

# Antiparasite behaviour in response to experimental brood parasitism in the great reed warbler: a comparison of single and multiple parasitism

Marcel Honza<sup>1</sup> & Csaba Moskát<sup>2</sup>

<sup>1</sup> Institute of Vertebrate Biology, AS CR, Květná 8, CZ-603 65 Brno, Czech Republic (e-mail: honza@brno.cas.cz)

<sup>2</sup> Animal Ecology Research Group of the Hungarian Academy of Sciences, c/o Hungarian Natural History Museum, Ludovika ter 2, H-1083 Budapest, Hungary (e-mail: moskat@nhmus.hu)

Received 19 Aug. 2005, revised version received 1 Oct. 2005, accepted 1 Oct. 2005

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. Fennici* 42: 627–633.

Rejection of parasitic eggs is one of the most important adaptations of avian hosts against brood parasites. Multiple brood parasitism is relatively rare in hosts of the common cuckoo (*Cuculus canorus*), but naturally occurs when the rate of parasitism is high. We experimentally parasitised great reed warbler (*Acrocephalus arundinaceus*) clutches with non-mimetic and moderately mimetic model cuckoo eggs. In the case of single parasitism, each egg type was rejected at the same rate (68%–75%), but in the case of multiple parasitism, the rejection rate significantly increased to 96%. So multiple parasitism is in some way facilitating anti-parasite behaviour in the host. We suggest that when parasitism rate reaches high levels, e.g. at the beginning of the coevolutionary arms race, multiple parasitism may be an important component of the host's adaptation to brood parasitism in general.

## Introduction

Brood parasitism by the common cuckoo (*Cuculus canorus*) represents a potential cost for at least one hundred species of small passerines (Moksnes & Røskaft 1995). Traditionally, the reproductive strategies of brood parasites and their hosts have been viewed as good models for the study of coevolutionary processes (Rothstein & Robinson 1998). Coevolutionary interactions lead to the evolution of a series of adaptations and counteradaptations at both sides of host-parasite pairs leading to an evolutionary arms race (Dawkins & Krebs 1979, Davies & Brooke

1988, Rothstein 1990), with winners of the arms race exhibiting the strongest counteradaptive mechanisms (Honza *et al.* 2004, Lovász & Moskát 2004).

Several host-specific races exist in the common cuckoo, and these are called “gentes” (e.g. Jourden 1925, Chance 1940, Davies 2000). Although some common cuckoo gentes parasitise several host species (Honza *et al.* 2001), the females of each gen lay eggs of a constant type that usually resembles the coloration of the main host species' eggs (Brooke & Davies 1988, Moksnes & Røskaft 1995). On the one hand, one could expect that the different eggshell

appearances (both in base-colour and markings) in cuckoo gentes result from selection pressures arising from the continuing arms race between the parasites and their hosts. On the other hand, host species are under strong selection pressure to discriminate alien eggs from their own, and this is probably the major selection pressure that favoured the evolution of different cuckoo gentes. In general, the act of parasitism is described whereby the cuckoo female alights on the host's nest, removes one or more of the host eggs randomly (Davies & Brooke 1988, Moskát & Honza 2002), and lays one of her own eggs directly into the nest (Gärtner 1981, Wyllie 1981, Moksnes *et al.* 2000, Honza *et al.* 2002).

In the light of this scenario, some researchers have studied the reactions of the hosts towards model cuckoo eggs with different appearances (e.g. Haartman 1976, 1981, Järvinen 1984, Davies & Brooke 1989a, Brown *et al.* 1990, Moksnes *et al.* 1990, Moskát & Fuisz 1999, Bártol *et al.* 2002) or eggs with varying sizes (Alvarez 2000, Marchetti 2000). However, most of these studies examined host responses to single parasitism, where one model or conspecific egg was swapped with one host egg, or alternatively, an alien egg was simply added to the host clutch. The situation where the host clutch is multiply parasitised, i.e. at least two foreign (natural or model) eggs appear in the host nest, has been largely unexplored. The proportion of multiply parasitised nests by the common cuckoo varies across host species, between populations and geographical regions of the same host species, although overall this phenomenon is relatively rare (i.e. only 469/11 268 clutches were found to be multiple parasitised in European museums; M. Honza *et al.* unpubl. data). Nonetheless, some localised host populations exhibit frequent multiple parasitism by cuckoos (e.g. in the great reed warbler (*Acrocephalus arundinaceus*) in Hungary it was 36% between 1940 and 1942 (Molnár 1944), and also 36% in 1998 and 1999 (Moskát & Honza 2002)). In North-American brood parasitic systems (*Molothrus* spp. and their hosts), where multiple parasitism is relatively common (Linz & Bolin 1982, Orians *et al.* 1989, Hauber & Russo 2000, Hauber 2001) several experimental multiple parasitism studies have been conducted (Rothstein 1982, Ward *et al.* 1996).

