

Post-ejection nest-desertion of common cuckoo hosts: a second defense mechanism or avoiding reduced reproductive success?

Csaba Moskát · Erik C. Rosendaal · Myra Boers ·
Anikó Zölei · Miklós Bán · Jan Komdeur

Received: 25 March 2010 / Revised: 13 August 2010 / Accepted: 3 November 2010
© Springer-Verlag 2010

Abstract Hosts of the common cuckoo (*Cuculus canorus*), an avian brood parasite, develop antiparasite defense mechanisms to increase their reproductive success. Ejection of the parasite egg and desertion of the parasitized nest are the most typical adaptations in response to brood parasitism, but nest desertion may also occur in response to partial clutch reduction, independently from parasitism. Some great reed warblers (*Acrocephalus arundinaceus*) showed both mechanisms in the same incidence of cuckoo parasitism: in 18% of successful ejections of the parasite eggs, they deserted their nests. We studied if such cases of post-ejection nest-desertion are caused by brood parasitism or reduced clutch value. We experimentally parasitized

clutches consisting of five or three host eggs with two painted conspecific eggs to mimic parasitic eggs, as multiple parasitism is frequent in the area. Although hosts ejected these parasitic eggs in both clutch categories (100% and 67% for the larger and smaller initial clutch sizes, respectively), we found that after manipulation, post-ejection nest-desertion frequently occurred at small (3-egg) clutches (40%), but rarely at large (5-egg) clutches (17%). The same phenomenon also occurred when unparasitized 3-egg clutches were reduced by two eggs, but not when 5-egg clutches were reduced in the same way. A logistic regression model revealed that only initial clutch size affected nest desertion of parasitized nests in our experiments. Therefore, we conclude that post-ejection nest-desertion is not a second antiparasite mechanism, which might serve as a redundant antiparasite defense, but a reaction to typically small and further decreased clutch size.

Communicated by M. Soler

C. Moskát (✉)
Animal Ecology Research Group, Hungarian Academy
of Sciences, c/o Hungarian Natural History Museum,
Ludovika ter 2., (Postal address: H-1431
Budapest P.O. Box 137, Hungary),
Budapest 1088, Hungary
e-mail: moskat@nhmus.hu

E. C. Rosendaal · M. Boers · J. Komdeur
Animal Ecology Group, Centre for Ecological and Evolutionary
Studies, University of Groningen,
Haren, The Netherlands

A. Zölei
Duna-Ipoly National Park Directorate,
Költő u. 21.,
Budapest 1121, Hungary

M. Bán
Behavioural Ecology Research Group,
Department of Evolutionary Zoology, University of Debrecen,
Debrecen, Hungary

Keywords Cuckoo · Great reed warbler · Antiparasite
defense · Clutch size · Clutch reduction

The common cuckoo (*Cuculus canorus*, hereafter “cuckoo”) is a well-known brood parasite, which parasitizes more than a hundred small passerine species breeding in the Palearctic (Wyllie 1981; Davies 2000; Payne 2005). However, the number of regularly used hosts is much smaller, probably just over 20, and at least 17 host-specific races of the cuckoo (the so-called “gentes”) with developed egg mimicry were previously found in Europe (Moksnes and Røskaft 1995; Alvarez 1994; Antonov et al. 2007), with additional species in Asia (Higuchi 1998; Lee and Yoo 2004; Takasu et al. 2009). The coevolutionary processes between cuckoos and their avian hosts are typically explained as a coevolutionary arms race (Dawkins and

Krebs 1979; Takasu 1998; Davies 2000), which leads to adaptations and counter adaptations between the hosts and the cuckoo (Davies and Brooke 1988; Moksnes et al. 1991; Krüger 2007). The host having adaptive mechanism will eventually win the coevolutionary arms race and escapes brood parasitism (e.g., Honza et al. 2004; Lovász and Moskát 2004; Stokke et al. 2004).

Brood parasitism often imposes a high cost on host breeding success and therefore hosts develop defense mechanisms against brood parasitism (Davies 2000). The most prominent antiparasite adaptations are based on the recognition of the parasite eggs (Hauber and Sherman 2001; Lahti and Lahti 2002; Moskát et al. 2010). Upon detection of a parasitic egg, the host may reject the egg through three known mechanisms (Rothstein 1974): (1) nest desertion, (2) ejection of the parasitic egg out of the nest, or (3) burial of the egg into the nest material. Hosts' antiparasite defense selects for mimetic eggs in cuckoos, resulting in similar eggs of the brood parasite to that of the host species (Brooke and Davies 1988; Kilner 2006). Highly mimetic parasitic eggs typically have a lower chance of being recognized and rejected by hosts than non-mimetic eggs (Davies 2000).

There are several mechanistic and functional explanations why nest desertion may occur. In hosts of brood parasites, it could be a form of antiparasite defense (Davies and Brooke 1988). It can be observed among the hosts of the brown-headed cowbird (*Molothrus ater*) (Rothstein and Robinson 1998) and also not rare among cuckoo hosts (Davies 2000). For example, meadow pipits (*Anthus pratensis*) normally reject parasitic eggs by nest desertion. In experimental parasitism by model cuckoo eggs, they showed a higher rejection rate when a cuckoo dummy was presented at the nests, indicating that nest desertion in parasitized clutches is clearly a response to cuckoo parasitism (Moksnes et al. 1993). Other cuckoo hosts use both egg ejection and nest desertion for the rejection of the parasite eggs. The great reed warbler (*Acrocephalus arundinaceus*) is such a species, where the frequency of desertion of naturally parasitized nests is significantly higher than frequency of desertions of non-parasitized nests (Bártol et al. 2002). A study of host nest desertion showed that activity of brown-headed cowbirds near the host's nest, and egg removal by the female cowbird, may lead to nest desertion by the host (Strausberger and Burhans 2001). Desertion could be a response to partial clutch or brood reduction and with that reduced value of the clutch or brood. Practically, nest desertion in this case is the consequence of nest predation (Hill and Sealy 1994). According to the parental investment theory, parents try to find an optimum between costs and reproductive success: if the benefits of deserting the nest are larger than the benefits from the current breeding attempt, the parents will desert

the nest (Pianka 1976; Sargent and Gross 1985; Winkler 1991). In some cases, only one of the parents deserts (Székely et al. 1996; Valera et al. 1997; van Dijk et al. 2007).

