model given the model set and which collectively sum to 1 for the entire model set.

Fixed factors in the model[a]	ΔAIC_c	K	w_i
PC1			
Date + trial[b]	0.00	4	0.466
Trial + date + time	1.43	5	0.228
Trial	1.63	3	0.206
Trial + time	3.40	4	0.085
Date	8.05	3	0.008
Date + time	9.88	4	0.003
Time	9.76	3	0.004
PC2			
Time[c]	0.00	3	0.446
Trial + time	1.00	4	0.270
Date + time	1.94	4	0.169
Trial + date + time	3.16	5	0.092
Trial	7.65	3	0.010
Date	7.90	3	0.009
Date + trial	9.69	4	0.004

[a] Explanatory variables used in models: trial = order of the trial (1–4), time = time of the day, date = date of the season; all models included nest identity as a random factor.
[b] AIC_c of the top model was 288.89.
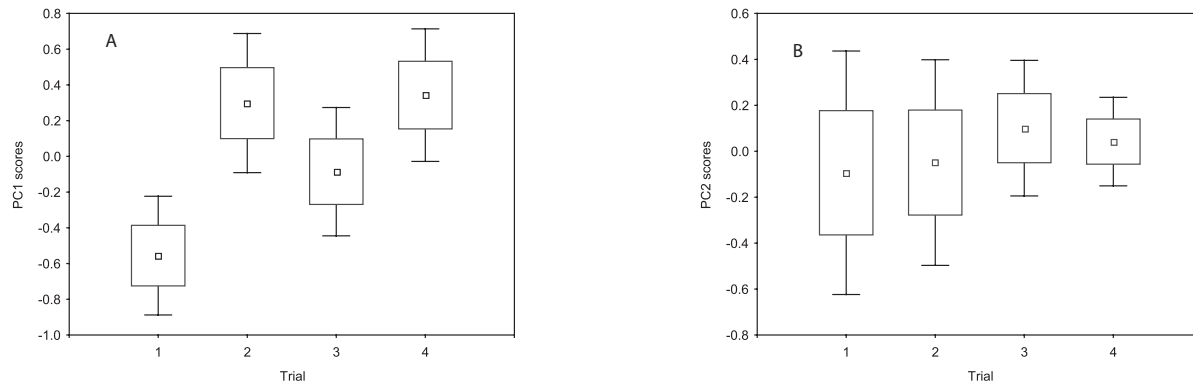[c] AIC_c of the top model was 287.12.

FIGURE 1. Nest-defense behavior of Eurasian Reed Warblers toward a mounted Common Cuckoo in four consecutive trials: (A) PC1 scores, (B) PC2 scores (means ± SE ± 1.96 SE given).

ANOVA $\chi^2 = 9.4$, df $= 3$, $n = 26$, $P = 0.025$; Fig. 1A): the nesting warblers significantly increased their aggressive behavior from trial 1 to trial 2, then sustained their response at the same intensity through trial 4 (Wilcoxon matched-pairs test trial 1 vs. trial 2: $Z = 3.4$, $P = 0.001$, trial 1 vs. trial 4: $Z = 3.0$, $P = 0.003$; other comparisons not significant; Fig. 1A). As the season progressed, however, the intensity of the tested birds' mobbing decreased ($\beta = -0.032$, $F = 4.0$, $P = 0.049$). A linear model without the random factor (nest identity) explained slightly more variance than the most parsimonious linear mixed-effects model, although this difference proved to be not significant (ΔAIC $= 0.73$, likelihood-ratio test $= 1.3$, $P = 0.260$), suggesting that identity of the tested pairs did not play a significant role in explaining the reed warbler's aggressive behavior.

The most parsimonious linear mixed-effects model explaining PC2 scores included the time of the day and nest's identity (Table 1). The model showed that PC2 scores significantly increased through the day ($\beta = 0.091$, $F = 8.4$, $P = 0.005$). A linear model without the random factor (nest identity) explained marginally significantly less variance than the most parsimonious linear mixed-effects model (ΔAIC $= 1.61$, likelihood ratio test $= 3.6$, $P = 0.058$). Across the four trials, however, the PC2 scores did not differ (Friedman ANOVA $\chi^2 = 0.9$, df $= 3$, $n = 26$, $P = 0.831$; Fig. 1b).

