Increased host tolerance of multiple cuckoo eggs leads to higher fledging success of the brood parasite

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In birds, multiple parasitism is the laying of two or more eggs by one or more parasitic females in a single host nest. Several cognitive mechanisms may explain how multiple parasitism could affect parasite egg discrimination by hosts. Rejection based on discordance predicts that multiple parasitism provides a perceptually more error-prone way for hosts to reject parasitism because more foreign eggs decrease the chance that any one egg is perceived as most dissimilar and recognized as foreign, unless parasite eggs are all similarly highly nonmimetic. In contrast, rejection based on clutch uniformity predicts that in multiple parasitism egg rejection is more error-proof if mimicry by parasite eggs is variable, because increased variation in egg appearance makes for easier egg rejection for hosts. Finally, true egg recognition, that is, rejection based on memory of the host's own eggs, predicts no differences in rejection rates from nests with single or multiple parasitism. We studied common cuckoos, *Cuculus canorus*, parasitizing a population of great reed warblers, *Acrocephalus arundinaceus*, in Hungary where multiple parasitism was frequent. Hosts rejected parasite eggs less often in nests with multiple parasitism than in nests with single parasitism. These observations were confirmed by experimental parasitism and support the rejection based on discordance hypothesis. As hosts were more likely to tolerate cuckoo eggs in nests with multiple parasitism, we found that multiple parasitism more than doubled cuckoos' reproductive output per host nest compared to single parasitism.

Avian obligate brood parasites lay their eggs in nests of host species, and leave parental care of their offspring to the unrelated foster parents (Davies 2000). Caring for a parasite offspring is a costly task for a host (Hauber 2006). For example, in evictor species the young brood parasite attempts to displace all nest content (Wyllie 1981; Honza et al. 2007a), including eggs and nestmates. Consequently, the brood parasite typically grows up alone, eliminating all host reproduction (Kilner 2005; Krüger 2007). Hosts can reduce the negative consequences of brood parasitism through antiparasite defence, involving aggression against the adult parasite (Davies & Brooke 1988; Røskaft et al. 2002a; Davies et al. 2003; Moskát 2005; Dyrcz & Halupka 2006; Honza et al. 2006), egg discrimination (e.g. Davies & Brooke 1989; Moksnes et al. 1991) and/or chick discrimination (Payne et al. 2001; Langmore et al. 2003; Schuetz 2005; Grim 2006; Anderson & Hauber 2007). Consequently, the evolution of both brood parasitism and host responses reflects naturally and sexually selected morphological and life history trade-offs within and across parasite taxa and refined perceptual and cognitive mechanisms of host species' defences (Krüger & Davies 2002; Garamszegi & Avilés

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2005; Hauber & Kilner 2007; Krüger et al. 2007; Parejo & Avilés 2007).

Consequences of Multiple Parasitism

When the relative population density of brood parasites is high compared to that of hosts, some host nests may contain more than one parasite egg, so that they are multiply parasitized (Wyllie 1981; Moskát et al. 2006). Irrespective of whether multiple parasitism (or superparasitism) is due to the laying of eggs by the same or different females (McLaren et al. 2003; Ellison et al. 2006), it is typically thought to be costly to brood parasites because parasitic chicks compete more vigorously than do host chicks (Hauber 2003), leading to the reduction of per capita egg-to-fledging success of the parasite (Trine 2000; Hoover 2003). Multiple parasitism is especially costly for evictor brood parasites whose chicks displace all eggs and nestmates following hatching (Honza et al. 2007a) and it has been hypothesized to be implicated in the evolution of both egg removal by laying parasites and the similarity between host and specialist parasite eggs (Davies & Brooke 1988; Brooker et al. 1990).

Multiple parasitism is common in some hosts of the brown-headed cowbird, *Molothrus ater* (Trine 2000; Hoover 2003; McLaren et al. 2003), the shiny cowbird, *Molothrus bonariensis* (Lea & Kattan 1998; Tuero et al. 2007), the bronzed cowbird, *Molothrus aeneus* (Ellison et al. 2006), and also in the great spotted cuckoo, *Clamator glandarius* (Martínez et al. 1998; Soler & Soler 1999). However, it is a relatively rare phenomenon in hosts of the common cuckoo, *Cuculus canorus* (hereafter 'cuckoo'), an evictor brood parasite, which are typically parasitized at a rate below 20% (e.g. Schulze-Hagen 1992; Davies 2000; Rutila et al. 2002; Avilés et al. 2005; Antonov et al. 2006, 2007; Stokke et al. 2007a). Thus, most cuckoo chicks that hatch successfully (Øien et al. 1998) do not need to compete with or evict other parasite eggs and chicks from parasitized broods. In contrast, an unusually high level (ca. 64%) of cuckoo parasitism occurs in the great reed warbler, *Acrocephalus arundinaceus*, in the Hungarian Great Plain (Moskát & Honza 2002), where a high rate of multiple parasitism has also been reported: 35% of the parasitized clutches ($N = 123$) were multiply parasitized by two to four cuckoo eggs, and so 58% of all cuckoo eggs ($N = 187$) were found in nests with multiple cuckoo eggs (Moskát & Honza 2002). Egg collections in Hungarian museums (C. Moskát, unpublished data) and other reports on historical data suggest that such a high level of parasitism has existed for at least the last 80–100 years (e.g. Baker 1942; Molnár 1944; Moskát & Honza 2002).

Behavioural Responses of Hosts

Multiple parasitism may also have critical implications for the host's reproductive success and behavioural responses to parasitism. At the fitness level, more parasite eggs mean greater chances of elimination or reduction of the host's own brood and caring for more genetically unrelated young, thus reducing the foster parents' current (Trine 2000; Hauber 2002; Hoover 2003) and future reproductive outputs (Payne & Payne 1998; Hauber 2002; Hauber & Montenegro 2002).