Another antiparasite defense mechanism, egg ejection, is much more specific to brood parasitism, whereas nest desertion is a pre-existing behavior, e.g., a response to nest predation (Hosoi and Rothstein 2000). Egg ejection shows a close relationship with nest sanitation behavior (Rothstein 1975). Birds eject foreign objects from nests (Ortega and Cruz 1988; Moskát et al. 2003; Guigueno and Sealy 2009) like leaves, small twigs, artificial objects, broken or debris eggs (Underwood and Sealy 2006). However, after successful ejection of the foreign objects, there is probably no need to desert the nest. Egg breakage in cuckoo hosts is not regarded as an antiparasite defense, when hosts accidentally break one or more of their own eggs during the ejection attempt of parasite eggs (often termed as “ejection cost”; Davies and Brooke 1988; Stokke et al. 2002). Additionally, some cuckoo hosts are able to destroy whole clutches of conspecifics, which are in the close vicinity of their nests (Hansson et al. 1997; Trnka et al. 2010), but this never seems to be applied against own eggs. In some situations, hosts may desert their nests after successfully ejecting the parasitic eggs. Nest desertion after egg ejection (we term it as “post-ejection nest-desertion”) is a rare, but not unknown phenomenon in brood parasitism (Antonov et al. 2008). However, there is almost no knowledge on the functional aspects of this behavior. For this reason, we investigate the functional significance of why nest desertion occurs after the successful ejection of the parasitic egg. Here, we demonstrate an experiment on a cuckoo host where we compare nest desertions after clutch reduction in non-parasitized nests and following the ejection of parasitic eggs.

We carried out experimental parasitism in a great reed warbler population in Hungary, to understand why nest desertion occurs after ejection of the parasitic egg. The way how hosts use cues concerning their risk being parasitized and how they use information from cues in their egg-rejection decisions are not fully understood (e.g., Servedio and Hauber 2006; Svernungsen and Holen 2010). In advance, we cannot exclude the possibility that in certain host individuals, under special circumstances (e.g., depending on parasite egg mimicry or number of eggs in clutch), both egg-ejection and nest-desertion mechanisms are manifested for the same task, i.e., the rejection of a foreign egg. This expectation is not unrealistic as these two mechanisms originated differently, as egg ejection is related to nest sanitation behavior, but nest desertion is a more general answer to changes in nest content, the sight of the brood parasite or external circumstances (e.g., weather) (Rothstein 1975; Kemal and Rothstein 1988; Moskát et al.

2003; Guigueno and Sealy 2009). In Hungary, the great reed warbler is unusually highly parasitized by cuckoos (41–68% of the clutches; Moskát et al. 2008a), with high proportion of multiple parasitism (ca. one third of the parasitized clutches contained more than one cuckoo egg; Moskát and Honza 2002; Hauber et al. 2006). A study on host-rejection behavior towards parasitic eggs showed 66% acceptance, 12% ejection, 20% desertion, and 2% egg burial (Moskát and Honza 2002). Some of the nests in this population were still monitored after the successful ejection of the cuckoo eggs, and in 18% of ejections, hosts deserted their nests (C. Moskát, unpublished; see “Methods” for further details). We hypothesized that “post-ejection nest-desertion” is a new form of hosts' antiparasite defense. If hosts are uncertain as to whether egg ejection was successful, they could still escape brood parasitism and its consequences by deserting the nest, so ejection and desertion could be a redundant antiparasite defense. By building a new nest, hosts get a new chance to avoid parasitism. We predict that the desertion rate will be higher in experimentally parasitized clutches after successful ejection of parasitic eggs than in experimentally reduced clutches that were not parasitized. Alternatively, we also hypothesized that nest desertion after successful ejection is due to reduced clutch size, so it is not the consequence of brood parasitism. In this case, we predict a higher nest desertion rate following clutch reduction than after ejection of parasitic eggs.

Methods

Study site and species

The research was performed in the surroundings of the village Apaj (47°07'N; 19°06'E) and the town Kunszentmiklós (47°02'N; 19°08'E), in central Hungary, ca. 40–60 km south of Budapest. The experiments were carried out on the great reed warbler in a ca. 20×35 km area, within an intensive system of small channels between 14 May and 14 June 2009. In this area, great reed warblers are heavily parasitized by common cuckoos (41–68%, Moskát et al. 2008a).

To find great reed warbler nests, we systematically searched the 2–4-m wide channel-side reed beds (*Phragmites australis*) once or twice a week. New nests were marked by small yellow tags at the edge of the reed beds to minimize predation, and the GPS coordinates of the nests were recorded (GPS 60, Garmin Co., Olathe, Kansas, USA) to help locate the nests later. The nests that we used for experiments were either freshly built or already contained a few eggs without cuckoo eggs. This way, we could follow the process of egg laying and avoid using nests where any

cuckoo eggs had already been ejected (for more details of the study area and on the basic methods, see Moskát et al. 2009). Multiple parasitism (two or more cuckoo eggs present in the nest) is relatively common in great reed warbler nests in our study area (36% of the parasitized clutches ($n=123$) contained multiple cuckoo eggs (23% nests contained 2, 10% contained 3, and only 3% contained 4 cuckoo eggs, Moskát and Honza 2002). Therefore, for manipulation, we used two non-mimetic parasitic eggs, instead of one, in order to achieve higher ejection rates than against one non-mimetic egg (Honza and Moskát 2005). This way, we tried to maximize the frequency of ejections to trigger the “post-ejection nest-desertion” of the hosts, in order to study this mechanism experimentally.

