

Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts

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Abstract Common cuckoo (*Cuculus canorus*) parasitism drastically reduces the reproductive success of their hosts and selects for host discrimination of cuckoo eggs. In a second stage of anti-parasite adaptation, once cuckoos can lay eggs that mimic those of their hosts, a high uniformity of host egg appearance within a clutch may favour cuckoo egg discrimination. Comparative evidence provides indirect support for this hypothesis although experimental support is currently lacking. Here, we studied the effect of experimentally decreased uniformity of host egg appearance on cuckoo egg discrimination by great reed warbler (*Acrocephalus arundinaceus*) hosts in a population in which long-term cuckoo parasitism has led to high levels of

cuckoo–host egg mimesis. We manipulated host clutch uniformity by adding extra spots to fresh host eggs just after they were laid. Rejection of non-mimetic experimental eggs added to these nests was compared with those in control nests in which uniformity was not altered. Previously, by over-painting real spots in a control group of nests, we showed a negligible effect of our paints on hosts' perception of their eggs. We show that for the great reed warbler, non-mimetic experimental eggs were relatively more tolerated in experimental nests, i.e. with lower uniformity (40%) than in control nests (5%). This is the first experimental study, to our knowledge, which demonstrates a reduced discrimination of foreign eggs as a consequence of an

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increase of egg phenotypes variation perception in a cuckoo host.

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Introduction

Common cuckoo (*Cuculus canorus*)–host parasitic relationships are among the classic textbook examples of co-evolutionary interactions. Hosts have evolved effective and finely tuned defensive mechanisms to reduce the harmful effects of cuckoo parasitism, which at the same time have selected for more sophisticated trickeries by the cuckoo to overcome host defences (Davies 2000). For instance, discrimination of cuckoo eggs is the most efficient host mechanism evolved to counteract cuckoo parasitism. Some hosts can learn how their eggs appear and discriminate and reject eggs unlike their own (Lotem et al. 1995). Experiments have shown that hosts of the cuckoo more often reject parasitic eggs that look dissimilar from their own (e.g. Davies 2000), supporting the view that in the evolutionary “arms race”, hosts have selected for improved cuckoo–host egg mimicry (Brooke and Davies 1988).

Once cuckoos mimic the eggs of their hosts, hosts are expected to produce more homogenous clutches in appearance (i.e. to reduce intra-clutch variation in egg appearance sensu Stokke et al. 1999) as a further stage in the “arms race” (Dawkins and Krebs 1979; Davies 2000; Takasu 1998; for reviews see Stokke et al. 2005, Kilner 2006 and Krüger 2007). In particular, discrimination of cuckoo eggs are expected to be facilitated by low variation in host egg appearance within a clutch (Davies and Brooke 1989), together with a higher variation in egg appearance among host individuals (i.e. inter-clutch variation), which hinders cuckoos to match their eggs to the proper host egg type (Davies and Brooke 1989). Evidence for a role of variation in egg appearance within clutches in egg discrimination came from comparative studies reporting the highest egg uniformity in clutches of hosts living sympatrically with the cuckoo (Øien et al. 1995; Soler and Møller 1996; Moskát et al. 2002; Stokke et al. 2002; Avilés and Møller 2003) or as a result of an arms race in the past (Davies and Brooke 1989). Intra-specific tests of the hypothesis have, so far, focused on reporting a link between egg uniformity within host clutches and probability of rejection of artificial eggs. Studies on good rejecters (Røskaft et al. 2002), who reject non-mimetic foreign eggs at almost 100% rate (e.g. great reed warblers *Acrocephalus arundinaceus*—Lotem et al. 1995, Moskát et al. 2002 and