Despite the great interest in cuckoo-host adaptations to brood parasitism, no studies have reported responses of hosts towards multiple parasitism. The great reed warbler is a well-known cuckoo host within its Palearctic range and parasitised nests have been found both in Europe (Molnár 1944, Moksnes *et al.* 1993, Moskát & Honza 2000, 2002) and Asia (Lotem *et al.* 1995, Higuchi 1998, Nakamura *et al.* 1998). To remedy this shortage of information on the behavioral responses of cuckoo hosts to both single and multiple parasitism, we conducted a series of experiments to explore reactions of the great reed warbler to several parasitic situations. More specifically, we studied the reaction of this species towards single and multiple parasitism. We hypothesise that multiple parasitism facilitates host-egg rejection, so we predict higher rejection rates when clutches were parasitised by two foreign eggs than in the cases when each clutch contained only one parasitic egg.

## Material and methods

### Study area

The study site was part of the irrigation and flood relief channels in the surroundings of the village Apaj (47°07'N, 19°06'E), about 50 km south of Budapest in Hungary. We searched systematically for great reed warbler nests during the breeding season between 15 May and 15 July in 1998–2001. We located the nests in vegetation consisting mostly of common reed (*Phragmites australis*), surrounding the channels in 3–5 m wide strips along both sides (for a more detailed description of the study area see Moskát & Honza 2000).

### Experimental procedures

Most nests were found during building stage or at the beginning of host egg laying. On the day when the fourth egg was laid (four eggs is median clutch size for this species — authors' unpubl. data) we replaced one of the host's eggs with one artificial egg of the two colour types (see below), resembling a real cuckoo egg. Two

colours were used randomly (colour codes were measured on the PANTONE 1995 scale): (1) “Bluish egg”: the background colour of this type was bluish (colour code: 317C). (2) “Beige egg”: the background colour was extra light sepia, similar to beige (colour code: 614C). Spots on both types of artificial eggs were painted using dark brown (code: 462C) and sepia (code 457C). In multiple parasitism experiments we followed the same procedure, except that here, two host eggs were replaced with either two artificial or two real painted host eggs. The artificial cuckoo eggs were similar in size and weight to real cuckoo eggs, were made of synthetic clay, and painted with acrylic paints. Real eggs were collected from abandoned or partially predated great reed warbler nests and painted by the same colour as artificial eggs to resemble model cuckoo eggs. As we did not find any difference in host responses in multiple parasitism towards model and painted real eggs, neither in rejection rate (Fisher exact test:  $p > 0.05$ ), nor in time of host reactions (Kolmogorov-Smirnov test:  $Z = 0.5$ ,  $p > 0.05$ ), so we combined multiple experiment results based on the two egg types. After the experimental trial, nests were monitored daily for six consecutive days, following the suggested protocol of Moksnes *et al.* (1990). If a clutch failed (i.e. was depredated or destroyed by bad weather), the nest was excluded from the experiments and the analyses.

In order to asses the quality of the mimicry of the experimental eggs, we photographed most of the clutches using a Nikon camera and either a circular flash, using Kodak 100 ASA film, or Kodak 200 ASA film without a flash. Photo-

graphs were taken in a standardised procedure: all eggs were placed on a Kodak Grey Card together with a Kodak Colour Card.

