Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*)

Bård G. Stokke¹, Arne Moksnes¹, Eivin Røskoft¹, Geir Rudolfsen¹ and Marcel Honza²

¹Department of Zoology, Norwegian University of Science and Technology, NTNU, N-7491 Trondheim, Norway

²Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Květná 8, 60 365 Brno, Czech Republic

Passerines that are exposed to brood parasitism can evolve reduced intraclutch variation in egg appearance to facilitate recognition and rejection of the parasitic egg. This has been shown to be true for European passerine species that are assumed to have participated in an evolutionary arms race with the cuckoo (*Cuculus canorus*). However, few investigations have been carried out with the aim of finding out whether there is a relationship between these two traits within a species. In this study, we compare the level of intraclutch variation in egg appearance and the rejection of an unlike parasitic egg within a population of reed warblers (*Acrocephalus scirpaceus*) in the south-eastern part of the Czech Republic. We parasitized reed warbler nests with an artificial non-mimetic cuckoo egg, and then monitored the reaction of the hosts. In 27 out of 48 nests (56.3%) the parasitic egg was rejected. The rejecter pairs had a statistically significantly lower intraclutch variation in egg appearance than the acceptor pairs. We discuss possible explanations for the observed relationship between rejection of unlike eggs and intraclutch variation in egg appearance within this population of reed warblers. The results are consistent with the evolutionary arms race hypothesis, but the intermediate rejection rate found in this population could also be maintained by an equilibrium between acceptors and rejecters due to rejection costs.

Keywords: brood parasitism; coevolution; cuckoo; intraclutch variation; reed warbler; rejection behaviour

1. INTRODUCTION

Interactions between avian brood parasites and their hosts are one of the most suitable model systems for studying coevolution (Rothstein & Robinson 1998). Recent investigations have shown that passerines that have been involved in a coevolutionary arms race with the cuckoo have developed, among other traits, less intraclutch variation in egg appearance than those that have not experienced such interactions (Øien *et al.* 1995; Soler & Møller 1996). The reason for the evolution of these traits by the host is thought to be an adaptation in the prevailing coevolutionary arms race (Swynnerton 1918; Dawkins & Krebs 1979; Brooke & Davies 1988; Davies & Brooke 1988, 1989a,b; Brown *et al.* 1990; Moksnes *et al.* 1990, 1991; Rothstein 1990; Øien *et al.* 1995). The reduced intraclutch variation among their own eggs is assumed to make it easier for the hosts to recognize a parasitic egg in their nest, even when the foreign egg is not very different in appearance from the host eggs (Øien *et al.* 1995).

Most investigations of variation in intraclutch egg appearance have so far focused on comparisons between species of passerines (Davies & Brooke 1989a; Øien *et al.* 1995; Soler & Møller 1996). However, to test the hypothesis that reduction in intraclutch egg variation is a stage in the coevolutionary arms race between host and parasite, it is also highly relevant to analyse the differences in

such variation within a species (see, for example, Victoria 1972; Lotem *et al.* 1995).

In this study, we recorded the host response to non-mimetic model cuckoo eggs in relation to intraclutch variation in the appearance of host eggs. We studied a reed warbler population in the Czech Republic, which is sympatric with the cuckoo and is regularly parasitized by it. According to the arms-race hypothesis (Davies & Brooke 1989b; Øien *et al.* 1995), we would expect that individuals from host populations that have been involved in coevolution with the cuckoo should have evolved rejection behaviour towards odd eggs, and also a low intraclutch variation in egg appearance to facilitate the recognition of a foreign, parasitic egg (Øien *et al.* 1995; Soler & Møller 1996). If these counter-adaptations against parasitism are working in accordance with this theory, we expect that rejecter individuals within a host population will show less intraclutch egg variation than acceptor individuals.

