

Nest defence and egg rejection in great reed warblers over the breeding cycle: are they synchronised with the risk of brood parasitism?

Csaba Moskát

Animal Ecology Research Group of the Hungarian Academy of Sciences, c/o Hungarian Natural History Museum, Ludovika ter 2, H-1088 Budapest, Hungary (e-mail: moskat@nhmus.hu)

Received 10 May 2005, revised version received 12 Aug. 2005, accepted 12 Aug. 2005

Moskát, C. 2005: Nest defence and egg rejection in great reed warblers over the breeding cycle: are they synchronised with the risk of brood parasitism? — *Ann. Zool. Fennici* 42: 579–586.

In avian host–brood parasite co-evolution, hosts develop antiparasite defence mechanisms against the brood parasite. Great reed warblers (*Acrocephalus arundinaceus*) exhibit intensive nest defence against common cuckoos (*Cuculus canorus*) and moderate egg rejection. Rejection of model cuckoo eggs is about two times greater than real eggs. Great reed warblers attacked a mounted cuckoo at nests in similarly high frequencies over the breeding cycle (86%–93%), but rejection rates of non-mimetic model cuckoo eggs increased from laying until early incubation from 69% to 92%, then decreased to 44% in late incubation. Temporal changes in the risk of parasitism were followed by the changes in egg rejection suggesting that egg rejection behaviour is primarily a risk-sensitive adaptation to brood parasitism, although hosts were not able to switch off egg rejection totally in the risk-free periods. In contrast, nest defence seems to be the compound effect of antiparasite defence and predator avoidance.

Introduction

The common cuckoo (*Cuculus canorus*; hereafter ‘cuckoo’) is a well-known avian brood parasite, exploiting passerine birds in the Palearctic (Wyllie 1981). Hosts of the cuckoo develop antiparasite defences against the brood parasite to reduce the cost of parasitism (e.g. Davies & Brooke 1988, 1989, Moksnes *et al.* 1990). They might recognise this brood parasite as a distinctive enemy (Duckworth 1991, but *see* Honza *et al.* 2004a). Nest defence against cuckoos in 53 potential cuckoo hosts in Europe was higher in sympatry than allopatry with the cuckoo (Røskaft *et al.* 2002). If nest defence is not successful,

hosts may have a second opportunity to reduce the consequences of brood parasitism by rejecting the parasitic eggs from nests (e.g. Davies & Brooke 1988, 1989, Moksnes *et al.* 1990). Nest defence and egg rejection in cuckoo hosts was highly correlated, representing the same level in the coevolutionary arms race (Moksnes *et al.* 1990). The strongest egg rejection and nest defence was found in abandoned hosts of the cuckoo, the winners of the arms race, including the red-backed shrike *Lanius collurio* (Lovász & Moskát 2004). A similar example is the black-cap *Sylvia atricapilla*, which shows high rejection rates against parasitic eggs (Honza *et al.* 2004b) and relatively high aggression against

cuckoos (Røskaft *et al.* 2002). Alternatively, in hosts of other brood parasites, nest defence and egg rejection might be antagonistic (Soler *et al.* 1999, Neudorf & Sealy 1992).

It is believed that intensity of an antiparasite defence mechanism is related to the risk of parasitism, which is high in a host's egg laying stage and absent after early incubation (Moskát & Honza 2002). For this reason changes of different antiparasite defence mechanisms in time may show similar patterns. On the other hand, cuckoos may predate host eggs (e.g. Alvarez 1994, Moksnes *et al.* 2000) or host nests with nestlings (e.g. Varga 1994, Kinoshita & Kato 1995, Kim & Yamagishi 1999), probably forcing hosts to re-nest when there is a lack of suitable nests (Gärtner 1981, Wyllie 1981). Cuckoos' predation on hosts' nests may reach a high level; in the reed warbler it was 2–4 times higher than clutch loss attributable to pure parasitism (Schulze-Hagen 1992). For this reason hosts might also regard cuckoos as nest predators, consequently aggression against cuckoos is expected to show a high level during the entire breeding cycle. Unfortunately, most studies on nest defence in cuckoo hosts is restricted to the egg laying period (but see Moksnes *et al.* 1990, Duckworth 1991, Grim 2005), and there is a paucity of information on the pattern of changes in this defence mechanism throughout breeding.