The quality of the mimicry was evaluated by four persons all of whom were unaware of the origin of the eggs that they were assessing. Slides of clutches were scaled from 1 to 5 for mimicry (1 = the best mimic and 5 = the poorest mimic, for details *see* Moksnes & Røskoft 1995). These measurements revealed that the beige colour egg had a mimicry score with the mean 3.64, S.D. = 0.68,  $n = 16$  and this evaluation, as assessed by humans, showed a high level of concordance ( $W = 0.59$ ,  $\chi^2 = 35.74$ , d.f. = 15,  $p < 0.001$ ). Bluish eggs exhibited greater mimicry with the mean 2.84, S.D. = 0.82,  $n = 25$ . Kendall’s coefficient of concordance:  $W = 0.64$ ,  $\chi^2 = 62.02$ , d.f. = 24,  $p < 0.001$ . The difference in mimicry of the two groups proved to be statistically significant ( $t = 3.12$ , d.f. = 39,  $p < 0.001$ ). Therefore, we considered “beige eggs” as poorly mimetic or non-mimetic, and “bluish eggs” as moderately mimetic.

Statistical analyses were carried out with SPSS v. 11 for MS Windows. All tests were two-tailed.

Results

Reactions towards the parasitic eggs

Hosts responses to experimental parasitism both in single and multiple parasitism are shown in Table 1. Host reactions, namely acceptances and rejections of the parasitic eggs did not show any

**Table 1.** Host responses towards parasitic eggs experimentally introduced in great reed warbler nests mimicking single and multiple parasitism ( $n$  = number of nests). (Beige and bluish reflects to the ground colour of artificial paintings on model cuckoo eggs. Both egg types were maculated with dark brown. Beige eggs mimicked poorly, but bluish eggs mimicked moderately the hosts’ eggs.)

Parasitism	Type of parasitic egg	Number of nests						Total  <i>n</i>
		Accepted		Deserted		Ejected		
		<i>n</i>	%	<i>n</i>	%	<i>n</i>	%	
Single	beige	6	31.6	0	0	13	68.4	19
	bluish	11	24.2	1	2.1	33	73.2	45
Multiple	beige and bluish	1	4	4	16	20	80	25

difference for the two egg types used in “single” parasitism experiments ( $\chi^2 = 0.08$ , d.f. = 1,  $p > 0.5$ ). When we pooled the data from the two experimental groups, the proportion of acceptances in single parasitised nests was higher (23.9%, 17/64) than in multiple parasitism (4%, 1/25) (Fisher exact test:  $p = 0.01$ ).

Most of the eggs were rejected within one day after experiments with the model cuckoo eggs started (Table 2). No difference was revealed between the two egg types in single parasitism (Kolmogorov-Smirnov test:  $Z = 0.5$ ,  $p > 0.05$ ), and between single and multiple parasitism (Kolmogorov-Smirnov test:  $Z = 0.63$ ,  $p > 0.05$ ). These results suggest that great reed warblers easily recognised and then rejected both colour variants of the experimental eggs. On one hand, multiple parasitism allows hosts to recognise brood parasitism more easily than single parasitism. On the other, hosts have to reject two alien eggs from their nests, which makes antiparasite defence more costly in multiple parasitism than in single parasitism because of higher recognition and ejection costs. Our results show that the sum of these opposite effects did not change hosts’ response time.

## Rejection costs

All painted real eggs added into the nests were ejected without any damage to the host eggs, but ejection attempts of the plastic eggs led to the occasional disappearance of the hosts’ own eggs. In single parasitised nests, in two out of 46 cases of rejection host eggs disappeared together with artificial eggs, whereas in multiply parasitised nests the proportion of such cases (5 out of 9) was significantly higher (Fisher exact test:  $p <$

0.05). Finally, only a single case of recognition error (where a host egg was missing instead of the parasitic egg(s)) took place out of 66 cases of ejection.

## Discussion

### Reactions towards parasitic egg(s)

There is general consensus that parasitic eggs tend to be rejected if they differ from host eggs, something which has been shown specifically in the great reed warbler (Bártol *et al.* 2002). The role of intraclutch variation in recognition and rejection of parasitic eggs is not so clear (Davies & Brooke 1989b). Stokke *et al.* (1999) found a negative relationship between intraclutch variation and rejection of non-mimetic artificial cuckoo eggs in the reed warbler. A positive effect of intraclutch variation on rejection rate was shown with the great reed warbler in Japan (Lotem *et al.* 1995), but experimentally increased intraclutch variation did not change the rejection rate of parasitic eggs in this host species in Hungary (Karcza *et al.* 2003). A comparison of our experimental results with those obtained on natural parasitism in the same area suggests similar rates of rejection — Moskát & Honza (2002) found that of 163 naturally parasitised nests, in 108 cases (66%) cuckoo eggs were accepted, but the acceptance rate was only 24% for moderately and poorly mimetic cuckoo eggs. In our experiments we used moderately mimetic eggs, and despite our study population suffering heavy parasitism, to our surprise a considerable proportion of parasitic eggs was accepted. These findings could be explained by migration from highly reproductive unparasitised populations to