Karcza et al. 2003; marsh warblers *A. palustris*—Antonov et al. 2006; common whitethroats *Sylvia communis*—Procházka and Honza 2003; blackcaps *S. atricapilla*—Honza et al. 2004 and Polacikova et al. 2007; red-backed shrikes *Lanius collurio*—Lovászi and Moskát 2004; chaffinches *Fringilla coelebs*—Stokke et al. 2004; yellowhammers *Emberiza citrinella*—Procházka and Honza 2004) have failed to find such a link. However, moderate rejecters (those who reject around 30–60% of non-mimetic foreign eggs, sensu Røskaft et al. 2002 and Stokke et al. 2005) might respond differently from good rejecters since Stokke et al. (1999) reported that rejecters of non-mimetic cuckoo eggs of reed warblers (*A. scirpaceus*) possessed a higher uniformity in egg appearance than acceptors. However, host egg uniformity within clutches remained non-manipulated, which raises the possibility that differences between acceptors and rejecters in egg appearance may simply reflect age-related rejection and egg appearance (e.g. Lotem et al. 1995) or a genetic link between egg appearance and rejection behaviour (e.g. Martín-Gálvez et al. 2006).

Hosts visually inspect their clutches before they reject cuckoo eggs (Soler et al. 2002; Honza et al. 2007). Although the exact mechanism for cuckoo egg recognition remains unclear, inspection of the clutch seems a likely first step. Here, we experimentally examine the assumption that a low variation in host egg appearance increases the chance of detecting cuckoo eggs in great reed warbler hosts. In a similar study, Karcza et al. (2003) exchanged great reed warbler eggs among nests and compared the rejection of artificial eggs in those nests with a control group of nests. They failed to find support for the hypothesis; however, they could not isolate the relative effects of either pattern of spottiness and eggshell background coloration on rejection. Here, we manipulated uniformity in the pattern of spottiness of host eggs, but left eggshell background coloration unaltered. We, therefore, expected that experimental increase of egg spottiness within a clutch causes a higher host tolerance toward parasitic eggs.

Materials and methods

Fieldwork was carried out around the village of Apaj, Hungary (47°07' N; 19°06' E) in 2007 and one of the experiments also in 2006 (see later). Great reed warblers breed in reed beds along small channels and are parasitised at unusually high (>50%) rates by cuckoos (Moskát and Honza 2002). We found similar levels of parasitism (53.3%, $N=45$ nests and 54.6%, $N=45$ nests in 2006 and 2007, respectively, when all nests having eggs were considered for calculation) and rejection rates against natural cuckoo eggs during the study period (45.8%, $N=24$ cuckoo eggs

and 30.4%, $N=23$ cuckoo eggs in 2006 and 2007, respectively; $\chi^2_1=0.62$, $P=0.4322$, with Yates continuity correction). Cuckoo eggs within this population showed a variable appearance with most typically weak ivory but also pale yellow, blue, green or pink background colours with brown spots, which closely resembled the appearance of host eggs as judged by humans (Moskát and Honza 2002) or by spectrophotometry (Cherry et al. 2007).

Manipulation of host egg uniformity

We used 41 nests for this experiment, which were assigned to one of the following three groups: (i) experimentally decreased uniformity of fresh eggs plus artificial parasitism ('decreased uniformity treatment'; $N=10$), (ii) natural uniformity plus artificial parasitism ('control uniformity'; $N=21$, including 15 experiments performed in 2006 where hosts showed similar rejection rates against the experimentally introduced eggs to 2007; Fisher exact test, $P=0.300$), and (iii) a control group was created to test the potential effect of painting ('control painting'; $N=10$). In the first group of nests, we added 10, 20 or 30 extra spots of about 1–2 mm in diameter with a brown fibre pen (Faber-Castel OHP colour code 78, size 1523) to the first three eggs laid by the host in a clutch (row 2 in Fig. 1). Each egg was manipulated just after it had been laid, i.e. in the morning on the day of laying (hosts typically lay in the early morning), and the sequence of extra spot categories (10, 20 or 30 spots) was chosen randomly. In the first two groups of nests, the fourth egg in the laying sequence was painted on day 4 to be non-mimetic and treated as the parasitic egg (see the next paragraph for the description of this egg). Typically, hosts laid four or five eggs per clutch,