In the year of the study, we observed two natural cases of post-ejection nest-desertions out of 13 clutches where a single cuckoo egg was ejected. In one case, the clutch contained one cuckoo egg and one host egg only and then the cuckoo egg was ejected. In the other, but uncertain case, three host eggs disappeared together with the cuckoo egg due to host ejection or partial predation. Interestingly, in both cases, clutch size was reduced to only one host egg. In our larger 12-year dataset, we found 11 cases of post-ejection nest-desertions out of 62 ejections (18%), where nest monitoring was continued after the ejection of the cuckoo egg (C. Moskát, unpubl.). At seven nests, one cuckoo egg was ejected together with one to three host eggs by mistake, while no such type of error occurred in the rest of nests. When hosts deserted their clutches, a low number of eggs remained in the nests (one host egg, $n=6$; two host eggs, $n=1$; one cuckoo egg, $n=3$; one host and one cuckoo egg, $n=1$). When a cuckoo egg remained in the nest, the nest was multiply parasitized by two ($n=2$) or three ($n=1$) cuckoo eggs. Besides these cases of post-ejection nest-desertions, in four nests, hosts did not eject any eggs, but cuckoos parasitized these nests at the one-host-egg stage. As cuckoos typically remove one egg from clutch when they lay (Wyllie 1981), consequently, no host egg remained in these nests, and hosts deserted them with a cuckoo egg.

Experimental treatments

We experimentally manipulated clutches during two stages of egg laying: (I) clutches containing five eggs (typically these clutches were complete), which is the modal clutch size of great reed warblers in the study area (Moskát et al. 2008a), and (II) clutches containing three eggs (typically representing the middle of the laying process). We carried out experiments on the days when the fifth or third egg was laid, depending on category (see below). This way, we could investigate the impact of clutch size on post-ejection nest-desertion.

Hosts desert their nests if only one host egg remains in a clutch as a response to partial clutch reduction (Rothstein (1982; Davies and Brooke 1988). Kosciuch et al. (2006) studied nest desertion in the Bell's vireo (*Vireo bellii*), which is the host of the brown-headed cowbird. They showed that cowbird eggs caused nest desertion when number of vireo eggs were reduced from 4 to 2 or less. However, if the original vireo's eggs were put back into nest on the morning after exchanging two host eggs with two cowbird eggs, hosts did not desert their nests. Similarly, we also applied a treatment when we replaced the hosts' original eggs but just after the ejection of the parasitic eggs. We expected that hosts might detect their complete clutches again, and not desert. Additionally, we also monitored control clutches with no treatments, which were checked with the same frequency as experimental nests. We only used nests for our results that were not depredated, parasitized naturally by cuckoos, or destroyed by storms.

For the three treatments (ii), (iv) and (v) (see Table 1), we used a non-mimetic egg, which is expected to be ejected in a high rate: We painted two great reed warbler eggs from another clutch dark brown for simulating non-mimetic foreign parasitic eggs (overlapping spots with a diameter between 4 and 5 mm, covering the eggshell for at least 98%). For all painting experiments, we used M-size dark brown waterproof fiber pens (Faber-Castel OHP-Plus permanent, size code: 1525; colour code: 78). This dark brown paint is similar to that of great reed warblers' most common spot type (Moskát et al. 2008b), so our experimental eggs resembled unusually highly pigmented eggs. Although highly overspotted or plain dark brown host or cuckoo eggs are not found in nature, this egg type was

frequently used as standard reference in previous studies on great reed warblers and closely related species (e.g., Lotem et al. 1995; Hauber et al. 2006; Dyrzcz and Halupka 2007; Moskát et al. 2008b). For this treatment (treatment (ii)), and the treatments (iv) and (v) below, we used conspecific eggs of the great reed warbler, which seem to be suitable for experimental parasitism due to their similar size as the cuckoo eggs (Hargitai et al. 2010). Great reed warbler eggs also proved to be superior for experimental parasitism than model cuckoo eggs, as a previous study revealed that using plastic eggs caused extra costs for the hosts when they ejected these eggs; the birds had to make a hole in the plastic eggs in order to eject them (Honza and Moskát 2008).

The modal clutch size in this great reed warbler population is five (Moskát et al. 2008a), as it was also observed in the present study (mean clutch size of our unmanipulated, control nests was 4.89; SE=0.169; $n=19$), so we started some of our experiments when the clutch was completed with five eggs, but we also used clutches with three eggs, representing an intermediate state in the laying process. We applied six different treatments, including controls (see details in Table 1).