**Table 2.** Time elapsed from experimental parasitism in great reed warbler nests until the rejection of the parasitic egg, used for experiments of single and multiple parasitism. (For more details on eggs see Table 1 and Material and methods.)

Parasitism	Type of parasitic egg	Day of rejection					Total <i>n</i>
		1	2	3	4	5	
Single	beige	5	2	3	3	0	13
	bluish	24	9	1	0	0	34
Multiple	beige and bluish	18	6	1	0	1	25

parasitised populations with low reproduction in a metapopulation structure (Moskát & Honza 2002, Barabás *et al.* 2004; *see also* Lindholm 1999). In addition, migration between unparasitised and parasitised populations delays evolution of host adaptations (Røskft *et al.* 2002, Barabás *et al.* 2004). Our results suggest that hosts were able to identify most of the model cuckoo eggs easily, therefore rejection rates were at least twice (over 68%) as high as those of real cuckoo eggs (34%; Moskát & Honza 2002). For the well-recognised model eggs hosts chose the ejection method of rejection, despite the hard shell of model cuckoo eggs.

### The evolutionary significance of multiple brood parasitism

Our results differ from a similar study on magpies (*Pica pica*), hosts of great spotted cuckoos (*Clamator glandarius*), where hosts rejected both the mimetic and non-mimetic model eggs at the same rate, regardless of whether parasitism was simulated in single or multiple experiments (Soler & Møller 1990). The recognition systems are concerned with the response of an evaluator to perceived cues and based on the dissimilarity of those cues compared with a template (Liebert & Starks 2004). This can be applied also for cuckoo-brood parasitic system. Starks *et al.* (1998) showed that discrimination thresholds become more restrictive and hosts are most likely to discriminate when more cues are present. Therefore it is natural to expect that multiple experimental parasitism on great reed warblers appears to facilitate egg recognition by hosts. This effect may play an important role in stages of the arms race when the parasitism rate is high. In new cases of parasitism, in particular, the parasitism rate may quickly rise to over 50%, but fall again later (Takasu *et al.* 1993). Another scenario might be when hosts form a metapopulation, and there is migration between parasitised and unparasitised subpopulations (Barabás *et al.* 2004). In such cases the parasitism rate might rise to over 50%, with high level of multiple parasitism, as was found in great reed warblers in Hungary (Moskát & Honza 2002).

### Rejection costs

In our experiments we recorded no rejection cost when great reed warblers rejected real experimental eggs, but in another Hungarian population about 80 km away from our study site Molnár (1944) reported recognition errors while rejecting parasitic egg in 28% of ejections. In addition, rejection costs to the hosts were relatively high in our naturally parasitised population (Moskát & Honza 2002). In the areas with poorer egg mimicry hosts make the mistake of ejecting or destroying their own eggs instead of parasite eggs more rarely (in Japan, less than 1%, Lotem *et al.* 1992). Rejection costs are normally high in good rejecter species, such as the red-backed shrike (*Lanius collurio*) (Moskát & Fuisz 1999), the blackcap (*Sylvia atricapilla*) (Honza *et al.* 2004) and the chaffinch (*Fringilla coelebs*) (Stokke *et al.* 2002), where a positive relationship exists between the degree of mimicry of parasitic eggs, and rejection costs. A possible explanation for this difference could be that natural cuckoo eggs were highly mimetic, as opposed to the experimental eggs we used in our experiments.

To summarize, our results suggest that multiple parasitism might have important evolutionary consequences. Recognition of the parasitic egg seems to be easier in multiple parasitism, which may help hosts in learning the parasitic eggs. Further research is needed to investigate how multiple parasitism may accelerate host defenses against the brood parasite.