An additional analysis of the original variables revealed that reed warbler behavior showed different patterns throughout the experiment (Fig. 2). While the latency to response, minimum distance, proportion of time spent within 1 m from the mount did not differ among the four trials (Friedman ANOVA $\chi^2 = 0.5$, $P = 0.915$, $\chi^2 = 3.4$, $P = 0.336$, $\chi^2 = 6.9$, $P = 0.074$, respectively), proportion of time spent singing and alarm calling differed significantly ($\chi^2 = 21.8$, $P < 0.001$, $\chi^2 = 17.8$, $P < 0.001$, respectively).

In two out of 26 nests tested a total of four eggs was damaged and later disappeared, whereas in only one of 17 control nests one egg was pecked and later disappeared. Between the experimental and control groups, the proportion of nests that lost eggs did not differ (Fisher's exact test $P = 0.664$).

DISCUSSION

It has been proposed that apparent differences among populations in variation of antiparasitic defenses could be explained by the host's phenotypic plasticity, which would be favored in environments where the risk of parasitism fluctuates (Lindholm 2000, Lindholm and Thomas 2000, Welbergen and Davies 2009). If hosts are indeed to defend their nests strategically with respect to the local parasitism pressure, they should be able to assess the risk of parasitism and modulate their behavior accordingly. In accordance with this assumption, we simulated a high risk of parasitism by repeatedly exposing mounted cuckoos near