Fig. 1 An example for our experimental manipulation on typical host eggs ('decreased uniformity treatment'). Row 1 (on the top)—the first three great reed warbler eggs in a clutch as they were naturally laid down. Row 2 (below)—clutch after uniformity was decreased by painting 30, 10 and 20 extra spots on the eggshells (from left to right) and one egg on the right was painted to be non-mimetic

and we left the fifth egg in its original state. Clutch size did not differ among the experimental and control groups (mean \pm standard deviation (SD) to (i) decreased uniformity treatment— 4.900 ± 0.567 , (ii) control uniformity— 4.476 ± 0.749 SD and (iii) control group— 4.40 ± 0.699 SD, one-way analysis of variance, $F_{2,38}=1.598$, $P=0.216$). Colour and size of added spots in our treatments resembled the dominant spot colour and size of great reed warbler eggshells in the population (Moskát et al. 2008; Fig. 1).

The effect of our manipulation on clutch uniformity was evaluated on digital pictures taken on a randomly selected sample of 20 great reed warbler clutches before and after manipulation. Clutches were photographed on Kodak grey card, and pictures were obtained with an Olympus Camedia E-20 camera. Nine persons unaware of the details of the experiment scored clutch uniformity following Øien et al. (1995) as follows: 1=no variation—all the eggs were similar; 2=at least one egg differed slightly from the others; 3=at least one egg differed markedly from the others; 4=at least one egg differed dramatically from the others; 5=all the eggs were different from one another.

Scores by the nine persons showed a high level of concordance (Kendall's coefficient of concordance ($N=40$, $W=0.133$, $\chi^2_8=42.711$, $P<0.001$). As expected, our manipulation decreased human perception of egg uniformity (before manipulation—median=2.4, range 1.1–3.7; after manipulation—median=2.65, range 1.8–3.7; Wilcoxon signed rank test, $z=-2.772$, $P=0.006$).

As a consequence of our manipulation host clutches differed in homogeneity between the decreased uniformity treatment group of nests and control nests with natural clutch uniformity (Fig. 1). However, paintings by brown fibre pens were used in the former group, which raised the possibility that differences in rejection were a response to the use of artificial paints in experimental nests. So, we tested the effect of this painting on the eggshell in the control painting group of nests: We painted over the natural brown spots (1–5 mm in size) of one egg in each of ten clutches and tested the reaction of the hosts to this manipulation. Painting effect should have manifested with rejection of painted control eggs. Acceptance, however, would indicate that we have effectively broadened the acceptance threshold of great reed warblers owing to more extensive phenotypic variability.

Experimental parasitism

Simulating natural parasitism (Moskát and Honza 2002), we manipulated one egg per clutch on the day when the fourth host egg was laid in every clutch, both in the treatment and control uniformity groups, by dying greenish yellow on the whole eggshell with a transparent yellow highlighter pen (Swan Stabilo Boss art No. 70/24). We also

painted 12 bigger spots with the diameter of 4–5 mm with a brown fibre pen (Faber-Castel OHP colour code 78, size 1525). Different shades of yellowish and greenish colours for natural cuckoo eggs are possible, although rare in our population (C. Moskát et al. unpublished). Therefore, although the size (volume) of cuckoo eggs is similar to that of great reed warbler hosts (Török et al. 2004), the use of the term “non-mimetic” artificial parasitism seems substantiated. In our study, we found a high intolerance against this egg type and to other non-mimetic experimental eggs applied earlier in our population, e.g. plain dark brown eggs (Hauber et al. 2006). We monitored nests for six consecutive days after manipulation and reported host responses as acceptance or ejection of the parasitic egg. No other response was observed. If the nest was depredated during the experiment, or a cuckoo laid her egg into the clutch, that case was not considered in the final analysis.

Statistical analyses

We used generalised linear models for the dependent variable (acceptance versus rejection), involving experimental treatments (decreased uniformity versus control) as independent fixed factors. Lotem et al. (1995) have suggested that young great reed warbler females may learn the appearance of their eggs during their first breeding attempt. Thus, young females may be more tolerant to our manipulation of uniformity than older females, which may have already learned the appearance of their eggs. To control for previous learning, we introduced clutch size as a fixed factor in our analysis. This is justified by clutch size being an age-related trait in passerines with young females often having smaller clutches than older ones (Bensch 1996). We entered laying time as a covariate since young great reed warbler females often lay in the middle of the breeding season, as it was revealed in Japan (Lotem et al. 1992); however, it has not been shown previously in our site (Moskát et al. 2002; Moskát and Hauber 2007).