We also discuss possible age-related patterns in rejection behaviour and intraclutch variation in the light of our data, together with the possible influence of conditional factors such as the level of cuckoo parasitism on hosts in different periods of the host's breeding season. Such patterns have suggested that the host response towards parasitic eggs could be explained by an evolutionary equilibrium model (see, for example, Lotem *et al.* 1992). This hypothesis states that the acceptance of

parasitic eggs by some individuals is a result of an equilibrium between various selective pressures including conditional responses (Zahavi 1979; Rohwer & Spaw 1988; Rohwer *et al.* 1989; Brooker & Brooker 1990; Røskaft *et al.* 1990; Petit 1991; Lotem *et al.* 1992, 1995; Lotem & Nakamura 1998).

2. MATERIAL AND METHODS

The fieldwork took place from 10 June to 10 July 1998 in Luzice, Southern Moravia, in the south-eastern part of the Czech Republic (47°40' N, 16°48' E), about 60 km south of the city of Brno. The most important breeding period for the reed warbler in this area is June through to mid-July (Hudec 1975), which means that most of the breeding period was studied. The study site is situated in a typical agricultural area, with interspersed villages and deciduous woods. The reed warbler nests were found in the littoral vegetation surrounding several fish ponds and mostly consisting of reeds (*Phragmites australis*) and to a lesser extent reedmace (*Typha angustifolia*) (Øien *et al.* 1998). The ponds are mainly surrounded by a belt of deciduous woodland. All the nests were given a number and were marked with a tiny yellow plastic sticker. No experimentally parasitized nests were naturally parasitized by cuckoos, and in addition no naturally parasitized nests were used in our experiments. Only nests that were found at the building stage, before the hosts had started their egg laying, were used in the study. These nests were visited every day and each egg was numbered with waterproof ink in consecutive order as laid. No indications of intraspecific parasitism were recorded. As far as we know, intraspecific brood parasitism has never been documented in the reed warbler.

Our intention was to use only first clutches in the experiment. Because we did not capture and mark any of the hosts, there exists a theoretical possibility that some second clutches could have been included in the experiment. However, our large sample size and study area, with a high breeding density of hosts (which reduces the risk of including clutches of the same individuals twice) would probably reduce this source of error to a marginal level.

To assess the rejection behaviour towards unlike eggs, we placed an artificial, immaculate blue, model cuckoo egg (redstart type) in the nest of the reed warbler hosts. The model eggs had approximately the same size and mass as real cuckoo eggs, and were made of plaster and painted with acrylic paint. All the nests used in the study were artificially parasitized the same day as the host had laid its fourth egg, so that the host could assess the intraclutch variation within the complete clutch (although a few females laid three or five eggs, which resulted in a mean clutch size slightly smaller than four; see §3). None of the host eggs were removed when the artificial egg was put into the nest, because this has been shown to have no influence on the host response (Davies & Brooke 1988; Moksnes & Røskaft 1989). The nests were visited every day for the next five days after parasitism. We regarded the model egg as accepted if the host had shown no rejection behaviour during the five days after parasitism; the blue egg was removed on the fifth day. In some other studies, the rejection behaviour has been monitored for somewhat longer (see, for example, Davies & Brooke 1988; Moksnes *et al.* 1990; Lotem *et al.* 1995). Of those reed warblers in our study area that, during 1992–1998, rejected naturally laid cuckoo eggs, 86% rejected the egg within the first five days after the parasitism, and 92% within six days (B. G. Stokke, A. Moksnes, E. Røskaft, G. Rudolfson and M. Honza,

unpublished data). However, because increasing the length of this observation period could also result in an increasing proportion of desertions for other reasons than parasitism, we decided to use five days as a limit. The parasitic egg was regarded as rejected if the hosts had deserted the nest, or had tried to puncture the artificial egg. The latter was made perceptible through small puncture holes in the plaster, which were easy to distinguish from the intact eggs in the nests of the acceptor pairs. A total of 48 nests were artificially parasitized in this study.

To be able to examine the intraclutch variation, we photographed the clutches in a standardized manner with a Canon EOS 100 camera with a ML-3 flashlight. The eggs were photographed on a greyish plate, and each clutch was given its own number. The intraclutch variation was later scored by four experienced test persons who did not know the fate of the nests in advance. These persons scored the intraclutch variation for each clutch according to the method used by Øien *et al.* (1995). With this method, the intraclutch variation in egg appearance, represented by colour and marking patterns, was scored from one to five according to the following scale.