In the present study I compared two types of great reed warblers' *Acrocephalus arundinaceus* antiparasite defence mechanisms against cuckoos, i.e. nest defence and egg rejection, focusing on their changes over the breeding cycle. I measured aggression against the brood parasite at host nests by using stuffed cuckoos, while egg rejection towards parasitic eggs by using non-mimetic model cuckoo eggs. I hypothesised that (i) egg rejection by hosts developed to avoid the consequences of brood parasitism, but nest defence had a wider role, because cuckoos are also nest predators. Although I predicted similar tendencies in changes of frequencies in nest defence and egg rejection in the egg laying period, high aggression against cuckoos and no or minimal egg rejection was expected in the rest of the breeding cycle. I also hypothesised that (ii) only egg rejection changed with the risk of brood parasitism during the breeding cycle. Thus

I expected similar patterns for the intensity of the risk of parasitism and egg rejection behaviour, but different patterns for the risk of parasitism and nest defence.

Material and methods

The study was conducted in the Hungarian Great Plain, ca. 40–50 km south of Budapest, in the surroundings of Bankháza and Apaj villages (47°07'N, 19°05'E). Great reed warbler nests were found in narrow, 3–5 m wide, strips of reed-beds along both sides of small channels (for more details see Moskát & Honza 2002). Great reed warblers are parasitised by cuckoos at an unusually high rate (ca. 64%; Moskát & Honza 2002), and immigration of hosts from unparasitised or lowly parasitised areas might be necessary to maintain this highly exploited host population (Barabás *et al.* 2004). Great reed warblers showed moderate rejection ability of real cuckoo eggs in natural parasitism (ca. 33%; Moskát & Honza 2002), and more intensive rejection of model cuckoo eggs (ca. 71%–76%; Bártol *et al.* 2002, Moskát *et al.* 2002).

Presenting a mounted brood parasite or its model at the nest is a suitable method to measure aggression of hosts towards the parasite (Sealy *et al.* 1998, Røskaft *et al.* 2002, Grim 2005). I placed a stuffed cuckoo 0.5 m from the nest at the same altitude and played cuckoos' 'bubbling calls' from a tape recorder during the experiment. Three stuffed cuckoo mounts were used to avoid pseudoreplication. Results were categorised as follows: (1) aggression (attack or mobbing); (2) no aggression (looking at or no reaction). I defined mobbing as follows: the hosts were flying around the dummy or diving at it, but did not touch it. In an attack the host vigorously attacked the dummy and touched it (Moksnes *et al.* 1990). Observation time was 5 minutes, but the experiment was abruptly finished when hosts attacked the cuckoo, in order to protect the mounted cuckoo from damage. Generally, birds fiercely attacked the mounted cuckoo within 1–3 minutes after it was positioned, and emitted loud alarm calls. No case of mobbing was observed in great reed warblers, but Bártol *et al.* (2002) reported one case (2.5%) out of 40 experiments.

They reported that great reed warblers more frequently (82.5%) attacked the mounted cuckoo than the collared dove *Streptopelia decaocto* (10%), which was used as a neutral (control) species. As the study by Bártol *et al.* (2002) was carried out within the period of the present study, in the same study area and on the same species, using the same protocol, and no year effect was found in hosts' egg rejection or nest defence (*see later*), for the sake of simplicity aggression experiments with the neutral species were not repeated in the present study.