The evidence suggests a negligible effect of multiple parasitism on recognition by hosts of nonevictor parasites. Indeed, experiments with *Molothrus* cowbird hosts have shown that single parasite eggs are as likely to be accepted or rejected as multiple foreign eggs (e.g. Rothstein 1975a; Davies 2000). Similar results were reported for magpie, *Pica pica*, hosts of great spotted cuckoos in Spain (Soler & Møller 1990). In contrast, although studies of multiple parasitism on hosts of evictor parasites are sparse (e.g. Brooker et al. 1990), these suggest that multiple parasitism may affect host recognition. For instance, Honza & Moskát (2005) experimentally parasitized great reed warbler clutches in Hungary

by two different, but both nonmimetic, model common cuckoo eggs, and found increased host rejection of the nonmimetic eggs relative to experimental single parasitism with a nonmimetic egg. However, in natural cases of cuckoo parasitism in the Hungarian great reed warbler population, the cuckoo eggs generally show a good visual match as judged by human eyes (Baker 1942; Southern 1954; Moskát & Honza 2002; Lovászi & Moskát 2004; Fig. 1) and spectrophotometry (Cherry et al. 2007a). If mimicry is so good, hosts may treat foreign eggs as their own (Hauber et al. 2006; Moskát & Hauber 2007). Therefore, the research by Honza & Moskát (2005) cannot be regarded as a typical case of parasitism in that naturally parasitized great reed warbler population. In addition, the use of two nonmimetic eggs in that earlier experiment did not allow a test for contrasting predictions of alternative cognitive explanations for egg rejection. Here, we designed a new treatment to simulate parasitism more realistically to add experimental data to observations of natural parasitism and to address alternative cognitive scenarios involved in the hosts' responses to multiple parasitism.

Alternative Cognitive Mechanisms of Host Responses

The rejection by discordance hypothesis (Rothstein 1975b, 1982; Marchetti 2000; Servedio & Lande 2003) assumes that egg appearance is perceived relative to the appearance of other eggs in the clutch so as to generate a distribution of pairwise dissimilarities. In this cognitive scenario, therefore, it is parasitism per se, rather than the identity of individual parasite eggs that is perceived by the host (Hauber et al. 2004; Hoover et al. 2006). Accordingly, this cognitive scenario predicts that multiple parasite eggs of different levels of mimicry will lead to lower rejection rates than single parasite eggs because more foreign eggs would reduce the chance that any single egg is considered the most dissimilar. In contrast, when two parasite eggs are highly dissimilar in multiple parasitism, each foreign egg is expected to be recognized, so this method would result in increased rejection rates.

Alternatively, the hypothesis that rejection is based on limited intraclutch variation (Davies & Brooke 1989; Stokke et al. 1999; Moskát et al. 2008a; Schulze-Hagen et al. 2009) predicts that through evolutionary time, host species or populations of a host species that are more frequently parasitized by cuckoos would evolve eggs more homogeneous in appearance within a nest than populations with lower rates of parasitism (Øien et al. 1995; Soler & Møller 1996; Moskát et al. 2002; Avilés & Møller 2003). From a cognitive perspective, individual hosts would use clutch uniformity of their perceived own eggs to identify parasitism (Stokke et al. 1999; Moskát et al. 2008a). Thus, provided that foreign eggs are nonmimetic (i.e. they cannot be considered among the host's own set of eggs), multiple parasitism in a host clutch will lead to increased recognition of the parasite eggs. If a nest contains two or more parasite eggs that differ in the extent of their mimicry relative to the host's eggs, this should also increase the perceived variation of the entire clutch within the nest and lead to increased rejection of parasitism.

Finally, the true egg recognition (recognition from memory) hypothesis predicts that birds compare the characteristics of eggs in a clutch to a memory template of their own or otherwise acceptable egg phenotype, which could be inherited and/or learned (Rothstein 1974; Moksnes 1992; Hauber & Sherman 2001; Hauber et al. 2006; Moskát & Hauber 2007). If the match of a parasite egg to the internal template is close, hosts would accept this egg as their own (Reeve 1989; Davies et al. 1996; Hauber et al. 2006; Moskát & Hauber 2007; Stokke et al. 2007b). Thus, this scenario predicts the same frequency of rejection for foreign eggs for single and multiple
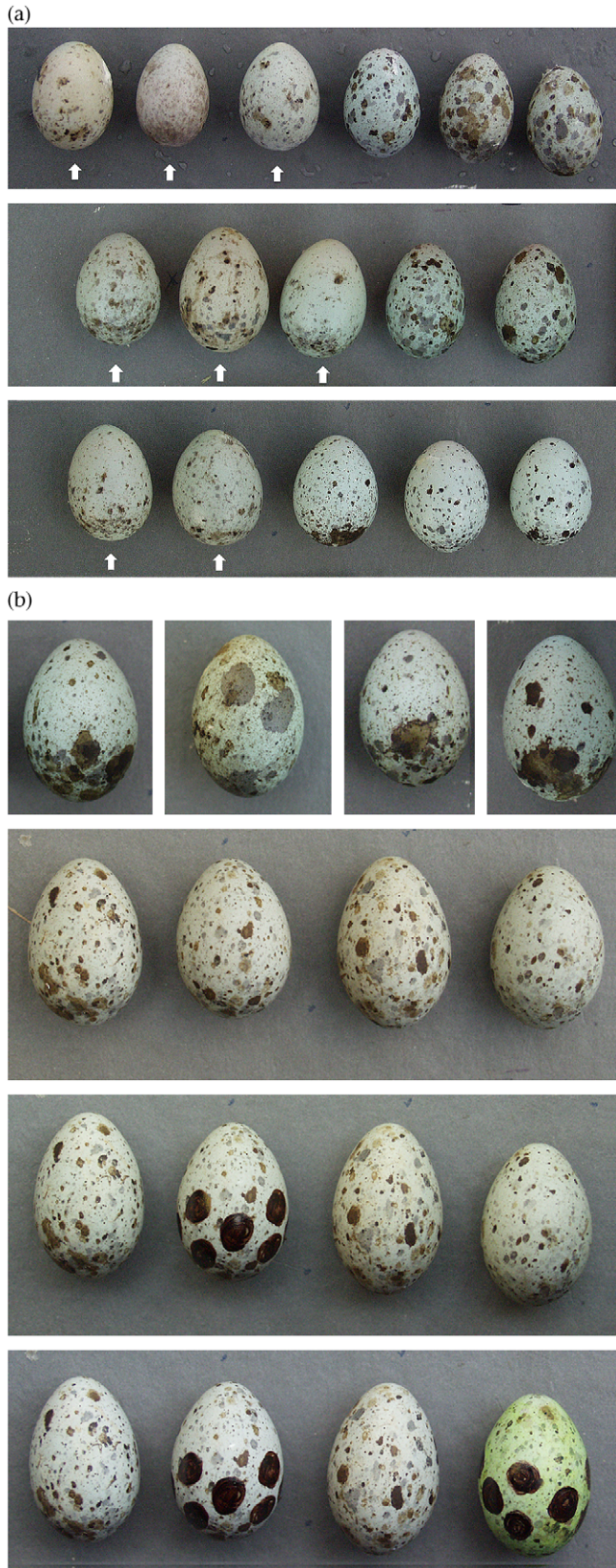
Figure 1. (a) Photos of great reed warbler clutches parasitized with multiple common cuckoo eggs. Parasite eggs are indicated by arrows. (b) Row 1: highly maculated great reed warbler eggs from central Hungary (rare type). Rows 2–4 provide an example of our experimental manipulation on typical host eggs. Row 2: the clutch before experimental manipulation; row 3: clutch with one 12-spot mimetic egg; row 4: clutch with one 12-spot mimetic and one yellow/12-spot nonmimetic egg.