- (1) No variation; all the eggs were similar.
- (2) At least one egg differed slightly from the others.
- (3) At least one egg showed marked differences from the other eggs.
- (4) At least one egg differed dramatically from the others.
- (5) All the eggs differed from one another.

The scores of intraclutch variation made by the different test persons were highly consistent as shown by a calculation of repeatability (Becker 1984; Lessels & Boag 1987). The intraclutch variation was normally distributed, so there was no need for normalization of this variable. The repeatability of intraclutch variation was 0.703 (s.e. = 0.055; $F = 10.460$, d.f. = 47, 144, $p < 0.001$). The total mean intraclutch variation for all four test persons was calculated and used in the analysis of the data. We used SPSS 8.0 for Windows to analyse the material statistically; all the tests are two-tailed.

3. RESULTS

The artificial parasitic egg was rejected in 27 (56.3%) out of the 48 host nests used in the experiment. This was statistically significantly higher than in the nests that were naturally parasitized in 1992–1998, where the parasitic egg was rejected in 73 out of 255 nests (28.6%) (B. G. Stokke, A. Moksnes, E. Røskaft, G. Rudolfson and M. Honza, unpublished data) ($\chi^2 = 13.94$, d.f. = 1, $p < 0.001$). Fourteen of the nests were deserted, and in 13 nests the foreign egg was considered rejected because the host had tried to puncture it (puncture ejection). The mean intraclutch variation in egg appearance for the rejecter pairs was 2.62 (s.d. = 0.69), which was statistically significantly lower than for the acceptor pairs, 3.41 (s.d. = 0.72) (figure 1, Mann–Whitney U , $Z = -3.407$, $n = 21, 27$, $p = 0.001$). We found no statistically significant differences in the distribution of acceptors and rejecters throughout the breeding season of the hosts (table 1, log-linear analysis, maximum likelihood $\chi^2 = 3.125$, d.f. = 3, $p = 0.370$). The overall level of natural cuckoo parasitism on reed warblers recorded in the area in 1998 was 11.7% (11 out of 94), and we found no differences in the rate of cuckoo parasitism throughout the part of the season when our experiment was done (table 1, log-linear analysis, maximum likelihood

Figure 1. Frequency distribution of intraclutch variation in egg appearance in rejecters (mean: 2.62, s.d. = 0.69, $n = 27$) and acceptors (mean: 3.41, s.d. = 0.72, $n = 21$) of non-mimetic model cuckoo eggs in a reed-warbler population in the south-eastern part of the Czech Republic (Mann-Whitney U , $Z = -3.407$, $n = 21, 27$, $p = 0.001$).

$\chi^2 = 1.898$, d.f. = 3, $p = 0.594$). Finally, the mean clutch size was similar in rejecter and acceptor pairs of non-mimetic parasitic eggs, 3.93 (s.d. = 0.62, $n = 27$) and 3.90 (s.d. = 0.44, $n = 21$), respectively (Mann-Whitney U , $Z = -0.08$, $n = 21, 27$, $p = 0.938$).

4. DISCUSSION

As predicted, we found a negative relationship among reed warblers between intraclutch egg variation and the ability to reject non-mimetic cuckoo eggs. This supports the arms-race hypothesis, which assumes that one stage in the coevolution between the cuckoo and the host would be selection for a reduction in intraclutch variation in egg appearance among hosts (Davies & Brooke 1989a; Øien *et al.* 1995; Soler & Møller 1996). This reduced intraclutch variation would make it easier for the host to distinguish a parasitic egg from its own eggs. As the eggs in the clutch become mutually less variable, the variation between clutches of different individuals may increase (Soler & Møller 1996). Such an increased interclutch variation would clearly make it more difficult for the cuckoo to mimic the host eggs, because there would be several 'egg types' in each host species (Øien *et al.* 1995; Soler & Møller 1996). To create this scenario, there must be a certain degree of intraclutch variation in egg appearance within a population at the start. This will allow selection on eggs with different appearance among the individuals by chance, as a host population is becoming involved in an arms race with the cuckoo. In addition, it is essential that the variation in egg appearance has a genetic foundation, so that a selection can take place. The relatively high intraclutch variation found in the acceptor pairs in this study, and in acceptor species by Øien *et al.* (1995), indicates that there is sufficient variation in egg

appearance within clutches to allow selection for a reduction in this variation and thereby an increasing interclutch variation when confronted with cuckoo parasitism.