focal nests and found that nesting reed warblers significantly increased their aggressive behavior toward the cuckoo from the first to the second trial and then their response remained at the same intensity. Such pattern of a host's responsiveness may be interpreted in the context of the "positive reinforcement" or so-called "revisitation" hypothesis (Knight and Temple 1986a, b). According to this hypothesis, an increase in intensity of nest defense is a methodological artifact of a researcher's repeated visits or presentations of a potential threat, which in this way becomes familiar to the parents. Such repeated encounters may reinforce parental responses because they always result in the departure of the threat, with the nest contents and parents left unharmed. Defending birds could thus learn that the enemy is not dangerous to them; however, they still view it as a threat to the nest contents. Thus, it is positive reinforcement and loss of fear that cause the parents to respond more vigorously the next time. However, we recorded such sensitization in the host's aggressive behavior only between the first and second trial; afterward the intensity of nest defense remained unchanged (at a high level). The reed warblers possibly reached an asymptotic level of nest defense immediately after the second
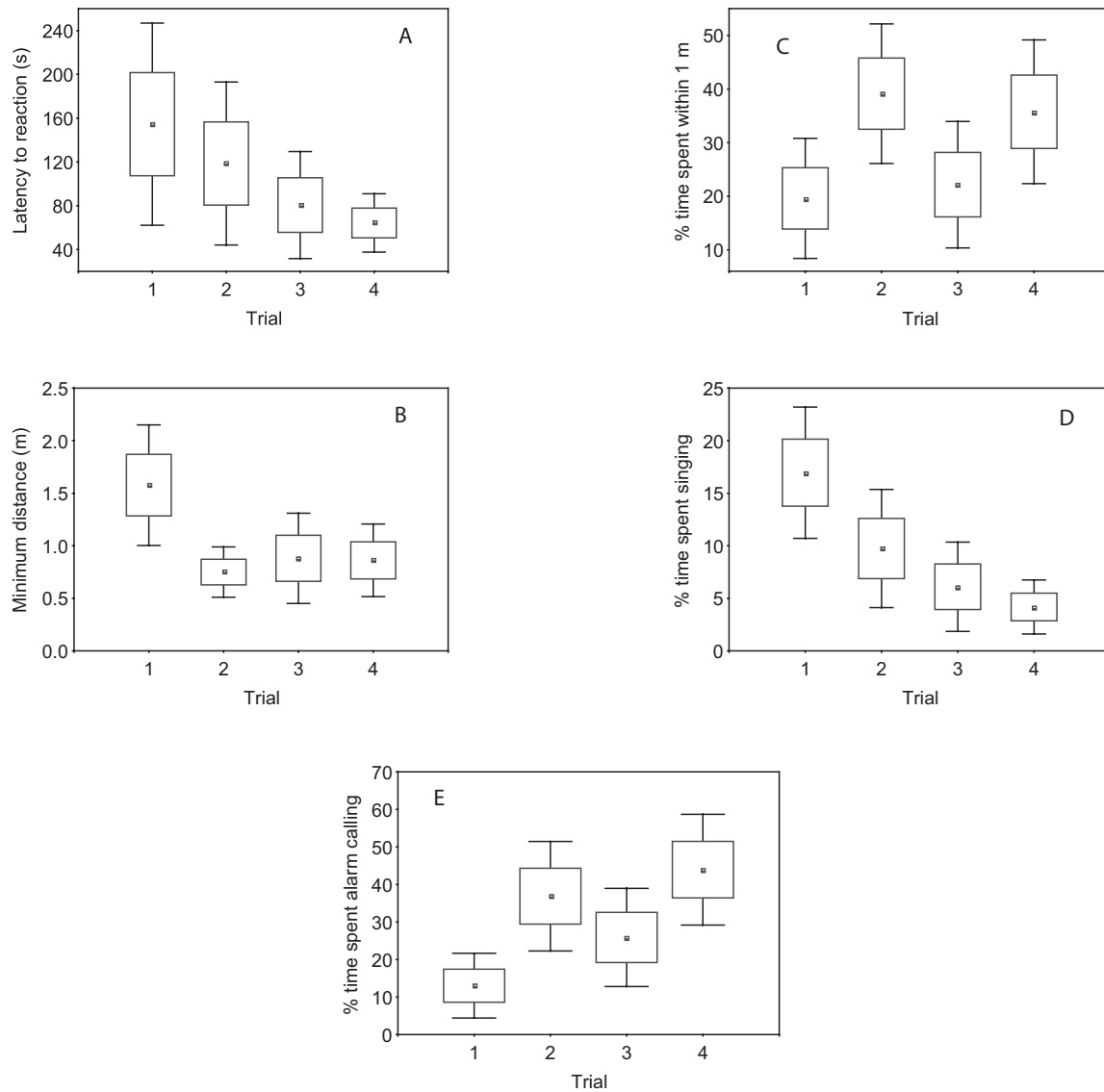
FIGURE 2.   Components of the Eurasian Reed Warbler's nest-defense behavior in four consecutive trials (means ± SE ± 1.96 SE given).