parasitism by parasite eggs that have the same degree of similarity to host eggs.

Importantly, these alternative cognitive mechanisms also make contrasting predictions about the method of parasite egg rejection (i.e. egg ejection or nest desertion). Specifically, the rejection by clutch uniformity and the true recognition hypotheses do not predict differences in the method of rejection between nests with single and multiple parasitism, but the rejection based on discordance hypothesis predicts more nest desertions than ejections for multiple parasitism because it is parasitism per se and not the identity of the foreign egg that is recognized (Servedio & Hauber 2006).

Our aim in this study was to contrast egg rejection behaviours of great reed warbler hosts towards real cuckoo eggs in nests with single or multiple cuckoo parasitism in the context of predictions of these alternative cognitive mechanisms of foreign egg recognition. We did not address instances of repeated or sequential parasitism of the same clutch in this study (i.e. parasitism of a host clutch with a previously ejected cuckoo egg, which represents novel cognitive challenges for cuckoo hosts: Hauber et al. 2006; Honza et al. 2007b) and we did not have the genetic tools to identify whether one or more female cuckoos were responsible for multiple parasitism. We compared these observations on natural parasitism with the outcomes of a consistent methodology of experimental single or multiple parasitism, where we artificially parasitized a set of non-parasitized host clutches by painting one or two of the hosts' own eggs.

Impact of Host Responses on Cuckoo Fitness

If the rejection rate of cuckoo eggs by hosts differed between nests with single versus multiple parasitism, we would also find an effect on cuckoos' reproductive success from clutches with single versus multiple parasitism. We therefore assessed whether more evictor parasite eggs represented a cost for individual cuckoo young because hatchling cuckoos may eliminate other parasite eggs and nestmates. Alternatively, more than one parasite egg in the same host nests may decrease host rejection rates of foreign eggs and, thus, increase the probability that at least one parasite egg hatches successfully in a parasitized clutch. To achieve these goals, we contrasted the proportions of parasitized clutches yielding a fledgling cuckoo between nests containing single versus multiple cuckoo eggs.

METHODS

Study Area and Species

We conducted the study in the surroundings of Apaj and Kiskunlacháza-Bankháza, central Hungary (47°07′N, 19°06′E), ca. 40–50 km south of Budapest (Moskát & Honza 2002). Great reed warblers breed in 2–4 m wide strips of reed along both sides of small channels. We collected observational data by monitoring great reed warbler nests and measuring behavioural responses to single and multiple parasitism by cuckoos across three years 1998–2000. Nests were found at the building stage, or at the start of the laying stage, and monitored daily during the egg-laying stage (day 0 = day of first egg laid), and for at least 6 consecutive days or until rejection if parasitism took place until rejection, or until successful fledging if rejection did not take place. Newly laid eggs were assigned to host or parasite species based on size and maculation and marked with a fibre pen for individual identification. Laying female cuckoos typically remove one egg from the clutch (86%), either a host egg or an already present cuckoo egg, but rarely two eggs (6%), or no egg (8%) at all (Moskát & Honza 2002).

Although spectrophotometry studies revealed a generally close match across all wavelengths between cuckoo and great reed warbler eggs in this population (Cherry et al. 2007a, b), a wide range of host–parasite egg mismatch was revealed by human scoring (28% perfect, 23% good, 27% moderate, 16% poor and 6% bad as reported by Moskát & Honza 2002, following the categories proposed by Moksnes et al. 1993). Furthermore, great reed warblers reject ca. 34% of naturally laid cuckoo eggs, and are more likely to reject more poorly mimetic eggs, as judged by human observations (Moskát & Honza 2002) or measured by spectrophotometry (Cherry et al. 2007a). Common cuckoo eggs are typically larger than eggs of most of their hosts (Krüger & Davies 2002); however, in our study site egg volumes of this relatively large cuckoo host and its brood parasite were similar (Török et al. 2004; see also Honza et al. 2001 for data from the Czech Republic), justifying the use of painted conspecific eggs as experimental cuckoo eggs (see below).