Data were analysed with SPSS version 9.0 (SPSS, Inc.) and STATISTICA version 5.1 (StatSoft, Inc.). The Levene's test was applied for testing homogeneity of variances prior to parametric tests.

Results

Interestingly, modifying uniformity in host egg appearance led to significant differences in tolerance toward non-mimetic eggs by great reed warblers (treatment effect— $\chi^2_{1,29}=5.89$, $P=0.015$). Pairs with experimentally decreased uniformity rejected only 60% of the parasitic eggs, while non-manipulated pairs rejected almost all parasitic eggs (95%;

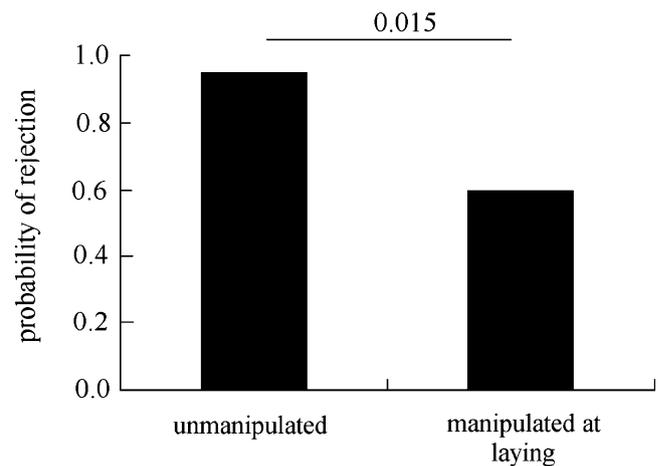


Fig. 2 Rejection rates of non-mimetic experimental eggs in non-manipulated natural clutches ($N=21$), and when egg uniformity was decreased experimentally on fresh host eggs ($N=10$)

Fig. 2). Neither laying date (laying date effect— $\chi^2_{1,27}=1.10$, $P=0.29$) nor clutch size (clutch size effect— $\chi^2_{1,28}=0.96$, $P=0.32$), which are possible traits influencing egg appearance and rejection in great reed warblers (e.g. Lotem et al. 1992), were related to probability of rejection.

Interestingly, great reed warblers did not show any reaction against those own eggs in their clutches where natural spots were carefully over-painted (all of the ten nests in the ‘control painting’ category accepted the manipulated own egg) or against the remaining host eggs in their clutch (all of the ten control nests accepted all their eggs once one own host egg was over-painted) so the use of brown paints did not affect host perception of its own eggs.

Discussion

The prediction that a low intra-clutch variation in egg appearance should increase in response to cuckoo parasitism rests on the key, but to date unproved, assumption that high uniformity in host egg appearance facilitates discrimination of cuckoo eggs (Davies and Brooke 1989). A number of non-experimental studies have failed to find support for this assumption (see “Introduction”, reviewed in Kilner 2006). Studies in which egg uniformity was not experimentally altered, however, cannot unambiguously provide support to the hypothesis, because uniformity in egg appearance may have already been increased as a result of the co-evolutionary process between hosts and cuckoos (Øien et al. 1995; Soler and Møller 1996; Moskát et al. 2002; Stokke et al. 2002; 2004; Avilés and Møller 2003) or simply because discrimination and egg appearance could simultaneously be age-related and/or genetically linked traits in hosts (e.g. Lotem et al. 1995; Martín-Gálvez et al. 2006). In the present study, we modified the appearance of

the host clutch by manipulating the pattern of spottiness of three host eggs. Manipulated eggs remained below the acceptance threshold of the hosts (sensu Hauber et al. 2006) and were recognised as hosts' own eggs. Interestingly, tolerance to the easily recognisable non-mimetic eggs increased in experimental great reed warbler nests in which uniformity was decreased. This result provides strong support for the assumption that high clutch uniformity in host eggs facilitates discrimination of cuckoo eggs.