Artificial cuckoo eggs were used to parasitise nests experimentally. Nests were parasitised at the following stages: egg laying (0–1 days, 2–3 days and 4–5 days after the first egg was laid), early incubation (1–3 days after clutch completion), late incubation (2–5 days before hatching) and nestling stage (1–4 days after hatching). Artificial eggs were made of plastic (synthetic clay); their size, weight and colour were standardised to a real non-mimetic cuckoo egg (for more details *see* Moskát *et al.* 2002). In experimental parasitism I exchanged one host egg with the experimental egg in naturally unparasitised great reed warbler nests. In the nestling stage I added the experimental egg to the clutch. Experimental nests were monitored daily for six additional days after experiments, or until rejection of the parasitic egg. In the late incubation stage experiments were finished if nestlings hatched from the eggs. Each experiment might give any of three alternative results: (1) acceptance, (2) ejection, and (3) nest desertion (*see* Moskát *et al.* 2002 for more details). Each nest was used only once, either for a nest defence experiment, or for one of the egg rejection experiments.

The study was carried out between 1998 and 2004. Previous studies evaluating egg rejection ability of great reed warblers with different egg types were not able to demonstrate any year-effect for the same period and study site (e.g. Karcza *et al.* 2003, C. Moskát, T. Székely, I. C. Cuthill & T. Kisbenedek unpubl. data). There was no difference in egg rejection in incomplete (in the laying stage) or complete (in the early incubation stage) clutches at the beginning of the experiments with non-mimetic model cuckoo eggs (Moskát *et al.* 2002). Because I did not find any year effect in host reactions against experi-

mental eggs nor cuckoo mounts in the present study (Fisher's exact test: $P > 0.50$ for all cases), I combined the data collected in different years into one category.

Statistical analyses were carried out with STATISTICA 6.0 and SPSS 10.0. All statistical tests were two-tailed.

Results

Eighty-two experiments with model cuckoo eggs proved to be successful i.e. were not depredated or lost for any reason (Table 1). Great reed warblers rejected almost all model cuckoo eggs by ejection, except in the first category, i.e. when the nest was still empty or only one host egg was in the clutch (3 ejections and 9 desertions out of 12 rejections). These responses differed from those in the second category, i.e. clutches with 2–3 eggs, where only 1 desertion, but 13 ejections were observed (Fisher's exact test: $P < 0.001$). Although hosts used methods for rejection in different frequencies in the first two categories, rejection rates proved to be the same (Fisher's exact test: $P = 1.000$). Ejection cost (*sensu* Davies & Brooke 1988), i.e. when one or more host eggs were ejected mistakenly when the parasitic egg was ejected successfully, was observed in 11 cases out of the 42 ejections from the egg-laying stages to the late incubation stage. (The nestling stage was not suitable for such type of comparison.) Generally one or two host eggs, and on one occasion 4 eggs, were mistakenly ejected from a clutch together with the model cuckoo egg (Table 1). The number of ejections in different stages of nests did not correlate with the number of nests where ejection had a cost ($R_{\text{Spearman}} = 0.395$, $P = 0.511$), and similarly, no correlation was revealed between the number of rejections and the number of rejections with cost (including nest desertions; *sensu* Stokke *et al.* 2002) ($R_{\text{Spearman}} = 0.730$, $P = 0.161$). In the early incubation stage hosts ejected the parasitic eggs with the lowest number of mistakes (Table 1), however, the highest ejection rate was also found in this stage. In the first stage, 'laying 0–1', was found to hold the highest proportions of errors both in ejection and rejection (Table 1). Although the sample size was low for ejections in this category (2 ejections with cost

Table 1. Host responses to experimental brood parasitism in different nesting stages (N = number of nests where acceptance or rejection of the model cuckoo egg occurred; time of ejection is given in days). n.c. = not comparable.