Recent investigations have focused on other causes of variation in rejection behaviour between individuals in the same population, and support has been found for the evolutionary equilibrium hypothesis (Lotem *et al.* 1992, 1995; Alvarez 1996; Brooke *et al.* 1998; Øien *et al.* 1998). Some studies have shown that rejection and acceptance of parasitic eggs may have a different distribution in the course of the breeding season (see, for example, Burgham & Picman 1989; Lotem *et al.* 1992, 1995; Alvarez 1996; Brooke *et al.* 1998; Øien *et al.* 1998). Lotem *et al.* (1992) observed that a population of the great reed warbler (*Acrocephalus arundinaceus*) in Japan had significantly more rejecter than acceptor individuals among the early and late breeders than among individuals that nested in the middle of the breeding season. Their interpretation of this was that naive first-year breeders need time to recognize their own eggs, and therefore do not eject an odd egg from their nests as readily as older individuals do. These naive individuals generally start their breeding season later than the adults (Lack 1968; Klomp 1970; Walker 1972) and therefore make up most of the breeding population in the middle of the season. At the end of the breeding season, the host breeding population again consists mostly of older birds that are re-nesting, or producing their second brood (Lotem *et al.* 1992). This scenario allows an evolutionary equilibrium to operate between rejecters and acceptors of odd eggs in a population of brood-parasite hosts. They also found some support for an age-specific pattern in the intraclutch variation in egg appearance: females showed a greater tendency to produce clutches with more intraclutch variation in egg appearance in their first breeding attempt than subsequently (Lotem *et al.* 1995). Due to the possible age-specific pattern in rejection behaviour and intraclutch variation, this could represent a potential source of error in the present study. However, the similar distribution of acceptors and rejecters through the breeding season indicates that there is no relationship between the timing of breeding and rejection behaviour in the population of reed warblers studied. An additional test to examine any possible age-specific rejection behaviour among reed warblers in the study area is related to differences in clutch size between young and old individuals. In passerines, first-time breeders generally have smaller clutches than older birds (Snow 1958; Campbell & Lack 1985). Following Lotem *et al.* (1995), we would therefore expect that the acceptors of parasitic eggs would have a smaller clutch size than the rejecters. We found no such difference in clutch size between rejecters and acceptors. These results indicate either that the distribution of young and old breeders is similar during the course of the season, or that there are no age-specific patterns of rejection and acceptance of odd eggs in this reed-warbler population. To sum up, there are no indications that the effect of age leads to any serious source of error concerning the observed relationship between intraclutch variation and rejection behaviour in this study.

If an allele for rejecting parasitic eggs exists, the spread of it in a particular host population will depend upon the

Table 1. *Rejection rate of artificial parasitic eggs, and rate of natural parasitism among reed warblers*

(The data included are from the part of the breeding season when the experiment was done (10–30 June). Figures in brackets are number of cases. Date of parasitism versus rejection rate: log-linear analysis, maximum likelihood $\chi^2 = 3.125$, d.f. = 3, $p = 0.370$. Date of parasitism versus rate of natural parasitism: log-linear analysis, maximum likelihood $\chi^2 = 1.898$, d.f. = 3, $p = 0.594$.)

