

The analysis of common cuckoo's egg shape in relation to its hosts' in two geographically distant areas

M. Bán¹, Z. Barta¹, A. R. Muñoz^{2,*}, F. Takasu², H. Nakamura³ & C. Moskát⁴

¹ Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Debrecen, Hungary

² Department of Information and Computer Sciences, Nara Women's University, Nara, Japan

³ Department of Biology, Faculty of Education, Shinsu University, Nagano, Japan

⁴ Animal Ecology Research Group of the Hungarian Academy of Sciences, Budapest, Hungary

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Correspondence

Miklós Bán, Behavioural Ecology Research Group, Department of Evolutionary Zoology, University of Debrecen, Egyetem tér 1, Debrecen 4032, Hungary.
Email: banm@vocs.unideb.hu

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Introduction

The common cuckoo *Cuculus canorus* is a brood parasite that exploits many passerine species (Davies, 2000). Cuckoo females lay their eggs into host nests during the hosts' laying period, and cuckoo chicks hatched in parasitized broods typically evict all other eggs or nestlings from the hosts' nests (Wyllie, 1981). This eviction behaviour and the misdirected parental care clearly reduce hosts' reproductive success (Davies & Brooke, 1988; Kilner, 2005). As a consequence, hosts typically develop antiparasite defence mechanisms against cuckoos and their eggs (for reviews, see Davies, 2000; Krüger, 2007). Hosts' discrimination against parasitic eggs (i.e. their recognition and rejection), in turn, selects for adaptations in the cuckoo to counteract hosts' defences to parasitism, leading to an evolutionary arms race (Dawkins & Krebs, 1979).

Generally, when a cuckoo egg is well matched to its host eggs, it has a greater chance to survive than those with poor matching (Davies & Brooke, 1988; Moksnes *et al.*, 1991; Hauber, Moskát & Bán, 2006; Cherry, Bennett & Moskát, 2007). Other factors, like uniformity of clutches, may also affect hosts' perceptual abilities in egg-rejection behaviour

Abstract

Evolutionary adaptations are required by common cuckoos *Cuculus canorus* to match host eggs. Hosts may discriminate against alien eggs; hence, accurate matching of the parasite egg to the hosts' is essential. Egg shape is the least-studied component of egg mimicry, and it may also have other functions: an optimal egg shape is necessary for effective incubation. For this reason, cuckoo eggs may show a wide range of variations in shape to a set of host species. Here, we compare cuckoo and host eggs by using egg shape parameters in two distant areas: from the nests of great reed warblers *Acrocephalus arundinaceus*, robins *Erithacus rubecula* and marsh warblers *Acrocephalus palustris* in Hungary, and oriental reed warblers *Acrocephalus orientalis*, bull-headed shrikes *Lanius bucephalus* and black-faced buntings *Emberiza spodocephala* from Japan. Our results suggest the lack of evolutionary adaptation of different cuckoo gentes to their corresponding hosts in terms of egg shape. However, our analyses revealed that cuckoo eggs showed a geographical difference in egg shape.

(Davies & Brooke, 1989; Stokke *et al.*, 1999; Lahti & Lahti, 2002; Moskát *et al.*, 2008a). As a consequence of this evolutionary arms race, cuckoo egg morphs are extremely diverse among geographical regions and host species due to specific mimicry to specific host eggs, leading to the formation of races among cuckoos (the so-called 'gentes', singular 'gens' Baker, 1942; Davies & Brooke, 1989; Moksnes & Røskaft, 1995). Cuckoos' egg mimicry is frequently evaluated on the basis of egg characteristics, like colour (Cherry & Bennett, 2001; Avilés & Møller, 2003, 2004; Takasu *et al.*, 2009; Antonov *et al.*, 2010; Landstrom, Heinsohn & Langmore, 2010) and patterns of spottedness (Moksnes & Røskaft, 1995; Antonov *et al.*, 2010; Polačiková & Grim, 2010; Stoddard & Stevens, 2010). In several experimental studies, painted model or foreign eggs, instead of real cuckoo eggs, have been used to investigate egg characteristics on egg-rejection behaviour, like the effects of colour (e.g. Honza, Polačiková & Procházka, 2007; Avilés, 2008; Cassey *et al.*, 2008; Vikan *et al.*, 2009), spottedness (López-de-Hierro & Moreno-Rueda, 2010) or both (Nakamura, Kubota & Suzuki, 1998; Moskát *et al.*, 2008b; Avilés *et al.*, 2010). In spite of the increasing number of such studies, egg shape has attracted little attention (Mason & Rothstein, 1986; Langmore, Hunt & Kilner,