	Breeding stage						Nesting stage
	0–1 egg	2–3 eggs	4–5 eggs	Early incubation	Late incubation		
Risk of parasitism ¹	high (ca. 36%)	high (ca. 30%)	high (ca. 30%)	low (ca. 4%)	no	no	
Response	5	6	6	1	5	5	
acceptance	12 (71%)	14 (70%)	11 (65%)	11 (92%)	4 (44%)	2 (29%)	
rejection							
Method of rejection							
ejection	3	13	11	11	4	2	
desertion	9 ²	1	0	0	0	0	
Ejected own eggs in successful ejection ³	1 + 1	2 + 1 + 1 ⁴	2 + 2 + 1	4	1	n.c.	
Ejections with cost ⁵	66.6%	23.0%	27.3%	9.1%	25.0%	n.c.	
Rejections with cost ⁶	91.7%	28.6%	27.3%	9.1%	25.0%	n.c.	
Rejection cost ⁷	0.22	0.43	0.45	0.36	0	n.c.	
Ejected own eggs in acceptance ⁸	0	0	1	0	3	n.c.	
Time of ejection (mean ± S.D.)	1.33 ± 0.58	2.07 ± 1.19	1.81 ± 1.08	2.09 ± 1.22	1.75 ± 0.96	3 ± 0	
N	17	20	17	12	9	7	

¹ calculation was based on the data from table 4 in Moskát and Honza (2002: p. 617), excluding uncertain cases and extra cases from outside the breeding cycle; $n = 141$ cuckoo eggs).

² three desertions occurred after the successful ejection of the parasitic egg.

³ number of host eggs/nest ejected mistakenly together with the parasitic egg.

⁴ the nest was deserted after the successful ejection of the parasitic egg.

⁵ percentage of nests where any host egg was missing after a successful ejection of the parasitic egg in relation to total number of ejections (*sensu* Davies & Brooke 1988).

⁶ percentage of nests where non-selective ejection (with cost) was observed and abandoned nests in relation to total number of nests (*sensu* Stokke *et al.* 2002).

⁷ the average of hosts' own eggs rejected together with 1 parasitic egg (including desertions; *sensu* Stokke *et al.* 2002).

⁸ recognition error (*sensu* Davies & Brooke 1988): number of mistakenly ejected hosts' own eggs/nest when the parasitic egg was accepted.

out of 3 ejections), hosts suffered rejection costs in 9 out of 17 nests due to the 6 nest desertions (Table 1). Recognition error, i.e. the rejection of hosts' own eggs without successful rejection of the parasitic egg (Davies & Brooke 1988) was found in only two cases (Table 1).

Hosts' responses to experimental parasitism during egg-laying, i.e. in the first three categories, proved to be highly analogous (χ^2 -test with continuity correction: $\chi^2 = 0.169$, $df = 2$, $P = 0.919$), therefore I combined the first three categories into one under the term 'laying stage' for further analyses (except for evaluation of time of rejection when a more detailed analysis was conducted). Hosts' responses to parasitism with non-mimetic cuckoo eggs showed significant differences over the whole breeding cycle when acceptances and rejections were compared in the laying, early incubation, late incubation and nestling stages (χ^2 -test with continuity correction: $\chi^2 = 9.888$, $df = 3$, $P = 0.020$). Frequency of rejections was 69% in the laying stage and increased to 92% in the early incubation stage (Fisher's exact test: $P = 0.187$). There was a significant change in hosts' responses from early incubation to late incubation as the rejection rate decreased from 92% to 44% (Fisher's exact test: $P = 0.046$). Rejection rates in late incubation and the nestling stage (29%) did not differ significantly (Fisher's exact test: $P = 0.633$). However, accidental expulsion of model eggs from nests by nestlings might also occur in the nestling stage, as nestlings on occasion reject unhatched eggs from nests (C. Moskát unpubl. data). This effect might increase rejection rate in the nestling stage.

Most ejections were observed in the 'laying 2–3', 'laying 4–5', 'early incubation' and 'late incubation' stages, where time of ejections were not significantly different (Table 1; ANOVA: $F = 0.191$, $P = 0.902$). In these categories hosts ejected the model cuckoo eggs within 1.75–2.07 days.