Host Responses to Natural Parasitism

Host reactions towards each cuckoo egg were categorized as acceptance or rejection with the mode of rejection specified (i.e. ejection, burial of the parasite egg or the desertion of the parasitized nest; for more details see Moskát & Honza 2002). In nests with more than one cuckoo egg, hosts showed the same reactions towards each of the two or more cuckoo eggs in clutches with multiple parasitism, except in one case when one of three cuckoo eggs was ejected, but the other two were accepted. This clutch was omitted from the data set because of its unsuitability for an analysis where the response variable was binary, that is, acceptance or rejection of all parasitism per nest. We also identified cases of ejection costs (Stokke et al. 2002) when host eggs disappeared together with the cuckoo eggs from the nests, while ejection errors were recorded when host eggs disappeared but cuckoo eggs remained in the nest.

Our quantitative analyses included clutches that contained one to four cuckoo eggs at the same time. In the present study we did not use data on repeated or sequential parasitism, that is, when the laying cuckoo removed a cuckoo egg, or a female cuckoo laid another egg after a burial or ejection of a previously laid cuckoo egg by the host. This ensures that we evaluated host reaction to multiple parasitism, that is, when the host had the chance to inspect two or more parasite eggs at the same time. Also, only clutches that had at least three eggs (host and parasite egg numbers combined) were considered (the modal clutch size in this population is five eggs: Moskát et al. 2008b). Great reed warblers' responses to parasitism are affected by the absence of their own eggs in the nest at the early laying stage (Moskát & Hauber 2007), so we considered parasitized clutches that contained at least one or, generally, more host eggs. However, we included two cases of egg burial in cases of single parasitism, when burial was incomplete and the upper half of the parasite eggs were visible in the clutch. The conclusions did not change when we omitted these two nests from the analyses.

Cuckoos lay an egg every second day (Wyllie 1981) and in parasitized clutches multiple cuckoo eggs are more likely to be laid on different days (91% of cases; Hauber et al. 2006). Although we did not analyse the parentage of the cuckoo eggs by molecular techniques (Marchetti et al. 1998), our photos of multiple parasitism showed that the same nests were typically parasitized with eggs that clearly differed in colour and pattern (for examples see Fig. 1a), suggesting that they were parasitized by different cuckoo females (cf Moksnes et al. 2008).

In our study area the first cuckoo eggs were laid in a nest at a mean stage ±SD of 0.9 ± 1.5 days (range -2 to 4, $N = 20$; day 0 = 1st egg laid). Additional cuckoo eggs were also laid after day 9. In an exceptional case, the first cuckoo egg was laid in the nest 2 days before the host female started her egg laying, and a second cuckoo egg was laid in the incubation stage, 2 days after the hosts completed the clutch.

Experimental Manipulations

Egg discrimination by great reed warblers in response to single versus multiple cuckoo parasitism was also tested through experimentation in 2006 with different egg types. Experimental eggs were produced by the manipulation of the hosts' own eggs; thus clutch size did not change, which simulated egg removal and replacement by the laying cuckoo.

Single experimental parasitism
Mimetic egg. For single parasitism we used two egg types. First, 12 dark-brown spots 4–5 mm in diameter were painted on the eggshell surface with a brown fibre pen (Faber-Castell OHP permanent, colour code 78, size 1525, Faber-Castell Inc., Stein, Germany; Fig. 1b, rows 3 and 4, second egg on the left). The colour of this pen was very similar to the dominant spot colour of hosts as revealed by spectrophotometry, and the size of these spots was within the range of natural spots (range < 1–6.1 mm; Moskát et al. 2008c). Typically the clutch needed a close inspection for humans to realize that the manipulated egg differed from the host's own eggs, so we called this egg type 'mimetic'. A previous experimental study revealed only 8% rejection rate for this egg type in single parasitism (one case out of 12 eggs and nests; Moskát et al. 2008c), and in the present study great reed warblers also tended to accept these eggs in clutches when no other eggs were manipulated (20% rejection of $N = 10$ eggs and nests) in similar frequencies (Fisher's exact test, two-tailed: $P = 0.571$). The disappearance of non-manipulated great reed warblers' own eggs at unparasitized nests (8.7%, in 4/46 nests between 1998 and 2005, C. Moskát, unpublished data) did not differ significantly from the rejection rate of these artificially spotted eggs in our population (Fisher's exact test: $P = 0.673$).

Nonmimetic egg. The mimetic egg type was expected to be rejected at a relatively low rate by hosts, so we also designed a less mimetic egg type, to be distinguishable from the host's own eggs, causing hosts to reject them at a relatively high rate. We modified host eggshell colour by painting the natural eggshell surface with a highlighter pen, because a previous study revealed that such changes in eggshell surface colours increased hosts' rejection rates significantly (Moskát et al. 2008c; see also Honza et al. 2007c for another species). So for the second egg type we painted the background colour of a host egg with a yellow highlighter pen (Stabilo Boss art No. 70/24, Stabilo Inc., Haroldsberg, Germany). This pen made the eggs a light greenish-yellow (Fig. 1b). We called this egg type nonmimetic. Many kinds of green and yellow shades can be found on both host and parasite eggshells in our population; however, these are very rare forms (<1% frequency, Moskát & Honza 2002; Moskát et al. 2008c). We also painted 12 brown spots as for the mimetic egg over the yellow highlighter marking (Fig. 1b, row 4, egg on the right), to ensure that the two egg types differed in only one parameter (i.e. background colour). Great reed warblers showed the same strong rejection responses (100% rejection) against this combined yellow/12-spot (nonmimetic) egg type as seen against other egg types used in previous experimental parasitism on which the overall background colour, not the maculation, of great reed warbler host eggs was manipulated (i.e. dark-brown-painted host eggs: 92% rejection rate; Hauber et al. 2006). We checked the content of

experimentally parasitized nests daily for 6 consecutive days to detect rejection.