	date of parasitism			
	11–15 June	16–20 June	21–25 June	26–30 June
rejection rate of artificial eggs (%)	60.0 (9/15)	57.1 (4/7)	61.9 (13/21)	20.0 (1/5)
rate of natural parasitism (%)	13.6 (3/22)	7.7 (1/13)	3.7 (1/27)	14.3 (1/7)

level of cuckoo parasitism, or in other words the selection pressure for host discrimination. With the relatively high rate of natural parasitism found in our study area (16.1%) (Øien *et al.* 1998), the overall rejection rate should be quite high (Davies *et al.* 1996; Brooke *et al.* 1998). The level of parasitism in our study area lies in the lower region of that experienced by a reed-warbler population in eastern England in 1985–1986 (16–26%) (Brooke *et al.* 1998). The rejection of the redstart-type model egg in this area was 69.2% in 1985–1986, but had declined to 24.6% in 1995–1997 when the level of parasitism had declined to a level as little as 2–6% (Brooke *et al.* 1998). The observed level of rejection in our study in 1998 (56.3%) corresponds quite well with these data, although the level of natural parasitism found this year (11.7%) was somewhat lower than in the previous years. In contrast to the high rejection rate for non-mimetic eggs, the rejection of mimetic eggs by cuckoo hosts is often much more infrequent. The rejection rate of natural cuckoo eggs by a population of reed warblers in England in 1985–1986 was thus only 19% (Davies & Brooke 1988; see also Davies & Brooke 1989b; Brown *et al.* 1990); in our study area the mean rate for 1992–1998 was 28.6%. The natural rejection rate for cuckoo eggs in our study area is thus much lower than the rejection rate for the artificial, non-mimetic eggs used in the experiment. The natural cuckoo eggs found in the area show at least some degree of mimicry of the host eggs (Moksnes *et al.* 1993), in contrast to the completely different artificial eggs used in the present study. Even though the blue model cuckoo egg we used was very different from reed-warbler eggs (seen with the human eye), 43.7% of them were accepted by the host. These acceptors had a higher intraclutch variation than the rejecters, but in spite of this it is reasonable to believe that the artificial egg was so different that it should have been possible for them to recognize it if they had such an ability (but see Alvarez 1999). It is therefore possible that the lack of rejection was not primarily due to high intraclutch variation, but to the lack of a ‘rejecter allele’. Following this line of argument, there could be a genetic linkage between the two traits found among the rejecters in this study: low intraclutch egg variation and a high ability to recognize odd eggs. In relation to this question it is interesting to note that in some passerine species it has been found that it is the female who is responsible for the ejection of foreign eggs (Moksnes *et al.* 1994; Palomino *et al.* 1998). It is believed that egg appearance is inherited by a daughter from her mother (see, for example, Punnett 1933; Collias 1993), because the genes responsible for such traits are thought to be located on the

female-specific W chromosome (Sheppard 1958; Jensen 1966). It thus seems that a possible linkage between intra-clutch variation and the ability to recognize odd eggs requires that the rejection of parasitic eggs is performed by the female.

To obtain more insight into these questions it is necessary to investigate the role of intraclutch variation when the parasitic egg shows better mimicry of the host eggs, for example whether there are any differences in intra-clutch variation between rejecters and acceptors of real cuckoo eggs. It is possible that rejecters of such eggs have the lowest intraclutch variation of all, if we assume that there is a genetic linkage between the traits. If, on the other hand, some conditional factors such as the presence of the cuckoo near the nest (Davies & Brooke 1988) or the short-term, natural level of parasitism are important, we should not expect such a close relationship between rejection behaviour and intraclutch variation. Such findings would support the evolutionary equilibrium hypothesis.

The level of cuckoo parasitism on reed warblers in different parts of Europe varies greatly, ranging from zero to 63%, with a mean of about 9% (Schreuers 1963; Schulze-Hagen 1992). The birds that have their origin in areas with no, or at least little, cuckoo parasitism would not be expected to have evolved any pronounced rejection behaviour against parasitic eggs. They are therefore expected to have a relatively high intraclutch variation in egg appearance along with a poor ability to reject odd eggs. Individuals that originate from areas with higher levels of parasitism would be expected to have evolved less intraclutch variation in egg appearance and a higher rejection rate for odd eggs. Gene flow could theoretically level off variations between populations, but differences in rejection behaviour have been found between populations that are separated by only a few kilometres (Brooke *et al.* 1998). It would be interesting to examine in more detail whether there are any differences in intraclutch variation between these populations.