### Acknowledgements

The study was supported by the Grant Agency of the Czech Republic (206/00/P046 and A6093203) operating to M.H. and by the Hungarian Scientific Research Fund (OTKA) No. T35015 and No. T48397 to C.M. Tibor Kisbenedek, Zsolt Karcza and István Bártol kindly helped in the fieldwork. The Duna-Ipoly National Park provided permission for research. Michael I. Cherry, Mark E. Hauber and Philip T. Starks greatly improved various versions of this manuscript.

### References

- Alvarez, F. 2000: Response to Common Cuckoo *Cuculus canorus* model egg size by a parasitized population of



- Rufous Bush Chat *Cercotrichas galactotes*. — *Ibis* 142: 683–686.
- 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., Røskft, 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, N. B. 1988: Egg mimicry by Cuckoos *Cuculus canorus* in relation to discrimination by hosts. — *Nature* 335: 630–632.
- Brown, R. J., Brown, M. N., Brooke, M. de L. & Davies, N. B. 1990: Reactions of parasitized and unparasitized populations of *Acrocephalus* warblers to model Cuckoo eggs. — *Ibis* 132: 109–111.
- Chance, E. 1940. *The truth about the cuckoo*. — Country Life, London.
- Davies, N. B. 2000: *Cuckoos, cowbirds and other cheats*. — T. & A. D. Poyser, London.
- 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. 1989a: 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. & Brooke, M. de L. 1989b: An experimental study of co-evolution between the cuckoo *Cuculus canorus*, and its hosts. II. Host-egg markings, chick discrimination and general discussion. — *J. Anim. Ecol.* 58: 225–236.
- Dawkins, R. & Krebs, J. R. 1979: Arms races between and within species. — *Proc. R. Soc. London B* 205: 489–511.
- Gärtner, K. 1981: Das Wegnehmen von Wirtsögeleirnen durch den Kuckuck (*Cuculus canorus*). — *Ornithologische Mitteilungen* 33: 115–131.
- Haartman, L. von 1976: The reaction of a regular Cuckoo host to foreign eggs. — *Ornis Fennica* 53: 96–98.
- Haartman, L. von 1981: Co-evolution of the Cuckoo *Cuculus canorus* and a regular Cuckoo host. — *Ornis Fennica* 58: 1–10.
- Hauber, M. E. 2001: Site selection and repeatability in Brown-Headed Cowbird (*Molothrus ater*) parasitism of Eastern Phoebe (*Sayornis phoebe*) nests. — *Can. J. Zool.* 79: 1518–1523.
- Hauber, M. E. & Russo, S. A. 2000: Perch proximity correlate with higher rates of cowbird parasitism of ground nesting Song Sparrows. — *Wilson Bulletin* 112: 150–153.
- Higuchi, H. 1998: Host use and egg color of Japanese Cuckoos. — In: Rothstein, S. I. & Robinson, S. K. (eds.), *Parasitic birds and their hosts: studies in coevolution*: 80–93. Oxford University Press.
- Honza, M., Moksnes, A., Røskft, E. & Stokke, B. G. 2001: How are different Common Cuckoo *Cuculus canorus* egg morphs maintained? An evaluation of different hypotheses. — *Ardea* 89: 341–352.
- Honza, M., Procházka, P., Stokke, B. G., Moksnes, A., Røskft, E., Čapek, M. Jr. & Mrfk, V. 2004: 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. & Røskft, E. 2002: Behaviour of female common cuckoos *Cuculus canorus* in the vicinity of host nests before and during laying: a radiotelemetry study. — *Anim. Behav.* 64: 861–868.
- Järvinen, A. 1984: Relationships between the Common Cuckoo *Cuculus canorus* and its host, the Redstart *Phoenicurus phoenicurus*. — *Ornis Fennica* 61: 84–88.
- Jourden, F. C. R. 1925: A study of parasitism in the cuckoo. — *Proc. Zool. Soc. London* 1925: 639–667.
- 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.
- Liebert, A. E. & Starks, P. T. 2004: The action component of recognition systems: a focus on the response. — *Ann. Zool. Fennici* 41: 747–764.
- Lindholm, A. K. 1999: Brood parasitism by the cuckoo on patchy reed warbler populations in Britain. — *J. Anim. Ecol.* 68: 293–309.
- Linz, G. M. & Bolin, S. B. 1982: Incidence of Brown-headed Cowbird parasitism on Redwinged Blackbirds. — *Willson Bulletin* 94: 93–95.
- 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 coevolution. — *Anim. Behav.* 49: 1185–1209.
- 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.
- Marchetti, K. 2000: Egg rejection in a passerine bird: size does matter. — *Anim. Behav.* 59: 877–883.
- Moksnes, A. & Røskft, E. 1995: Egg-morphs and host preference in the Common Cuckoo (*Cuculus canorus*): an analysis of Cuckoo and host eggs from European museum collections. — *J. Zool. London* 236: 625–648.
- Moksnes, A., Røskft, E., Bičík, V., Honza, M. & Øien, I. J. E. 1993: Cuckoo (*Cuculus canorus*) parasitism on (*Acrocephalus*) warblers in Southern Moravia in the Czech Republic. — *J. Ornithol.* 134: 425–434.
- Moksnes, A., Røskft, E., Braa, A. T., Korsnes, 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., Røskft, E., Greger Hagen, L., Honza, M., Mørk, C. & Olsen P. H. 2000: Common Cuckoo (*Cuculus canorus*) and host behaviour 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. 1999: Reactions of Red-backed Shrikes (*Lanius collurio*) to artificial Cuckoo (*Cuculus canorus*) eggs. — *J. Avian Biol.* 30: 175–181.