Multiple experimental parasitism

At our study site, half of naturally laid cuckoo eggs showed good to perfect mimicry and the other half showed moderate to bad mimicry (Moskát & Honza 2002). For this reason, we induced multiple parasitism experimentally by introducing one of our mimetic eggs and one of our nonmimetic eggs on day 4 in the hosts' egg-laying period. As we manipulated two host eggs from each nest, the clutch size remained the same, as in natural cuckoo parasitism (see above). This approach was specifically aimed at testing the prediction of the decreased clutch uniformity hypothesis by introducing two different artificially manipulated egg types into nests to simulate multiple parasitism.

Control

We also used a control group of nonparasitized host clutches in the year of the experiment where we did not manipulate eggs, but only checked and marked them as in cases of experimental parasitism. No egg was ejected or buried and no nest was abandoned or showed recognition error ($N = 8$), which is the same result obtained in previous years for control clutches (0/13 desertions, Hauber et al. 2006; 0/12 desertions, Moskát et al. 2008c), indicating no host sensitivity for nest checks. However, this is a relatively small sample size for monitoring recognition errors.

Cuckoo Reproductive Success

We monitored the fate of parasitized nests until the cuckoo chick fledged. We calculated hatching success of cuckoos as the proportion of nests with cuckoo chicks that hatched. We also calculated fledging success as the proportion of nests that produced a cuckoo fledgling, in relation to the number of parasitized clutches. Both hatching and fledging success were calculated for single and multiple parasitized nests separately, with depredated nests removed from the analyses.

Statistical Tests

Individual breeding pairs of hosts were not colour-banded in the population, but only a single observation or experiment was recorded from each territory and breeding philopatry is generally low in this population (Moskát et al. 2008b), thereby limiting the possibility of pseudoreplication. All statistical tests were two-tailed. Analyses were carried out using the programs Statistica 5.1 (Statsoft Inc., Tulsa, OK, U.S.A.) and Statview 5.0.1 (SAS Institute Inc., Cary, NC, U.S.A.), and binary logistic regressions were computed in SPSS version 9.0 (SPSS Inc. Chicago, IL, U.S.A.). For the binary logistic regression analyses, the host's response was the dependent variable (accept or reject), with the number of cuckoo eggs, host clutch size, laying date (Gregorian day) and year treated as covariates in the initial model. Stepwise variable selection was applied by choosing the option 'backward conditional' with standard criteria.

Ethical Note

Our observational data came from monitoring the nesting attempts of wild birds as part of a long-term project on the breeding biology of great reed warblers. No birds abandoned nests because of our visits. The experimental test of our hypotheses also required the manipulation of some great reed warbler eggs. No great reed warbler eggs were crushed during our treatments, and we detected no effect of the manipulation on egg hatchability in comparison with nonexperimental nests. Our study was licensed by the Duna-Ipoly National Park, the Kiskunság National Park and the Hungarian Inspectorate for Environment, Nature and Water.

RESULTS

Host Responses to Natural Parasitism

Altogether, 45 cases of single parasitism and 34 cases of multiple parasitism with 78 cuckoo eggs (two, three or four cuckoo eggs in the frequency of 25, 8 and one, respectively) were detected in this study. Rejection rates of great reed warblers towards cuckoo eggs differed significantly between naturally parasitized clutches with single versus multiple parasitism (40% and 12% rejection rates in nests of single and multiple natural parasitism, respectively; Fisher's exact test: $P = 0.004$; Fig. 2). Rejection rates did not differ whether nests were parasitized by two or three to four cuckoo eggs (12% and 11% rejection rates with corresponding sample sizes of $N = 25$ and $N = 9$, respectively; Fisher's exact test: $P = 1.0$). A binary logistic regression (with the Wald statistic, W) revealed that laying date was not significantly related to rejection rates ($\beta = -0.036$, $W_1 = 1.5$, $P = 0.30$; laying date was removed at step 2), nor was the year of observation ($\beta = 0.65$, $W_1 = 2.4$, $P = 0.13$; year was removed at step 3). In the final model, the rejection rate of cuckoo eggs by great reed warbler hosts was negatively associated with the increasing number of cuckoo eggs per clutch ($\beta = -1.76$, $W_1 = 6.6$, $P = 0.010$) and positively with number of host eggs ($\beta = 0.84$, $W_1 = 7.8$, $P = 0.005$). The discriminatory ability of the logistic model was 77.6%, and the Hosmer–Lemeshow goodness-of-fit test was not statistically significant ($\chi^2_7 = 8.9$, $P = 0.26$), indicating good power and good calibration of the model, respectively. Nests deserted during the laying stage had no chance of being completed and, consequently, they had smaller clutches, which resulted in the negative relationship between clutch size and egg rejection (Spearman rank correlation: $r_S = -0.31$, $P = 0.006$). None the less, even without the clutch size term included, the relative contributions of each predictor variable to the overall model remained similar (model discriminative power: 72.4%; the number of cuckoo eggs per nest: $\beta = -1.7$, $W_1 = 6.8$, $P = 0.009$; laying date: $P = 0.72$; year: $P = 0.18$).
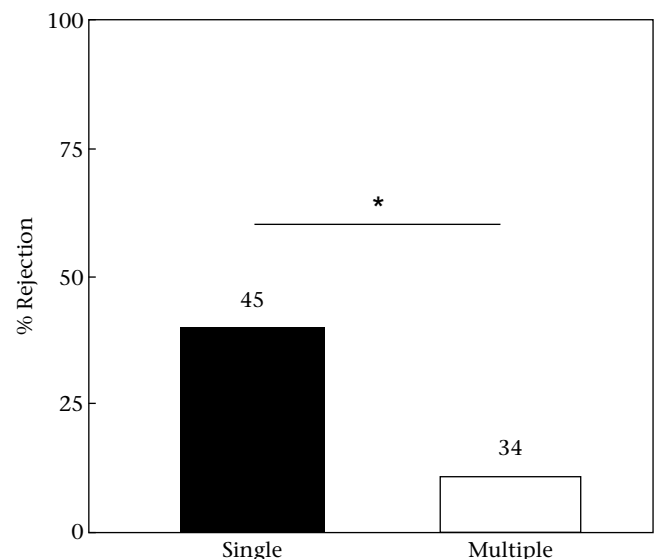

Figure 2. Rejection rate in response to real cuckoo eggs in nests naturally parasitized by one ('single') and two or three ('multiple') parasite eggs. In calculations a multiply parasitized nest was considered as one case. Numbers above bars indicate numbers of cases. *$P < 0.005$; Fisher's exact test.