In this study we have concluded that our results support the evolutionary arms-race hypothesis (see above). However, even if low intraclutch variation in host eggs has evolved as a counter-adaptation against mimetic cuckoo eggs, the results of this study do not permit us to reject the evolutionary equilibrium hypothesis. It is still possible that intermediate rejection rates are maintained by an equilibrium between acceptors and rejecters due to rejection costs (see, for example, Davies & Brooke 1988; Rohwer *et al.* 1989; Moksnes *et al.* 1991; Marchetti 1992; Røskaft *et al.* 1993; Takasu *et al.* 1993; Lotem *et al.* 1995; Davies *et al.* 1996; Takasu 1998). In theory, there are, for

example, many possibilities for variation in rejection behaviour due to conditional responses at different levels of intraclutch variation. These questions should be further analysed by carrying out more detailed field experiments.

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REFERENCES

- Alvarez, F. 1996 Model cuckoo *Cuculus canorus* eggs accepted by rufous bush chats *Cercotrichas galactotes* during the parasite's absence from the breeding area. *Ibis* **138**, 340–342.
- Alvarez, F. 1999 Attractive non-mimetic stimuli in cuckoo *Cuculus canorus* eggs. *Ibis* **141**, 142–144.
- Becker, W. A. 1984 *Manual of quantitative genetics*. Pullman, WA: Academic Enterprises.
- Brooke, M. de L. & Davies, N. B. 1988 Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335**, 630–632.
- Brooke, M. de L., Davies, N. B. & Noble, D. G. 1998 Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proc. R. Soc. Lond. B* **265**, 1277–1282.
- Brooker, L. C. & Brooker, M. G. 1990 Why are cuckoos host specific? *Oikos* **57**, 301–309.
- 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.
- Burgham, M. C. J. & Picman, J. 1989 Effect of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. *Anim. Behav.* **38**, 298–308.
- Campbell, B. & Lack, E. (eds) 1985 *A dictionary of birds*. Calton, UK: T. & A. D. Poyser.
- Collias, E. C. 1993 Inheritance of egg-color polymorphism in the village weaver (*Ploceus cucullatus*). *Auk* **110**, 683–692.
- 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.
- Davies, N. B., Brooke, M. de L. & Kacelnik, A. 1996 Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc. R. Soc. Lond. B* **263**, 925–931.
- Dawkins, R. & Krebs, J. R. 1979 Arms races between and within species. *Proc. R. Soc. Lond. B* **205**, 489–511.
- Hudec, K. 1975 Density and breeding of birds in the reed swamps of southern Moravian ponds. *Acta Sci. Nat. Brno* **9**, 1–40.
- Jensen, R. A. C. 1966 Genetics of cuckoo egg colour polymorphism. *Nature* **209**, 827.
- Klomp, H. 1970 The determination of clutch-size in birds. A review. *Ardea* **58**, 1–124.
- Lack, D. 1968 *Ecological adaptations for breeding in birds*. London: Methuen.
- Lessels, C. M. & Boag, P. T. 1987 Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116–121.
- Lotem, A. & Nakamura, H. 1998 Evolutionary equilibria in avian brood parasitism. An alternative to the 'arms race-evolutionary lag' concept. In *Parasitic birds and their hosts, studies in coevolution* (ed. S. I. Rothstein & S. K. Robinson), pp. 223–235. Oxford University Press.
- 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.
- Marchetti, K. 1992 Costs of host defence and persistence of parasitic cuckoos. *Proc. R. Soc. Lond. B* **248**, 41–45.
- Moksnes, A. & Røskaft, E. 1989 Adaptations of meadow pipits to parasitism by the common cuckoo. *Behav. Ecol. Sociobiol.* **24**, 25–30.
- Moksnes, A., Røskaft, 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., Røskaft, E. & Braa, A. T. 1991 Rejection behavior by common cuckoo hosts towards artificial brood parasite eggs. *Auk* **108**, 348–354.
- Moksnes, A., Røskaft, E., Bicik, V., Honza, M. & Oien, I. J. 1993 Cuckoo *Cuculus canorus* parasitism on *Acrocephalus* warblers in southern Moravia in the Czech Republic. *J. Ornithol.* **134**, 425–434.
- Moksnes, A., Røskaft, E. & Solli, M. M. 1994 Documenting puncture ejection of parasitic eggs by chaffinches *Fringilla coelebs* and blackcaps *Sylvia atricapilla*. *Fauna Norv. (Cinclus)* **C17**, 115–118.
- Oien, I. J., 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.
- Oien, I. J., Moksnes, A., Røskaft, E. & Honza, M. 1998 Costs of cuckoo *Cuculus canorus* parasitism to reed warblers *Acrocephalus scirpaceus*. *J. Avian Biol.* **29**, 209–215.
- Palomino, J. J., Martin-Vivaldi, M., Soler, M. & Soler, J. J. 1998 Females are responsible for ejection of cuckoo eggs in the rufous bush robin. *Anim. Behav.* **56**, 131–136.
- Petit, L. J. 1991 Adaptive tolerance of cowbird parasitism by prothonotary warblers: a consequence of nest-site limitation? *Anim. Behav.* **41**, 425–432.
- Punnett, G. W. 1933 Genetic studies in poultry. IX. The blue egg. *J. Genet.* **27**, 465–470.
- Rohwer, S. & Spaw, C. D. 1988 Evolutionary lag versus bill-size constraints: a comparative study of the acceptance of cowbird eggs by old hosts. *Evol. Ecol.* **2**, 27–36.
- Rohwer, S., Spaw, C. D. & Røskaft, E. 1989 Costs to northern orioles of puncture-ejecting parasitic cowbird eggs from their nests. *Auk* **106**, 734–738.
- Rothstein, S. I. 1990 A model system for coevolution: avian brood parasitism. *A. Rev. Ecol. Syst.* **21**, 481–508.
- Rothstein, S. I. & Robinson, S. K. (eds) 1998 *Parasitic birds and their hosts, studies in coevolution*. Oxford University Press.
- Røskaft, E., Orians, G. H. & Beletsky, L. D. 1990 Why do red-winged blackbirds accept eggs of brown-headed cowbirds? *Evol. Ecol.* **4**, 35–42.