Great reed warblers attacked the mounted cuckoo in 86% of cases (12/14) in the egg laying stage, 93% (13/14) in the late incubation stage, and 88% (7/8) in the nestling stage. None of the differences between categories proved to be significant ($\chi^2 = 0.382$, $df = 3$, $P = 0.826$).

Rejection rates and intensity of the nest defence in the laying, late incubation and nes-

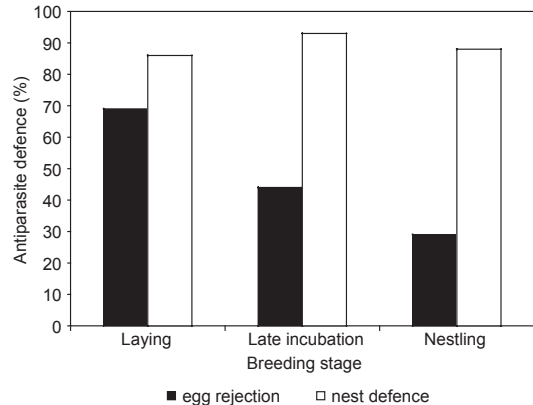


Fig. 1. Changes of rejection rate and nest defence over the breeding cycle in the great reed warbler. Rejection rate (rejection/all experiments expressed as percentages) was measured by using non-mimetic model cuckoo eggs and nest defence measured as aggression against stuffed cuckoo (aggression/all trials expressed as percentages).

tlng stages are presented in Fig. 1. These two types of antiparasite defence showed high similarity in the laying stage (Fisher's exact test: $P = 0.319$), but rejection rate decreased in the later stages while nest defence remained the same. In the latter two categories differences between frequencies of aggression and rejection proved to be significant (Fisher's exact test: $P = 0.018$ and $P = 0.040$ in the late incubation and nestling stages, respectively).

Discussion

My study provided two key results: (i) Nest defence and egg rejection showed a different pattern during the breeding cycle, i.e. the frequency of egg rejection was more variable than the stable and robust nest defence. (ii) The pattern of changes in egg rejection related better to the risk of parasitism than to the pattern of nest defence throughout the entire breeding cycle. Hosts reduced egg rejection when the risk of parasitism disappeared. This seemingly superfluous egg rejection ability may increase efficiency of this antiparasite defence mechanism against unusually late parasitisms, and the cost in maintenance of this ability is probably low or negligible. However, I observed some cost of

rejection in almost all of the categories over the breeding cycle, indicating that maintaining the rejection behaviour by great reed warblers is not cost-free, similarly to cases of natural cuckoo parasitism (Moskát & Honza 2002). The latter study on natural cuckoo parasitism revealed a higher level of recognition errors (i.e. when the parasitic egg was accepted but one or more host eggs were ejected from nest) than the present study for non-mimetic model cuckoo eggs, suggesting that non-mimetic cuckoo eggs are easier to recognise and reject for this host species than natural cuckoo eggs. In the present study I found the highest egg rejection after clutch completion. Some rejecters do not inspect their clutches closely until they are complete and incubation begins. A similar effect was observed in the reed warbler *Acrocephalus scirpaceus* (Davies & Brooke 1989) and the red-backed shrike (Moskát & Fuisz 1999). Although there was no risk of parasitism in late incubation and in the nestling stage, I observed an intensive nest defence and a moderate egg rejection in these stages. Egg rejection seems to be unnecessary from the middle of incubation until nestlings fledge out of nests. In accordance with these findings Honza *et al.* (2002) revealed with radio-tracked cuckoos that females visited nests in any stage from 'before laying' to 'late incubation/hatching', but they only laid their eggs into nests in the egg-laying stage.