We checked nests' contents twice a day, once in the morning (ca. 8–11 h Central European Time) and once in the afternoon (ca. 16–19 h CET) for all treatments (including the control group). We checked nests for six consecutive days if no response was observed on days 1–6, or until the nest was deserted (cold eggs) and no rotation of the eggs was detected in 3 days (we oriented the sharp poles of the eggs towards each other in the center of the nests and checked for changes in this configuration). If the

Table 1 Hosts' responses to experimental treatments: (i) “clutch reduction from five to three eggs”; (ii) “swapping at clutch size=5”, i.e., swapping two host eggs with two parasitic eggs; (iii) clutch reduction (three to one egg); (iv) “swapping at clutch size=3”, i.e.,

swapping two host eggs with two parasitic eggs; (v) “swapping and restoration at clutch size=3”, i.e., swapping two host eggs with two parasitic eggs, and just after the ejection of the parasitic eggs, hosts' original eggs were set back into the nest; (vi) controls

Treatments					Hosts' responses				<i>n</i>
Code	No. of host eggs at exp.	Reduction (no. of host eggs)	No. of parasitic eggs ^a added	Renew (no. of original eggs placing back) ^b	Acceptance%	Desertion%	Ejection%	Post-ejection-nest desertion % of ejections	
(i)	5	2	–	–	100	0	n.a.	n.a.	12
(ii)	5	2	2	–	0	0	100	17	12
(iii)	3	2	–	–	58	42	n.a.	n.a.	12
(iv)	3	2	2	–	33	0	67	40	15
(v)	3	2	2	2	27	0	73	25	11
(vi)	3–5	–	–	–	100	0	n.a.	n.a.	19

Acceptance no reaction toward the clutch, females incubates it, irrespectively if it was parasitized or not, *Ejection* ejection of the parasitic eggs, i. e., the two dark brown conspecific eggs per clutch used for experimental parasitism (in all cases of ejections, hosts ejected both of these parasitic eggs from a clutch), *Desertion* desertion of a clutch, irrespectively if it was parasitized or not, *Post-ejection nest-desertion* desertion of a clutch following the successful ejection of the parasitic eggs, *n* sample size, *n.a.* not applicable

^a Two conspecific eggs painted brown (overspotted with dark brown spots, covering at least 98% of the eggshell surface)

^b Only if the parasitic eggs were ejected

parasitic eggs were ejected in treatments (ii), (iv), and (v), we also checked these nests after ejection for 6 days or until nest desertion. Video records revealed that in great reed warblers, females were typically responsible for nest checking and egg-rejection behavior (Pozgayová et al. 2009), so hosts' reactions are mainly attributable to females in this species.

Statistical analyses

We constructed a set of multinomial logistic regression models in SPSS v. 17 (SPSS Inc.) to evaluate which parameters affect nest desertion, based on data from categories (i), (ii), (iii), and (iv). In the full model, we included “nest desertion” as the binary dependent variable, “laying date”, and “clutch size at experiment” (just before manipulation) as covariates, and the “usage of parasitic eggs” as a fixed factor. No interaction was revealed among the variables. Laying date was included in the full model, as Lotem et al. (1992) revealed age-dependent structure of laying in the oriental reed warbler (*Acrocephalus orientalis*, previously considered as a subspecies of the great reed warbler). We defined laying date as the laying of the first egg in a clutch, where laying date of the earliest clutch was defined as 1. “Clutch size at experiment” showed if the experiment was started on a clutch with five or three host eggs. In two cases, we started the experiments with six eggs, instead of five, 1 day later than normal. These nests were found with five fresh eggs, and an increment in number of eggs on the next day justified their usable state for experiment. We treated each experiment as an independent data point, although hosts were not color-ringed, but only a single experiment was recorded from each territory (see Moskát et al. 2009 for justification), thereby limiting the possibility of pseudoreplication. The “usage of parasitic eggs” shows if a clutch was experimentally parasitized by two conspecific eggs painted dark brown (see above) or not. Model selection was based on weighted Akaike information criteria (Burnham and Anderson 2002; Anderson 2008), corrected for small sample bias.

Results

Altogether, 62 experiments and 19 controls proved to be successful, i.e., not depredated or parasitized by cuckoos and not destroyed by harsh weather (Table 1). No nest desertion was observed in the control group of nests, indicating that no important effects contributed to nest desertions in unmanipulated nests. Our results revealed that hosts did not desert their clutches when clutch size was reduced from 5 to 3 (0/12; treatment (i)), and only 2 desertions were observed just after the ejection of the

brown parasitic eggs (2/12; treatment (ii)). However, in both deserted nests we observed some yolk on the eggs, suggesting that hosts broke an egg when they ejected the brown eggs, and consequently, they deserted the clutch with yolk on the eggshells resulting in eggs “glued” together. No other egg breakage was observed in the other treatments and controls. Comparing the outcomes of these experiments using a clutch size of 5, the experiments using clutch size of 3 showed that both desertion rate (5/12; treatment (iii)), and post-ejection nest-desertions (4/10; treatment (iv)) increased considerably (Fig. 1). We found a significant difference when we compared the ratio of nest desertions and acceptances (combined with corresponding values for post-ejection nest-desertions) in the 5- and 3-egg categories (2/22 for treatments (i) and (ii), and 9/18 for treatments (iii) and (iv) in Table 1) (Fisher's exact test, two-tailed, $P=0.042$). The variant of the swapping (treatment (v)) experiment gave a similar result, i.e., 2/8 post-ejection nest-desertions, to treatment (iv) (acceptances vs. rejections: Fisher's exact test, two-tailed, $P<1.000$; post-ejection nest-desertions vs. no desertion following ejections: Fisher's exact test, two-tailed, $P=0.638$). No clutch was deserted in the control group of nests within the 6-day monitoring period.