encounter with the cuckoo and then either did not or could not respond more vigorously. As the cuckoo is always dangerous to the nest contents and is likely to return to a host's nest even several times, it would not be adaptive for the hosts to decrease the intensity of their nest defense but to stay alert and aggressive.

Alternatively and perhaps more likely, our findings may be explained by the pattern of the reed warbler's nest attendance over the course of egg laying. In this species, the modal clutch size is four eggs, and incubation starts usually after the laying of the penultimate egg (Cramp 1992), which corresponds to the second or the third (in cases of five-egg clutches) trial in our experimental setting. Reed warblers attend their nests less frequently at the two-egg stage than later during laying and after

the commencement of incubation (Davies et al. 2003), which may reflect also the pattern of nest defense that we recorded throughout the experiment. Duckworth (1991) documented a similar effect of the host's nest attendance on its nest-defense behavior. In his study, reed warblers tended to approach the mounted cuckoo more closely once incubation had started. According to Davies et al. (2003), presentations of dummy cuckoos at nests during egg laying lead to the host's increasing its nest attendance. Because of this pattern of nest attendance and nest defense in the reed warbler, it seems to be adaptive for the cuckoo to parasitize nests early in the period of laying (Davies 2000, Moksnes et al. 2000, Honza et al. 2002).

Our study further revealed that the reed warbler's nest-defense behavior decreased over the breeding season. Since

specific aggressive responses toward the cuckoo may have a learned component (Davies and Welbergen 2009) and young birds breed on average later than old birds (Lotem et al. 1992, 1995), we suggest that the age of the breeders might be responsible for the decline in nest defense over the breeding season. Alternatively, because in some populations parasitism pressure decreases at the end of the breeding season (Brooke et al. 1998, Welbergen and Davies 2009), the probability of encounters with the brood parasite at the nest may decrease at the end of the breeding season, which, in turn, could negatively influence the propensity of the late breeders to mob. In the population we studied, however, the incidence of parasitism did not significantly depend on date of laying (GLM: $\beta = -0.050$, $P = 0.069$), so in this case this explanation does not necessarily apply.

We also found that the intensity of nest defense decreased through the day, a pattern difficult to explain in terms of the known daily schedule of the reed warbler's nest attendance. Reed warblers do not spend significantly more time at the nest in the morning than in the afternoon (Moksnes et al. 2000, Honza et al. 2004). Nevertheless, Davies and Brooke (1988) found that reed warbler clutches are warmer in the morning than in the afternoon after the second egg is laid. If we use clutch temperature as a simple measure of parental attendance, we can infer that reed warblers spend less time on their nests incubating their clutches in the afternoon, so they are less likely to detect the cuckoo and thus defend their clutches later during the day. Hosts' lower nest attendance in the afternoon may plausibly explain why the cuckoo often parasitizes nests at this time (Seel 1973, Davies and Brooke 1988, Honza et al. 2002), as afternoon laying may reduce the risk of being spotted by the host (Davies 2000). Davies and Brooke (1988) tested this hypothesis by placing mimetic model eggs into reed warbler nests and found that those placed at dawn were more likely to be rejected than those placed in the afternoon. Afternoon laying is therefore an important part of the Common Cuckoo's trickery. However, laying in the afternoon is not a general strategy among brood parasites because some species, such as the Brown-headed Cowbird (*Molothrus ater*), Jacobin Cuckoo (*Clamator jacobinus*), Horsfield's Bronze Cuckoo (*Chrysococcyx basalis*), and Shining Bronze Cuckoo (*C. lucidus*) lay in the morning (Gaston 1976, Brooker et al. 1988, Neudorf and Sealy 1994). In contrast to the Common Cuckoo, the Brown-headed Cowbird parasitizes its host's nests before sunrise when the hosts are absent from the nest (Scott 1991). Hence it seems that different species of brood parasites lay at different times of the day to avoid being spotted by the hosts.

As reed warblers have been shown to assess the local parasitism risk and modify their behavioral responses adequately (Welbergen and Davies 2009), we expected that multiple encounters with a dummy cuckoo would increase the host's probability of damaging or ejecting its own eggs in the absence of a cuckoo egg in the nest (i.e., true recognition errors, Røskaft et al. 2002b, Stokke et al. 2002). However,

encountering a cuckoo at the nest is not the only stimulus that hosts may use to assess their risk of parasitism. The probability of committing a recognition error is also likely to be influenced by the actual frequency of parasitism in the population and the frequency of rejecters (which is 29% in our population, Kleven et al. 2004). The incidence of recognition errors may be an important selective force behind acceptance of parasitic eggs, leading to a balance between rejecters and accepters in a host population (equilibrium hypothesis, Davies et al. 1996); documentation of such errors, however, is extremely difficult. Although reed warblers in our experiments faced repeated presentations of a dummy cuckoo, we failed to reveal any significant differences between experimental and control nests in the frequency of recognition errors. This result is in accordance with the previous experimental study by Røskaft et al. (2002b) based on single presentations of a dummy cuckoo at reed warbler nests.

In summary, by simulating repeated visits of a brood parasite we found that the hosts increased the intensity of their nest defense, though only from the first to the second trial. Afterward, the nest defense remained at the same intensity. The increase can be explained in the light of the positive-reinforcement hypothesis or it may simply result from nest attendance increasing through laying. Despite the repeated exposures of a brood parasite, hosts did not commit more recognition errors, in accordance with the general rarity of such errors in *Acrocephalus* warblers (Røskaft et al. 2002b).

ACKNOWLEDGMENTS

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