The other antiparasite defence, nest defence, seems to be different from egg rejection, because hosts presented a constantly high level of nest defence against the cuckoo over the whole breeding cycle. Duckworth (1991) revealed a tendency for reed warblers to approach the cuckoo mount placed at nests more closely once incubation had started, and there were no apparent changes between incubation and nestling stages. However, the reed warbler is not very aggressive towards the cuckoo. While in the present study great reed warblers attacked the cuckoo mount in almost all cases, reed warblers rarely attack it (Duckworth 1991, Lindholm & Thomas 2000, Røskaft *et al.* 2002).

Beside cuckoos, the main avian predator of great reed warbler nests in my study area is the magpie *Pica pica*, but locally the hooded crow *Corvus cornix* also could be important. Mag-

pies and cuckoos use somewhat similar tactics in searching for great reed warbler nests. They usually use the same trees as vantage points, sometimes flying over the reedbeds. In other areas of Hungary gulls *Larus* spp., and the marsh harrier *Circus aeruginosus* could also have an impact on great reed warbler nests (Batáry *et al.* 2004). However, great reed warblers might also destroy closely built nests of conspecifics (Hanson *et al.* 1997). I observed this phenomenon on experimentally placed great reed warbler nests (C. Moskát unpubl. data). Small mammals also can predate on eggs or nestlings of nests placed above the ground at reedbed edges. In my study area great reed warblers learn to recognise cuckoos well, because of the unusually high parasitism rate and density of the brood parasite. This could be the reason for the high level of attacks against cuckoos (86%–93%).

My results on the nest defence of great reed warblers against the cuckoo resemble the pattern of the nest defence found in the least flycatcher *Empidonax minimus*, a host of the brown-headed cowbird *Molothrus ater*. The least flycatcher responded similarly to the mount of cowbirds over the nesting cycle, suggesting that this host species may have responded to the cowbird as a predator at later nest stages (Briskie & Sealy 1989). Yellow warblers *Dendroica petechia* responded to the taxidermic mounts of brown-headed cowbirds with two unique behaviours (seet calling and nest-protection behaviour) more intensively at the laying stage than later, but responded to the avian nest predator common grackle *Quiscalus quiscula* more intensively in the nestling stage than earlier (Gill & Sealy 1996). Red-winged blackbirds *Agelaius phoeniceus*, gray catbirds *Dumetella carolinensis*, northern orioles *Icterus galbula* and cedar waxwings *Bombycilla cedorum* showed a wide range of responses against the cowbird mounts. The cedar waxwing was non-aggressive, gray catbirds and northern orioles showed a general response. Although the latter three species are all capable of rejecting the cowbird egg, the acceptor red-winged blackbird was the most aggressive to cowbird mounts in the laying stage (Neudorf & Sealy 1992).

Hosts may attack cuckoos during parasitism attempts (Wyllie 1981), and after an unsuccessful

attempt the female cuckoo may repeat her trial of parasitism, if necessary several times, increasing her chances of success (C. Moskát pers. obs.). However, aggression towards the brood parasite might be effective to avoid parasitism. Molnár (1944) reported a case when great reed warblers at their nest attacked a cuckoo so heavily that the cuckoo was drowned in water. Reed warblers were able to discriminate cuckoos from non-cuckoo predators, however, aggression was even higher towards cuckoos than non-cuckoo predators (Duckworth 1991). Birds showed a dynamic risk assessment of the risk of predation, regarding predator type, nest height and predator distance in three *Acrocephalus* warblers (Kleindorfer *et al.* 2005). Davies *et al.* (2003) reported that at the beginning of breeding male reed warblers guarded nests against conspecific intruders, but increased nest guarding in response to cuckoos in the egg laying stage. However, maintaining an intensive nest guarding is costly for a bird, because it reduces the time available for feeding (Komdeur & Kats 1999). Arcese and Smith (1988) provided surplus food for song sparrows *Melospiza melodia*, which lowered the rate of parasitism by brown-headed cowbirds, suggesting that birds had more time for nest guarding.

I conclude that results revealed different patterns for changes of nest defence and egg rejection in the great reed warbler over the breeding cycle. Results suggest that both the risk of parasitism and risk of cuckoo predation may contribute to the development of antiparasite defence in cuckoo hosts.