- Røskoft, E., Rohwer, S. & Spaw, C. D. 1993 Costs of puncture ejection compared with costs of rearing cowbird chicks for northern orioles. *Ornis Scand.* **24**, 28–32.
- Schreuers, T. 1963 Vogelwelt an Niederheinischen Gewässern. *Limnol. Schr. R. (Gewässer und Abwässer)* A **32**, 7–43.
- Schulze-Hagen, K. 1992 Parasitierung und Brutverluste durch den Kuckuck (*Cuculus canorus*) bei Teich- und Sumpfrohrsänger (*Acrocephalus scirpaceus*, *A. palustris*) in Mittel- und Westeuropa. *J. Ornithol.* **133**, 237–249.
- Sheppard, P. M. 1958 *Natural selection and heredity*. London: Hutchinson.
- Snow, D. W. 1958 *A study of blackbirds*. London: Allen & Unwin.
- Soler, J. J. & Møller, A. P. 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.
- Swynnerton, C. F. M. 1918 Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. *Ibis* **60**, 127–154.
- Takasu, F. 1998 Why do all host species not show defense against avian brood parasitism: evolutionary lag or equilibrium? *Am. Nat.* **151**, 193–205.
- 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**, 819–839.
- Victoria, J. K. 1972 Clutch characteristics and egg discriminative ability of the African village weaverbird *Ploceus cucullatus*. *Ibis* **114**, 367–376.
- Walker, J. E. S. 1972 Recent studies on reed and sedge warblers. *Ibis* **114**, 585.
- Zahavi, A. 1979 Parasitism and nest predation in parasitic cuckoos. *Am. Nat.* **113**, 157–159.