In both treatments (ii) and (iv), hosts ejected non-mimetic parasitic eggs, but number of eggs differed when experiments started (5 vs. 3, respectively). Number of host eggs remained in nests just after a quick ejection of the parasitic eggs also differed (3 vs. 1, in categories (ii) and (iv), respectively). Interestingly, ejections and post-ejection

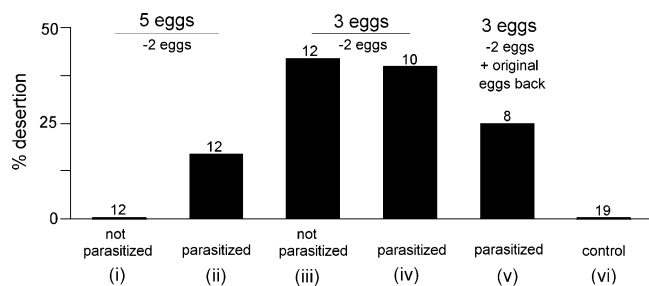


Fig. 1 Post-ejection nest-desertions of hosts in treatments where parasitic eggs were present (treatments (ii), (iv), and (v)) and nest desertions of hosts where parasitic eggs were not present (treatments (i), (iii), and (vi)). Treatments: (i) “clutch reduction from five to three eggs”; (ii) “swapping at clutch size=5”, i.e., swapping two host eggs with two parasitic eggs; (iii) “clutch reduction from three to one egg”; (iv) “swapping at clutch size=3”, i.e., swapping two host eggs with two parasitic, conspecific eggs (painted dark brown); (v) “swapping and restoration at clutch size=3”, i.e., swapping two host eggs with two parasitic eggs, and just after the ejection of the brown eggs, hosts' original eggs were set back into the nest; (vi) controls (see also Table 1). n denotes sample size (note that sample sizes slightly differ in some of the categories from that of in Table 1, because cases of acceptances are presented in Table 1 (five and three in treatments (iv) and (v), respectively), but these are excluded from this figure, where post-ejection nest-desertions are evaluated)

nest-desertions differed in these categories (Fisher's exact test, $P=0.029$), which reflects to the importance of ejections in relation to reduced egg numbers. The comparison of the effects of treatments (iii) and (iv) is also informative as both treatments left birds with one host egg in nest, but only (iv) involved ejection of non-mimetic eggs (acceptances vs. desertions (iii) or post-ejection nest-desertions (iv); Fisher's exact test, $P=0.448$), which shows no importance whether the nest was parasitized or not.

In treatments (iii) and (iv), when we manipulated clutches at that time when they had three eggs, hosts had the chance to continue their egg laying, as typical clutch size of great reed warblers is 5 (4–6) in our study area (Moskát et al. 2008a). In treatment (iii), in 67% of nests, we found one or more new eggs on the next days (one new egg in one nest, two new eggs in six nests, and three new eggs in one nest). All except one of these nests showed acceptance for the manipulated clutch, but the one nest with one new egg was deserted. Of all the other nests, where hosts deserted their clutches, the hosts made their decision quickly and deserted their nests within 1 day. The two sets of nests in category (iii), where hosts continued laying or did not, showed significant difference in host responses (acceptance or desertion) (Fisher's exact test, two-tailed, $P=0.010$). For category (iv), we found a very similar result: all birds that deserted the nest did so within a day and did not lay any new egg into their clutch ($n=4$), while those which continued laying until four ($n=2$) or five ($n=6$) eggs, accepted their reduced clutch (Fisher's exact test, two-tailed, $P=0.005$).

The multinomial logistic regression model, which included all of our variables (model 4; Table 2), revealed that “clutch size at experiment” had a significant effect on nest desertions (Table 2). All other models revealed the

Table 2 Parameter estimates in logistic regression models exploring the effect of “laying date” (LD), “clutch size at experiment” (CE), and “using brown eggs” (BE) on “nest desertion” of great reed warblers

Model	Parameter	<i>B</i>	S.E.	Wald	<i>df</i>	<i>P</i>
1	Intercept	2.62	1.51	2.98	1	0.084
	CE	-0.99	0.42	5.64	1	0.018
2	Intercept	2.95	1.62	3.32	1	0.068
	CE	-1.01	0.42	5.75	1	0.017
	BE	-0.50	0.76	0.44	1	0.507
3	Intercept	5.80	2.45	5.60	1	0.018
	CE	-1.43	0.51	7.93	1	0.005
	LD	-0.17	0.10	2.80	1	0.095
4	Intercept	6.75	2.78	5.89	1	0.015
	CE	-1.53	0.54	8.09	1	0.004
	BE	-0.80	0.84	0.91	1	0.341
	LD	-0.19	0.11	3.06	1	0.080

same effect of this variable (Table 2), regardless of whether the other covariates and the factor were included or not. All of the other parameters had non-significant effects in all of the models (Table 2). The full model (model 4) and model 3 showed the worst parameters of model evaluation (Table 3). The smallest Akaike information criterion was revealed for the model when only the covariate “clutch size at experiment” was included for independent variables (model 1; Table 2), and the corresponding Akaike weight indicated that the likelihood that this model was the best ($w_1=0.97$). Model probability was much smaller for model 2 (0.03), so only model 1 was acceptable. This clearly led to our conclusion that post-ejection nest-desertion was mainly affected by the clutch size at experiment.

Discussion

Our results clearly supported the hypothesis that post-ejection nest-desertion was due to reduced clutch size and not related to brood parasitism. We found nest desertions when experiments resulted in one egg, but no desertions were found when clutch size was reduced to three eggs. This behavior could be explained by the higher future benefits to be obtained from clutches with higher number of eggs. Hosts' desertion rate might decrease when the hosts may gain higher prospective benefits from a larger clutch (for example, when three eggs remained in the clutch instead of one egg, the value of the clutch is higher). Similarly, reduced desertion rates in hosts of brood parasites were found at the end of the breeding season (Alvarez 1999). Although we did not find this effect in our study (our research was not conducted at the end of the season, when some birds have their second brood season), it has never manifested in any previous study on cuckoo parasitism in our study area (e.g., Moskát and Honza

Table 3 Logistic regression models exploring the effect of “laying date” (LD), “clutch size at experiment” (CE), and “using brown eggs” (BE) on “nest desertion” of great reed warblers