Acknowledgements

The study was supported by the Hungarian Scientific Research Fund (OTKA, No. T48397). The author is indebted to Tibor Kisbenedek, Zsolt Karcza, István Bártol and Miklós Bán for their help in the fieldwork. I thank Zoltán Barta for his constructive comments. I am grateful to Brandon Anthony for improving the English. The Duna-Ipoly National Park provided permission for research.

References

Arcese, P. & Smith, J. N. M. 1988: Effects of population density and supplemental food on reproduction in song sparrows. — *J. Anim. Ecol.* 57: 119–136.

- Alvarez, F. 1994: Cuckoo predation on nests of nearest neighbours of parasitised nests. — *Ardea* 82: 269–270.
- Barabás, L., Gilicze, B., Takasu, F. & Moskát, C. 2004: Survival and anti-parasite defense in a host metapopulation under heavy brood parasitism: a source-sink dynamic model. — *J. Ethol.* 22: 143–151.
- 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.
- Batáry, P., Winkler, H. & Báldi, A. 2004: Experiments with artificial nests on predation in reed habitats. — *J. Ornithol.* 145: 59–63.
- Briskie, J. V. & Sealy, S. G. 1989: Changes in nest defense against a brood parasite over the breeding cycle. — *Ethology* 82: 61–67.
- Davies, N. B. & Brooke, M. de L. 1988: Cuckoos versus reed warblers: adaptations and counteradaptations. — *Anim. Behav.* 36: 262–284.
- Davies, N. B. & Brooke, M. de L. 1989: An experimental study of co-evolution between the cuckoo *Cuculus canorus*, and its hosts. I. Host egg discrimination. — *J. Anim. Ecol.* 58: 207–224.
- Davies, N. B., Butchart, S. H. M., Burke, T. A., Chaline, N. & Stewart, I. R. K. 2003: Reed warblers guard against cuckoos and cuckoldry. — *Anim. Behav.* 65: 285–295.
- Duckworth, J. W. 1991: Responses of breeding reed warblers *Acrocephalus scirpaceus* to mounts of sparrowhawk *Accipiter nisus*, cuckoo *Cuculus canorus* and jay *Garulus glandarius*. — *Ibis* 133: 68–74.
- Gärtner, K. 1981: Das Wegnehmen von Wirtsvogeleiern durch den Kuckuck *Cuculus canorus*. — *Ornithologische Mitteilungen* 33: 115–131.
- Gill, S. A. & Sealy, S. G. 1996: Nest defence by yellow warblers: recognition of a brood parasite and an avian predator. — *Behaviour* 133: 263–282.
- Grim, T. 2005: Host recognition of brood parasites: implications for methodology in studies of enemy recognition. — *Auk* 122: 530–543.
- Hansson, B., Bensch, S. & Hasselquist, D. 1997: Infanticide in great reed warblers: secondary females destroy eggs of primary females. — *Anim. Behav.* 54: 297–304.
- Honza, M., Grim, T., Capek, M., Moksnes, A. & Røskaft, E. 2004a: Nest defence, enemy recognition and nest inspection behaviour of experimentally parasitized reed warblers *Acrocephalus scirpaceus*. — *Bird Study* 51: 256–263.
- Honza, M., Procházka, P., Stokke, B. G., Moksnes, A., Røskaft, E., Capek, M. Jr. & Mrlík, V. 2004b: Are black-caps current winners in the evolutionary struggle against the common cuckoo? — *J. Ethol.* 22: 175–180.
- Honza, M., Taborsky, B., Taborsky, M., Teuschl, Y., Vogl, W., Moksnes, A. & Røskaft, E. 2002: Behaviour of female common cuckoos, *Cuculus canorus*, in the vicinity of host nests before and during egg laying: a radio telemetry study. — *Anim. Behav.* 64: 861–868.
- Karcza, Z., Moskát, C., Cherry, M. I. & Kisbenedek, T. 2003: Experimental manipulation of intraclutch variation in the great reed warbler shows no effect on rejection of parasitic eggs. — *Ethology* 109: 15–22.