We therefore conclude that discrimination of parasite eggs in nests with higher intra-clutch variation in egg appearance seems to be more difficult for great reed warblers than in nests with lower intra-clutch variation. In this experiment, hosts had the chance to inspect their eggs and learn their appearances before the nest was experimentally parasitised on day 4. Rejection of parasitic eggs is the behavioural component of a series of maternal traits involving egg appearance and a visual system of recognition (Davies 2000). In many host species, like in great reed warblers, egg recognition is related to the memory templates of their own eggs, containing inherited and learned components (Lotem et al. 1992, 1995; Hauber and Sherman 2001; Hauber et al. 2006; Moskát and Hauber 2007). Learned components related to discrimination of parasitic eggs can be acquired by female hosts during their first breeding attempt by learning the appearance of their eggs while laying, although it could also be reinforced in successive breeding attempts (Lotem et al. 1995). Our manipulation probably affected the set of learned components by great reed warbler hosts during their laying, which led to constraints on the cognitive mechanisms used for egg discrimination.

Noteworthy, we detected a lower rejection of non-mimetic eggs in nests with lower clutch uniformity, despite the fact that the parasitic egg greatly differed in appearance from those of the great reed warbler host. This finding stresses the importance of only small variations in clutch uniformity for discrimination of cuckoo eggs (Davies and Brooke 1989; Stokke et al. 1999) and suggests that hosts may use uniformity of the whole clutch (own and foreign eggs) to identify parasitism.

Cherry et al. (2007) have suggested that the effect of host egg uniformity on cuckoo egg discrimination is mimicry dependent. We found that egg uniformity affected hosts' rejections against non-mimetic eggs, but we did not reveal any effect of clutch size and season on discrimination. Clutch size was related to age of great reed warblers in Japan (Lotem et al. 1992) and so may indicate previous knowledge of hosts on their egg appearance. In our population, template-based egg discrimination was evident when hosts rejected approximately 22% of cuckoo eggs laid into empty nests, just before egg laying started (Moskát and Hauber 2007). However, our results from the egg-laying

period suggest that prolonged learning of hosts' own egg patterns could be particularly advantageous for females having variable eggs in their clutches. A similar result was concluded from a mathematical model developed by Stokke et al. (2007), where the importance of clutch characteristics and learning for anti-parasite adaptations were evaluated. In the great reed warbler, prolonged learning of egg appearances may increase hosts' knowledge of the various characteristics of their own eggs (Lotem et al. 1995).

In conclusion, our findings suggest that great reed warbler hosts may use uniformity of their eggs in a clutch as a cue for cuckoo egg discrimination as Davies and Brooke (1989) proposed. Because we experimentally manipulated host egg uniformity within their clutches, this study constitutes the first unambiguous support for the role of intra-clutch variation in parasite egg-discrimination. Further experimental studies are needed, however, to evaluate the effect of experimental manipulation of host egg appearance in other host systems and with variable levels of cuckoo–host egg mimesis to ascertain the generality of our findings.

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References

- Antonov A, Stokke BG, Moksnes A, Røskft E (2006) Egg rejection in marsh warblers (*Acrocephalus palustris*) heavily parasitised by common cuckoos (*Cuculus canorus*). *Auk* 123:419–430
- Avilés JM, Møller AP (2003) Meadow pipit (*Anthus pratensis*) egg appearance in cuckoo (*Cuculus canorus*) sympatric and allopatric populations. *Biol J Linn Soc* 79:543–459
- Bensch S (1996) Female mating status and reproductive success in the great reed warbler: is there a potential cost of polygyny that requires compensation? *J Anim Ecol* 65:283–296
- Brooke M de L, Davies NB (1988) Egg mimicry by Cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 335:630–632
- Cherry MI, Bennett ATD, Moskát C (2007) Host intra-clutch variation, cuckoo egg matching and egg rejection by great reed warblers. *Naturwissenschaften* 94:41–447
- Davies NB (2000) Cuckoos, cowbirds and other cheats. Poyser, London
- Davies NB, Brooke M de L (1989) 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 NB, Krebs JR (1979) Arms races between and within species. *Proc R Soc Lond B* 205:489–511
- 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