The method of rejection differed consistently between cases of single and multiple parasitism: in clutches with single parasitism ($N = 18$ of 45 nests) ejection was the most frequent method of rejection (13/18, 73%) with the remaining cases being 11% of burial and 16% of nest desertion. In multiple parasitism, hosts rarely rejected cuckoo eggs (4/34 nests, 7/78 eggs). Egg ejection was observed in only one case (1/4 nests, 1/7 eggs) and all other rejections were by desertion (3/4 nests, 6/7 eggs). Thus, nest desertion was the more frequent method of rejection at nests with multiple parasitism (Fisher's exact test: $P = 0.046$), and ejection the more frequent response in nests with single parasitism (Fisher's exact test: $P = 0.005$).

Ejection costs were observed only in nests with single parasitism (4/13 nests, i.e. 31% of nests where the cuckoo egg was ejected). Typically one host egg was lost per nest, but in one case three host eggs disappeared. Ejection errors were observed in four nests where the cuckoo eggs were accepted, but only in cases of single parasitism (4/27 cases, i.e. 15% of nests where the parasite egg was accepted, with the loss of three eggs in one nest and one egg in each of the other three nests).

Experimental Parasitism

With respect to the nonmimetic egg, great reed warblers rejected all manipulated eggs in response to single parasitism (14 nonmimetic eggs in 14 nests). When hosts were exposed to experimental parasitism by the two different egg types (multiple parasitism with one mimetic and one nonmimetic experimental eggs), they rejected 60% of nonmimetic eggs (nine nonmimetic eggs in 15 nests; Fig. 3). The mimetic egg was also rejected in six cases from 15 nests of multiple experimental parasitism (40%) together with a nonmimetic egg. The rejection rate of the mimetic egg when it was introduced together with a nonmimetic egg did not differ significantly from that when the mimetic egg was introduced alone (two mimetic eggs rejected in 10 nests, 20%;

Fisher's exact test: $P = 0.68$). In contrast to natural parasitism, only ejection was observed as the method for rejection of the parasite eggs in both single and multiple experimental brood parasitism.

Hosts with multiple experimental parasitism showed a significantly lower rate of rejection compared to single parasitism with respect to the nonmimetic egg only (binary logistic regression: $\beta = -2.6$, $W_1 = 4.7$, $P = 0.032$; model discriminative power was 84%). Neither laying date ($P = 0.37$) nor clutch size ($P = 0.34$) had an effect on rejection, and they were removed from the binary logistic model by the stepwise procedure ($\beta = 0.16$, $W_1 = 0.79$, $P = 0.37$ and $\beta = 0.91$, $W_1 = 0.91$, $P = 0.34$ for laying date and clutch size, respectively). The lack of laying date and clutch size effects suggests similarities in the putative age and quality of host parents between our experimental treatments (Lotem et al. 1992).

Cuckoo Reproductive Success

In a counterintuitive pattern of this evictor parasite's breeding success, having more than one cuckoo egg per host clutch increased the chance that a cuckoo egg would be accepted and eventually hatch. This meant that a greater proportion of multiply parasitized nests contained a cuckoo hatchling than did singly parasitized nests (19/64 and 15/28 in single and multiple parasitism, respectively; Fig. 4, $\chi^2_1 = 4.2$, $P = 0.041$).

In each case only a single cuckoo chick survived and there was no difference in the hatching-to-fledging survival rate of cuckoo chicks between clutches with originally single versus multiple parasitism: 93% of hatched cuckoo chicks fledged successfully from nests with single parasitism ($N = 14$ hatchlings), and 75% from multiply parasitized nests ($N = 20$ hatchlings, with four nests containing two cuckoo hatchlings; $\chi^2_1 = 0.17$, $P = 0.68$). We also found similar productivities of those nests where at least one cuckoo egg hatched (single parasitism: 93%, $N = 14$ nests; multiple parasitism: 94%, $N = 15$ nests; $\chi^2_1 < 0.01$, $P = 0.99$). In contrast, the proportion of host broods with the cuckoo chick surviving to fledging (ca. 18–21 days; C. Moskát, unpublished data) in nests with multiple parasitism proved to be greater than that in nests with single parasitism (13/59 and 15/30 in single and multiple parasitism, respectively; $\chi^2_1 = 7.2$, $P = 0.007$; Fig. 5).
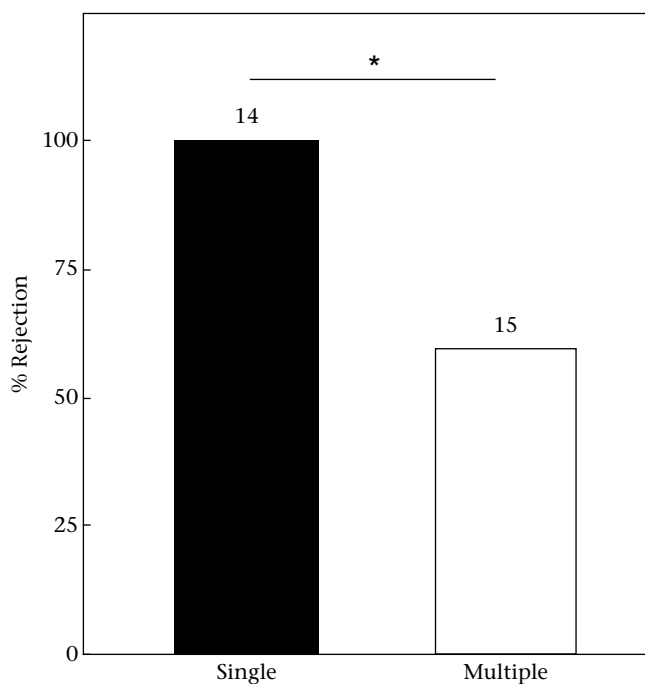