- Kim, C.-H. & Yamagishi, S. 1999: Nestling crow-tits *Paradoxornis webbiana* ejected from their nest by common cuckoo *Cuculus canorus*. — *The Raffles Bulletin of Zoology* 47: 295–297.
- Kinoshita, M. & Kato, C. 1995: Killing nestling stonechats by the common cuckoo. — *Jap. J. Ornithol.* 44: 99–100.
- Kleindorfer, S., Fessl, B. & Hoi, H. 2005: Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. — *Anim. Behav.* 69: 307–313.
- Komdeur, J. & Kats, R. K. H. 1999: Predation risk affects trade-off between nest guarding and foraging in Seychelles warblers. — *Behav. Ecol.* 6: 648–658.
- Lindholm, A. K. & Thomas, R. J. 2000: Differences between populations of reed warblers in defences against brood parasitism. — *Behaviour* 137: 25–42.
- Lovász, 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., Braa, A. T., Kornses, L., Lampe, H. M. & Pedersen, H. C. 1990: Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. — *Behaviour* 116: 64–89.
- Moksnes, A., Røskaft, E., Hagen, L. G., Honza, M., Mørk, C. & Olsen, P. H. 2000: Common cuckoo *Cuculus canorus* and host behavior at reed warbler *Acrocephalus scirpaceus* nests. — *Ibis* 142: 247–258.
- Molnár, B. 1944: The cuckoo in the Hungarian Plain. — *Aquila* 51: 100–112.
- Moskát, C. & Fuisz, T. I. 1999: Reactions of red-backed shrikes *Lanius collurio* to artificial cuckoo *Cuculus canorus* eggs. — *J. Avian Biol.* 30: 175–181.
- 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., Szentpéteri, J. & Barta, Z. 2002: Adaptations by great reed warblers to brood parasitism: a comparison of populations in sympatry and allopatry with the common cuckoo. — *Behaviour* 139: 1313–1329.
- Neudorf, D. L. & Sealy, S. G. 1992: Reactions of four passerine species to threats of predation and cowbird parasitism: enemy recognition or generalized responses? — *Behaviour* 123: 84–105.
- Røskaft, E., Moksnes, A., Stokke, B. G., Bicík, V. & Moskát, C. 2002: Aggression to dummy cuckoos by potential European cuckoo hosts. — *Behaviour* 139: 613–628.
- Schulze-Hagen, K. 1992: Parasitism and egg losses due to the cuckoo (*Cuculus canorus*) in reed and marsh warblers (*Acrocephalus scirpaceus*, *A. palustris*) in central and western Europe. — *J. Orn.* 137: 181–192.
- Sealy, S. G., Neudorf, D. I., Hobson, K. A. & Gill, S. A. 1998: Nest defense by potential hosts of the brown-headed cowbird. — In: Rotstein, S. I. & Robinson, S. K. (eds.), *Parasitic birds and their hosts: studies in coevolution*: 194–211. Oxford University Press, New York.
- Soler, J. J., Soler, M., Pérez-Contreras, T., Aragón, S. & Møller, A. P. 1999: Antagonistic antiparasite defences: nest defence and egg rejection in the magpie host of the great spotted cuckoo. — *Behav. Ecol.* 10: 707–713.
- Stokke, B. G., Honza, M., Moksnes, A., Røskaft, E. & Rudolfsen, G. 2002: Costs associated with recognition and rejection of parasitic eggs in two European passerines. — *Behaviour* 139: 629–644.
- Varga, F. 1994: *Cuckoo observations around the source of the River Zagyva*. — Salgótarján: Hungary. Published by the author.
- Wyllie, I. 1981: *The cuckoo*. — Batsford, London.