- Honza M, Procházka P, Stokke BG, Moksnes A, Røskaft E, Capek M Jr, Mrlík V (2004) Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *J Ethol* 22:175–180
- Honza M, Pozgayová M, Procházka P, Kadlec E (2007) Consistency in egg rejection behaviour: responses to repeated brood parasitism in the blackcap (*Sylvia atricapilla*). *Ethology* 113:344–351
- Karca Z, Moskát C, Cherry MI, 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
- Kilner RM (2006) The evolution of egg colour and patterning in birds. *Biol Rev* 81:383–406
- Krüger O (2007) Cuckoos, cowbirds and hosts: adaptations, trade-offs and constraints. *Phil Trans R Soc B* 362:1873–1886
- 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
- 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
- Martín-Gálvez D, Soler JJ, Martínez JG, Krupa AP, Richard M, Soler M, Møller AP, Burke T (2006) A quantitative trait locus for recognition of foreign eggs in the host of a brood parasite. *J Evol Biol* 19:543–550
- 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, Szentpéteri J, Barta Z (2002) Adaptations by great reed warblers to brood parasitism: a comparison of populations in sympatry and allopatry with the cuckoo. *Behaviour* 139:1313–1329
- Moskát C, Székely T, Cuthill IC, Kisbenedek T (2008) Hosts' responses to parasitic eggs: which cues elicit hosts' egg discrimination? *Ethology* 114:186–194
- Øien JJ, Moksnes A, Røskaft E (1995) Evolution of variation in egg color and marking pattern in European passerines: adaptations in a coevolutionary arms race with the cuckoo, *Cuculus canorus*. *Behav Ecol* 6:166–174
- Polaciková L, Honza M, Procházka P, Topercer J, Stokke BG (2007) Colour characteristics of the blunt pole: cues for recognition of parasitic eggs as revealed by reflectance spectrophotometry. *Anim Behav* 74:419–427
- Procházka P, Honza M (2003) Do common whitethroats (*Sylvia communis*) discriminate against alien eggs? *J Orn* 144:354–363
- Procházka P, Honza M (2004) Egg discrimination in the yellowhammer. *Condor* 106:405–410
- Røskaft E, Moksnes A, Stokke BG, 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
- Soler JJ, Møller AP (1996) A comparative analysis of the evolution of variation in appearance of eggs of European passerines in relation to brood parasitism. *Behav Ecol* 7:89–94
- Soler M, Martín-Vivaldi M, Pérez-Contreras T (2002) Identification of the sex responsible for recognition and the method of ejection of parasitic eggs in some potential common cuckoo hosts. *Ethology* 108:1093–1101
- Stokke BG, Moksnes A, Røskaft 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 Lond B* 266:1483–1488
- Stokke BG, Moksnes A, Røskaft E (2002) Obligate brood parasites as selective agents for evolution of egg appearances in passerine birds. *Evolution* 56:199–205
- Stokke BG, Rudolfsen G, Moksnes A, Røskaft E (2004) Rejection of conspecific eggs in chaffinches: the effect of age and clutch characteristics. *Ethology* 110:459–470
- Stokke BG, Moksnes A, Røskaft E (2005) The enigma of imperfect adaptations in hosts of avian brood parasites. *Ornithol Sci* 4:17–29
- Stokke BG, Takasu F, Moksnes A, Røskaft E (2007) The importance of clutch characteristics for antiparasite adaptations in hosts of avian brood parasites. *Evolution* 61:2212–2228
- Takasu F (1998) Modelling the arms race in avian brood parasitism. *Evol Ecol* 12:969–987
- Török J, Moskát C, Michl G, Péczely P (2004) Common cuckoos (*Cuculus canorus*) lay eggs with larger yolk but not more testosterone than their great reed warbler (*Acrocephalus arundinaceus*) hosts. *Ethol Ecol Evol* 16:271–277