Figure 3. Rejection rates by great reed warblers against nonmimetic eggs when nests were experimentally parasitized with one nonmimetic egg ('single'), or with one mimetic and one nonmimetic egg each ('multiple'). Numbers above bars indicate numbers of cases. *$P < 0.005$; Fisher's exact test.
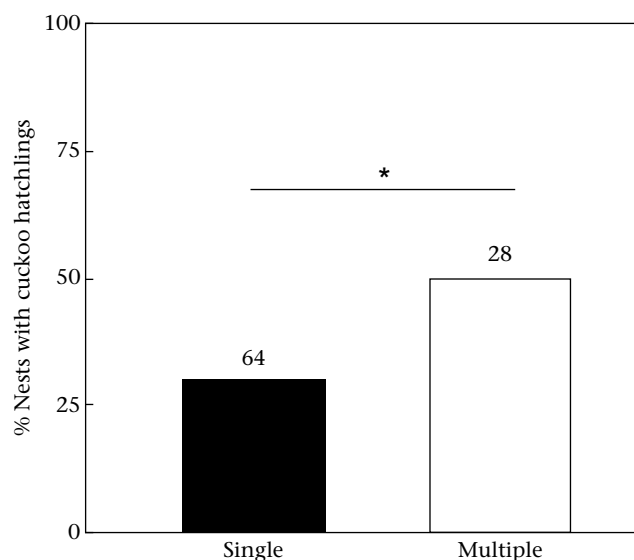

Figure 4. Percentage of host nests with cuckoo hatchlings from clutches with single or multiple parasitism. Numbers above bars indicate numbers of cases. *$P < 0.05$; chi-square test (see Results).

As cuckoo fledging rates were significantly greater in nests with multiple parasitism, we expected lower survival rates of cuckoo eggs in single parasitism. However, survival rates to fledging did not differ statistically in single and multiple parasitism (13 fledglings from 96 cuckoo eggs (0.135 fledgling/egg) in single parasitism, and 15 fledglings from 118 cuckoo eggs found in 50 nests (0.127 fledgling/egg) in multiple parasitism; $\chi^2_1 = 0.02$, $P = 0.88$). We explain this finding by the lower survival rate of cuckoo eggs on a per capita basis in nests with multiple than single parasitism (see above), which overcompensated for the effect of the hosts' lower rejection rate in nests with multiple parasitism.

DISCUSSION

Our results revealed a consistent difference, in both the observational cases and the experimental results, in great reed warblers' responses to variable numbers of cuckoo eggs, as we detected higher rejection rates to natural cuckoo eggs or experimental eggs in nests with single versus multiple parasitism. Thus, we reject the hypothesis of cuckoo egg rejection by clutch uniformity which predicts that more cues from more parasite egg appearances aid hosts to improve egg discrimination by decreasing egg similarity within the clutch and, thus, presumably by increasing behavioural rejection of foreign eggs. The significant differences in host responses between nests with varying numbers of cuckoo eggs also allow us to discount the true recognition scenario that predicts that rejection rates would be similar (and low for mimetic parasite eggs) in host nests with single or multiple parasitism.

In contrast, the hypothesis of rejection based on discordance was supported by both the observational and the experimental results. Specifically, this scenario predicts that more foreign eggs decrease the ability of the hosts to discriminate their own from foreign eggs based on pairwise differences between egg appearances (Marchetti 2000; Servedio & Lande 2003; Servedio & Hauber 2006) in parasitized clutches. The methods of the rejection of cuckoo eggs were also in support of the rejection by discordance hypothesis (as predicted by the model of Servedio & Hauber 2006), because cuckoo eggs were more likely to be rejected by ejection from nests with single parasitism while nests with multiple parasitism were more likely to be deserted. Increased rejection costs

and rejection errors of hosts' own eggs were associated with the increased rejection rates of single cuckoo eggs as they were documented only in nests with single parasitism.

A previous study revealed different results on great reed warblers' egg discrimination in multiple parasitism, yet they all seem to be the simple consequences of the mimicry of the experimental eggs: Honza & Moskát (2005) found that two types of experimental eggs, both rejected at a high rate (68–75%) in single parasitism, were rejected at about 96% when both were used for multiple experimental parasitism. In contrast to our present experiments, in previous experiments both of the parasite eggs fell outside the hosts' acceptance threshold for their own eggs (Hauber et al. 2006) and the two easily recognizable eggs appeared to facilitate the hosts' egg discrimination, in support of the discordance mechanism (see Introduction). Both the model cuckoo eggs used in the multiple parasitism experiments by Honza & Moskát (2005) and the natural cuckoo eggs in our study area (cf Moskát & Honza 2002) showed different levels of mimicry to host eggs (measured by the method of Moksnes & Røskaft 1995; Kruskal–Wallis test: $\chi^2_2 = 15.010$, $N = 158$, $P = 0.001$), which explains the differences in egg rejection rates in multiple parasitism by Honza & Moskát (2005) and the present study (96% versus 12%; Fisher's exact test: $P < 0.001$).