Models	<i>k</i>	AIC _{C,i}	Δ_i	w_i
1 CE	2	10.41	0	0.97
2 CE+BE	3	17.27	6.86	0.03
3 CE+LD	3	31.07	20.66	3.17e-5
4 CE+BE+LD	4	42.11	31.70	1.27e-7

Models are ranked from the best to the worst based on Akaike information criteria (corrected for small sample bias) (k =number of parameters, including all independent and the dependent variables, AIC_C=Akaike information criteria, corrected for small sample bias, $\Delta_i=AIC_{C,i}-AIC_{C,\min}$, w_i =Akaike weight, which is the likelihood that the single model with the lowest AIC_C value is the best exploratory model)

2002). Another study on great reed warblers at the same location revealed that hosts rejected less parasitic eggs when the chance of rejection costs or errors was higher, i.e., when clutch size was larger (Moskát and Hauber 2007). In our present study, we found the opposite pattern (12/12 ejections when clutch size was 5 in treatment (ii) and 10/15 when clutch size was 3 in treatment (iv)). We explain this difference on cognitive backgrounds. Great reed warblers use both discordancy and template recognition for foreign egg discrimination (Moskát et al. 2010). Hosts ejected less parasitic eggs in treatment (iv) when the clutch contained one own egg and two parasitic eggs than in treatment (ii) when the clutch contained three own eggs and two parasitic eggs. If the parasitic eggs are in the majority of the clutch, this may reduce the effectiveness of egg recognition by discordancy.

Interestingly, in treatment (iv), hosts did not desert any clutch when they contained the parasitic eggs, but we observed desertions just after the parasitic eggs were ejected, as we call this post-ejection nest-desertion. As in category (iii) (one host egg), we found 42% desertions, and in category (iv) (one host+two parasitic eggs) 0% desertions, but 40% post-ejection nest-desertions. This points out that great reed warblers are not able to assess the value of the clutch and make decision on staying with the nest or desert until they have ejected the parasitic eggs. These results also suggest that clutch reduction may induce nest desertion.

In one of our treatments (v), we tried to eliminate clutch size effect by introducing hosts' original eggs just after they rejected the two parasitic eggs. It had no effect on hosts' rejection rates when compared either with treatments (ii) or (iv). In this way, we could not eliminate clutch size effect although we checked nests twice a day. This result suggests that great reed warblers could have recognized the parasitic eggs quickly. Some of the hosts may recognize the foreign egg almost at once (Honza et al. 2005), and a study on great reed warblers in the Czech Republic revealed that in the first 90 min after experimental parasitism with non-mimetic eggs, females pecked the parasitic eggs about ten times, indicating a quick recognition of the foreign eggs (Pozgayová et al. 2009). Based on this, we assume that we probably replaced the original eggs too late, so the hosts had already made their decisions to desert the nests.

Rothstein (1982, 1986) revealed in cowbird parasitism that hosts responded by nest desertion to partial clutch reduction. The possible reason is that hosts had more time for the adaptation to partial clutch reduction, which is an ancient selection pressure, than to cowbird parasitism, which should have evolved later.

Our study suggests that nest desertion by great reed warbler hosts, following the successful ejection of the parasitic egg, can be explained by clutch reduction. The

same phenomenon was revealed in experiments when the clutch size of great reed warblers was reduced. However, sensitivity of hosts to clutch size reduction was higher when clutches were reduced from three to one eggs than from five to three eggs, and post-ejection nest-desertion was also higher when hosts ejected two parasitic eggs from smaller (incomplete) clutches than from larger (complete) clutches. We also revealed that hosts, those that continued laying after the number of eggs was reduced from three to one, did not desert. Our results are in concordance with Rothstein's logically different experiments on cowbird hosts (e.g., Rothstein 1982), which suggested the importance of partial clutch reduction.

When can we expect post-ejection nest-desertion in natural or experimental brood parasitism? (1) The ejection of one parasitic egg which reduces clutch size with one egg rarely induces nest desertion, except when it happens at the beginning of laying when the number of eggs have not reached the typical clutch size. (2) The chance for post-ejection nest-desertion is expected to be higher in multiply parasitized nests, when more than one parasite eggs are ejected. (3) When a host successfully ejects a foreign egg and mistakenly eject one or more of its own eggs ("ejection cost", c.f. Davies and Brooke 1988; Stokke et al. 2002), this may also induce post-ejection nest-desertion. The ejection cost was higher when smaller *Acrocephalus* hosts, e.g., marsh warblers (*Acrocephalus palustris*), ejected the cuckoo eggs than in the larger great reed warbler (Antonov et al. 2006). The shells of the cuckoo eggs are thicker and harder than that of the *Acrocephalus* hosts (Honza et al. 2001; Hargitai et al. 2010). Hosts having small bills are forced to puncture parasitic eggs before removing them, but larger-billed hosts, like the great reed warbler, are able to grasp it (Moksnes et al. 1991), or the larger and stronger bill probably let them puncture the cuckoo eggs easily. In the latter, species ejection costs were reported when clutches were larger (Moskát and Hauber 2007). So these three forms of parasite egg ejections cause severe clutch size reduction, which may lead to nest desertion just after the successful ejection of the parasite egg(s). We can conclude that the type of partial clutch reduction seems to be not important in the mechanism of post-ejection nest-desertion.

Acknowledgments The study was supported by the Office of Academy-supported Research Groups Affiliated with Universities and Other Institutions of the Hungarian Academy of Sciences (to C. M.) and by the Groningen University Grant (to E.R. and M.B.). Timea Protovin, Michael G. Anderson, and István Zsoldos kindly helped in the fieldwork. We thank Hannah Dugdale (Groningen University, Netherlands/Sheffield University, UK) for her valuable comments on the manuscript. The Middle-Danube-Valley Inspectorate for Environmental Protection, Nature Conservation and Water Management provided permission for research.