- Moskát, C. & Honza, M. 2000: Effect of nest and nest site characteristics on the risk of Cuckoo (*Cuculus canorus*) parasitism in the great reed warbler (*Acrocephalus arundinaceus*). — *Ecography* 23: 335–341.
- 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.
- Nakamura, H., Kubota, S. & Suzuki, R. 1998: Coevolution between the Common Cuckoo and its major hosts in Japan. — In: Rothstein, S. I. & Robinson, S. K. (eds.), *Parasitic birds and their hosts: studies in coevolution*: 94–112. Oxford University Press.
- Orians, G. H., Røskft, E. & Beletsky, L. D. 1989: Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds? — *Willson Bulletin* 101: 599–605.
- PANTONE 1995: *Color formula guide 1000*. — Pantone Inc., New Jersey.
- Røskft, E., Moksnes, A., Stokke, B. G., Moskát, C. & Honza, M. 2002: The spatial habitat structure of host populations explains the pattern of rejection behavior in hosts and parasitic adaptations in cuckoos. — *Behav. Ecol.* 13: 163–168.
- Rothstein, S. I. 1982: Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. — *Am. Zool.* 22: 547–560.
- Rothstein, S. I. 1990: A model system for coevolution: avian brood parasitism. — *Annual Review Ecology Systems* 21: 481–508.
- Rothstein, S. I. & Robinson, S. K. 1998: The evolution of avian brood parasitism. — In: Rothstein, S. I. & Robinson, S. K. (eds.), *Parasitic birds and their hosts: studies in coevolution*: 3–56. Oxford University Press.
- Soler, M. & Møller, A. P. 1990: Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. — *Nature* 343: 748–750.
- Starks, P. T., Fischer, D. J., Watson, R. E., Melikian, G. L. & Nath, S. D. 1998: Context-dependent nestmate discrimination in the paper wasp, *Polistes dominulus*: a critical test of the optimal acceptance threshold model. — *Anim. Behav.* 56: 449–458.
- Stokke, B. G., Honza, M., Moksnes, A., Røskft, E. & Rudolfsen, G. 2002: Costs associated with recognition and rejection of parasitic eggs in two European passerines. — *Behaviour* 139: 629–644.
- Stokke, B. G., Moksnes, A., Røskft, E., Rudolfsen, G. & Honza, M. 1999: Rejection of artificial Cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). — *Proc. R. Soc. London B* 266: 1483–1488.
- Takasu, F., Kawasaki, K., Nakamura, H., Cohen, J. E. & Shigesada, N. 1993: Modeling the population dynamics of a cuckoo-host association and the evolution of host defenses. — *Am. Nat.* 142: 812–839.
- Ward, D., Lindholm, A. K. & Smith, J. M. N. 1996: Multiple parasitism of the Red-winged Blackbird: Further experimental evidence of evolutionary lag in a common host of the Brown-headed cowbird. — *Auk* 113: 408–413.
- Wyllie, I. 1981: *The cuckoo*. — Batsford, London.