Apart from mimicry (Honza & Moskát 2005 versus this study), intraclutch variation in host eggs (Stokke et al. 1999; Cherry et al. 2007a; Moskát et al. 2008a), hosts' age (Lotem et al. 1992, 1995), nonrandom selection of hosts (Hauber 2001; Grim 2002; Hauber et al. 2004; Garamszegi & Avilés 2005; Parejo & Avilés 2007), previous experience with the parasite egg (Rodríguez-Gironés & Lotem 1999; Hauber et al. 2006; Honza et al. 2007b) and variable host genetic backgrounds (Martín-Gálvez et al. 2006) may also affect rates of hosts' egg rejection in response to multiple parasitism. In the great reed warbler, other important factors include the host's sighting of a cuckoo near the nest (Bártol et al. 2002), experience with its own eggs throughout the laying stage (Moskát & Hauber 2007), breeding stage (Moskát 2005) and time of day (Dyrcz & Halupka 2007). Habitat structure and immigration of parasite-naïve individuals (Takasu et al. 1993; Røskaft et al. 2002b, 2006), through a metapopulation effect (Barabás et al. 2004; Hauber et al. 2004), might also affect antiparasite defence in our population. However, our results revealed no statistical relationship with laying date or interannual differences in rejection rate from nests with single versus multiple parasitism, and so increased tolerance to parasite eggs in multiple parasitism seems to be a fairly robust effect.

Surprisingly, fitness correlates of the parasite with multiple parasitism in our observational data set yielded an increased egg-to-fledging success of parasite eggs, owing to reduced rejection of parasite eggs in multiple parasitism. Yet, as with all observational data sets, consistent variation in rejection rates of cuckoo eggs by hosts in naturally parasitized nests can be explained by parameters not measured in the observational portion of our study. For example, differences in visit rates to host nests by prospecting and laying parasites have been implicated in shifting acceptance thresholds of cuckoo eggs by other host species (e.g. Brooke et al. 1998). However, we recorded this last confound in our experimental approach because we increased the variability of eggs in nests with simulated multiple parasitism solely by using two different egg types compared with one egg type in host nests with simulated single parasitism. This in turn resulted in the same directional change of decreasing host rejection rates as seen in the naturally parasitized nests. Nevertheless, experimental work is required to determine the factors influencing which evictor cuckoo chick survives in the nest with multiple parasitism, such as hatching asynchrony or sex-specific development of the parasite
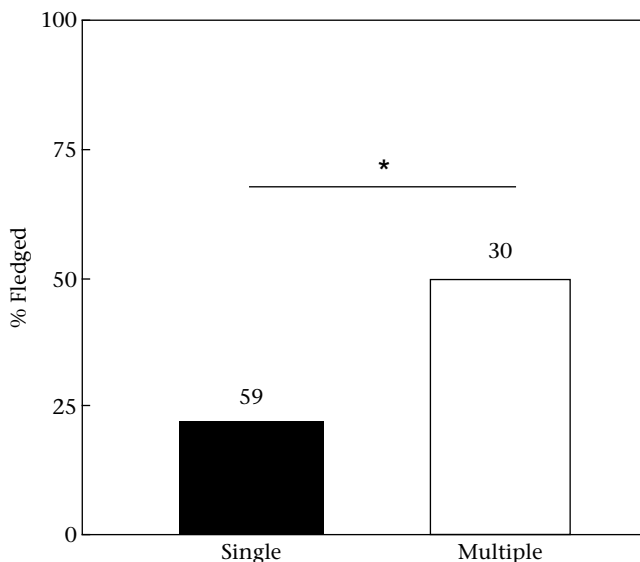

Figure 5. Percentage of nests with fledged cuckoo chicks from clutches with single or multiple parasitism. Numbers above bars indicate numbers of cases. $^*P < 0.01$; chi-square test (see Results).

(Tonra et al. 2008). In our study, only one cuckoo chick survived per parasitized brood but in some hosts of the cuckoo, including the redstart, *Phoenicurus phoenicurus*, in Finland, multiple cuckoo chicks can survive per host brood, alongside the hosts' own chicks (Rutila et al. 2002; Grim et al. 2009), implying that perhaps genetic, host race differences might also mediate cuckoo success in the presence versus absence of multiple parasitism.

From the perspective of the brood parasites, counter to expectations for an evictor brood parasite whose chicks do not tolerate other host or parasite chicks in the nest (Hauber & Moskát 2008), our results surprisingly show that multiple parasitism seems not to be detrimental, because hosts' antiparasite defences against multiple parasite eggs in a clutch are weaker than against single parasite eggs. In the absence of genetic data on these eggs, we do not know for certain whether multiple cuckoo eggs were laid by the same females. None the less, our photos of nests with multiple cuckoo eggs showed consistent differences between parasite eggs, suggesting laying by different females (Moksnes et al. 2008), as seen in other avian brood parasite taxa (Martínez et al. 1998; McLaren et al. 2003; Ellison et al. 2006). The reduced rate of rejection of cuckoo eggs from multiply parasitized nests might also act against the evolution of the recognition and rejection of other parasite eggs by laying female cuckoos (Brooker et al. 1990; Brooker & Brooker 1998).

In conclusion, we have found that multiple natural parasitism may play a key factor in cuckoo egg discrimination of great reed warblers, causing a highly significant reduction of rejection rates. We demonstrated this shift in multiple experimental parasitism by using simultaneously one mimetic and one nonmimetic egg. As a consequence of hosts' limited egg rejection responses to multiple parasitism, cuckoos' reproductive success was higher in clutches with multiple parasitism. However, multiple parasitism is also costly for cuckoos: because of the multiple eggs invested in the same nest only one cuckoo chick can fledge (Wyllie 1981). An equilibrium between an individual female cuckoo's benefits of increased hatching and fledging success of her young and the costs of losing eggs and chicks to intraspecific competition by evictor parasite chicks may exist in populations exposed to a longstanding high parasitism pressure and a consistently high proportion of nests with multiple parasitism.

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