References

- Alvarez F (1994) A gens of cuckoo *Cuculus canorus* parasitizing rufous bush chat *Cercotrichas galactotes*. *J Avian Biol* 25:239–243
- Alvarez F (1999) Attractive non-mimetic stimuli in cuckoo *Cuculus canorus* eggs. *Ibis* 141:142–144
- Anderson DR (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York
- Antonov A, Stokke BG, Moksnes A, Kleven O, Honza M, Røskaft E (2006) Eggshell strength of an obligate brood parasite: a test of the puncture resistance hypothesis. *Behav Ecol Sociobiol* 60:11–18
- Antonov A, Stokke BG, Moksnes A, Røskaft E (2007) First evidence of regular common cuckoo, *Cuculus canorus*, parasitism on eastern olivaceous warblers, *Hippolais icterina elaeica*. *Naturwiss* 94:307–312
- Antonov A, Stokke BG, Moksnes A, Røskaft E (2008) Does the cuckoo benefit from laying unusually strong eggs? *Anim Behav* 76:1893–1900
- Bártol I, Karcza Z, Moskát C, Røskaft E, Kisbenedek T (2002) Responses of great reed warblers *Acrocephalus arundinaceus* to experimental brood parasitism: the effects of a cuckoo *Cuculus canorus* dummy and egg mimicry. *J Avian Biol* 33:420–425
- Brooke M de L, Davies NB (1988) Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 35:630–632
- Burnham KP, Anderson DR (2002) Model selection and multimodal inference. A practical information-theoretic approach. Springer, New York
- Davies NB (2000) Cuckoos, cowbirds and other cheats. T. & A.D. Poyser, London
- Davies NB, Brooke M de L (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. *Anim Behav* 36:262–284
- Dawkins NB, Krebs JR (1979) Arms races between and within species. *Proc R Soc Lond B* 205:489–511
- Dyrz A, Halupka K (2007) Why does the frequency of nest parasitism by the cuckoo differ considerably between two populations of warblers living in the same habitat? *Ethology* 113:200–213
- Guigueno MF, Sealy SG (2009) Nest sanitation plays a role in egg burial by yellow warblers. *Ethology* 115:247–256
- Hansson B, Bensch S, Hasselquist D (1997) Infanticide in great reed warblers: secondary females destroy eggs of primary females. *Anim Behav* 54:297–304
- Hargitai R, Moskát C, Bán M, Gil D, López-Rull I, Solymos E (2010) Eggshell characteristics and yolk composition in the common cuckoo *Cuculus canorus*: are they adapted to brood parasitism? *J Avian Biol* 41:177–185
- Hauber ME, Sherman PW (2001) Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends Neurosci* 24:609–616
- Hauber ME, Moskát C, Bán M (2006) Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. *Biol Lett* 2:177–180
- Higuchi H (1998) Host use and egg color of Japanese cuckoos. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts. Studies in coevolution. Oxford University Press, New York, pp 80–93
- Hill DE, Sealy SG (1994) Desertions of nests parasitized by cowbirds: have clay-coloured sparrows evolved an anti-parasite defence? *Anim Behav* 48:1063–1070
- Honza M, Moskát C (2005) Antiparasite behaviour in response to experimental brood parasitism in the great reed warbler: a comparison of single and multiple parasitism. *Ann Zool Fenn* 42:627–633
- Honza M, Moskát C (2008) Egg rejection behaviour in the great reed warbler (*Acrocephalus arundinaceus*): the effect of egg type. *J Ethol* 26:389–395
- Honza M, Picman J, Grim T, Novák V, Capek MJr, Mrlik V (2001) How to hatch from an egg of great structural strength. A study of the common cuckoo. *J Avian Biol* 32:249–255
- Honza M, Procházka P, Stokke BG, Moksnes A, Røskaft E, Capek MJr, Mrlik V (2004) Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *J Ethol* 22:175–180
- Honza M, Kuiper SM, Cherry MI (2005) Behaviour of African turdid hosts towards experimental parasitism with artificial red-chested cuckoo *Cuculus solitarius* eggs. *J Avian Biol* 36:517–522
- Hosoi SA, Rothstein SI (2000) Nest desertion and cowbird parasitism: evidence for evolved responses and evolutionary lag. *Anim Behav* 59:823–840
- Kemal RE, Rothstein SI (1988) Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. *Anim Behav* 36:175–183
- Kilner RM (2006) The evolution of egg colour and patterning in birds. *Biol Rev* 81:383–406
- Kosciuch KL, Parker TH, Sandercock BK (2006) Nest desertion by a cowbird host: an antiparasite behavior or a response to egg loss? *Behav Ecol* 17:917–924
- Krüger O (2007) Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Phil Trans R Soc B* 362:1873–1886
- Lahti DC, Lahti AR (2002) How precise is egg discrimination in weaverbirds? *Anim Behav* 63:1135–1142
- Lee J-W, Yoo J-C (2004) Effect of host egg color dimorphism on interactions between the vinous-throated parrotbill (*Paradoxornis webbianus*) and common cuckoo (*Cuculus canorus*). *Korean J Biol Sci* 8:77–80
- Lotem A, Nakamura H, Zahavi A (1992) Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. *Behav Ecol* 3:128–132
- Lotem A, Nakamura H, Zahavi A (1995) Constraints on egg discrimination and cuckoo-host co-evolution. *Anim Behav* 49:1185–1209
- Lovászi P, Moskát C (2004) Break-down of arms race between the red-backed shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). *Behaviour* 141:245–262
- Moksnes A, Røskaft E (1995) Egg-morph and host preferences in the common cuckoo (*Cuculus canorus*): an analysis of cuckoo and host eggs from European museum collections. *J Zool Lond* 236:625–648
- Moksnes A, Røskaft E, Braa AT, Korsnes L, Lampe H, Pedersen HC (1991) Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* 116:64–89
- Moksnes A, Røskaft E, Korsnes L (1993) Rejection of cuckoo (*Cuculus canorus*) eggs by meadow pipits (*Anthus pratensis*). *Behav Ecol* 4:120–127
- Moskát C, Honza M (2002) European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus arundinaceus* population. *Ibis* 144:614–622
- Moskát C, Hauber ME (2007) Conflict between egg recognition and rejection decisions in common cuckoo (*Cuculus canorus*) hosts. *Anim Cogn* 10:377–386
- Moskát C, Székely T, Kisbenedek T, Karcza Z, Bártol I (2003) The importance of nest cleaning in egg rejection behaviour of great reed warblers *Acrocephalus arundinaceus*. *J Avian Biol* 34:16–19
- Moskát C, Hansson B, Barabás L, Bártol I, Karcza Z (2008a) Common cuckoo *Cuculus canorus* parasitism, antiparasite defence and gene flow in closely located populations of great

- reed warblers *Acrocephalus arundinaceus*. *J Avian Biol* 39:663–671
- Moskát C, Székely T, Cuthill IC, Kisbenedek T (2008b) Hosts' responses to parasitic eggs: which cues elicit hosts' egg discrimination? *Ethology* 114:186–194
- Moskát C, Hauber ME, Avilés JM, Bán M, Hargitai R, Honza M (2009) Increased host tolerance of multiple cuckoo eggs leads to higher fledging success of the brood parasite. *Anim Behav* 77:1281–1290
- Moskát C, Bán M, Székely T, Komdeur J, Lucassen RWG, van Boheemen LA, Hauber ME (2010) Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. *J Exp Biol* 213:1976–1983
- Ortega CP, Cruz A (1988) Mechanisms of egg acceptance by marsh-dwelling blackbirds. *Condor* 90:349–358
- Payne R (2005) Cuckoos, Cuculidae. Oxford University Press, Oxford
- Pianka ER (1976) Natural selection of optimal reproductive tactics. *Am Zool* 16:775–784
- Pozgayová M, Procházka P, Honza M (2009) Sex-specific defence behaviour against brood parasitism in a host with female-only incubation. *Behav Process* 81:34–38
- Rothstein SI (1974) Mechanisms of avian egg recognition: possible learned and innate factors. *Auk* 91:796–807
- Rothstein SI (1975) An experimental and teleonomic investigation of avian brood parasitism. *Condor* 77:250–271
- Rothstein SI (1982) Success and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *Amer Zool* 22:547–560
- Rothstein SI (1986) A test of optimality: egg recognition in the eastern phoebe. *Anim Behav* 34:1109–1119
- Rothstein SI, Robinson SK (1998) The evolution and ecology of brood parasitism. In: Rothstein SI, Robinson SK (eds) Parasitic birds and their hosts: studies in coevolution. Oxford University Press, New York, pp 3–56
- Sargent RC, Gross MR (1985) Parental investment decision rules and the Concorde fallacy. *Behav Ecol Sociobiol* 17:43–45
- Servedio M, Hauber ME (2006) To eject or to abandon? Life history traits of hosts and parasites interact to influence the fitness payoffs of alternative anti-parasite strategies. *J Evol Biol* 19:1585–1594
- Stokke BG, Honza M, Moksnes A, Røskoft E, Rudolfsen G (2002) Costs associated with recognition and rejection of parasitic eggs in two European passerines. *Behaviour* 139:629–644
- Stokke BG, Rudolfsen G, Moksnes A, Røskoft E (2004) Rejection of conspecific eggs in chaffinches: the effect of age and clutch characteristics. *Ethology* 110:459–470
- Strausberger BM, Burhans DE (2001) Nest desertion by field sparrows and its possible influence on the evolution of cowbird behavior. *Auk* 118:770–776
- Svenningsen TO, Hølen OH (2010) Avian brood parasitism: information use and variation in egg-rejection behaviour. *Evolution* 64:1459–1469
- Székely T, Webb JN, Houston AI, McNamara JM (1996) An evolutionary approach to offspring desertion in birds. *Curr Ornithol* 13:271–330
- Takasu F (1998) Modelling the arms race in avian brood parasitism. *Evol Ecol* 12:969–987
- Takasu F, Moskát C, Muñoz AR, Imanishi S, Nakamura H (2009) Adaptations in the common cuckoo (*Cuculus canorus*) to host eggs in a multiple-hosts system of brood parasitism. *Biol J Linn Soc* 98:291–300
- Trnka A, Prokop P, Batáry P (2010) Infanticide or interference: does the great reed warbler selectively destroy eggs? *Ann Zool Fennici* 47:272–277
- Underwood TJ, Sealy SG (2006) Influence of shape on egg discrimination in American robins and gray catbirds. *Ethology* 112:164–173
- Valera F, Hoi H, Schleicher B (1997) Egg burial in Penduline Tits *Remiz pendulinus*: its role in nest desertion and female polyandry. *Behav Ecol* 8:20–27
- van Dijk RE, Szentirmai I, Komdeur J, Székely T (2007) Sexual conflict over parental care in Penduline Tits *Remiz pendulinus*: the process of clutch desertion. *Ibis* 149:530–534
- Winkler DW (1991) Parental investment decision rules in tree swallows: parental defense, abandonment, and the so-called Concorde Fallacy. *Behav Ecol* 2:133–142
- Wyllie I (1981) The cuckoo. Batsford, London