2003) and still remains an often-neglected component in the study of cuckoo–host coevolution.

Avian eggs, nevertheless, vary not only in colour and spottedness but in shape too, which is possibly related to efficient heat transfer during incubation in different-sized clutches (Barta & Székely, 1997). This variation points to the potential importance of egg shape in cuckoo–host coevolution. First, it might facilitate more perfect mimicry. Second, in order to achieve efficient heat transfer, the shape of the cuckoo eggs should match that of the host eggs.

In the present study, we investigated whether cuckoo eggs were similar to host eggs in their shape by comparing the egg shape characteristics of several host species and their corresponding brood parasites. As far as we know, this is the first attempt to examine the role of egg shape in the cuckoo–host relationship. We predict similarity in shape between eggs of a particular host species and its particular cuckoo gens, that is, the cuckoos adapted to host eggs shape in order to ensure more perfect mimicry. We also predict that cuckoos' adaptation to host eggs in shape may vary in geographically distant areas, as cuckoo races specialized on host populations vary in time and space (c.f. Davies, 2000).

Material and methods

We photographed parasitized clutches of great reed warblers *Acrocephalus arundinaceus*, marsh warblers *Acrocephalus palustris* and robins *Erithacus rubecula* in the egg collection of the Mátra Museum, Gyöngyös, Hungary (Fig. 1). These eggs were typically collected in the 1950s, 1960s and 1970s in southern Hungary. We also took pictures in the field on parasitized clutches in two study areas: (1) Kiskunság National Park, Hungary, c. 50 km south of Budapest, around the village Apaj (47°07'N; 19°06'E; great reed warblers), and (2) Nobeyama highlands (35°57'N, 138°28'E; oriental reed warblers *Acrocephalus orientalis*, bull-headed shrikes *Lanius bucephalus* and black-faced buntings *Emberiza spodocephala*, c. 120 km south of Nagano City, central Japan (Fig. 1). All clutches were photographed on a Kodak Grey Card by digital cameras (Olympus Camedia E20P, Olympus Co., Tokyo, Japan and Nikon COOLPIX 995, Nikon Co., Tokyo, Japan). Kodak Colour Control Patches were also placed near the eggs on each photo as a reference. We took the pictures at different

phases of egg laying; therefore, we have no information on the final clutch sizes in most of the cases.

We applied the method originally developed by Barta & Székely (1997) and improved by Mónus & Barta (2005) for measuring egg shape parameters from digital pictures, based on the circle transformation technique by Thompson (1942) and Todd & Smart (1984). To measure the eggs' shape, we used the ImageJ software (Abramoff, Magelhaes & Ram, 2004). We set up mark points around the eggs' edges: two points on the two opposite tips of the eggs, which determined the longitudinal axis of eggs, and seven roughly equally distributed points along each of the two edges of the shape (Fig. 2a). We fitted second-order polynomials to the coordinates of the mark points (Fig. 2b). We used three parameters of the polynomial to describe egg shape. The first (c_0) parameter is the compression ratio relative to a circle (Fig. 3); the smaller the c_0 , the more elongated the egg. The other two parameters describe the level of asymmetry of the eggs (c_1 , larger c_1 means more pointed egg) and roundness of the tips (c_2 , larger c_2 means more blunted tips) (Fig. 3). Consequently, the three polynomial parameters describe egg shape together.

We measured eggs from 135 clutches belonging to six host species (Table 1) in Hungary and Japan. In the analyses, we used one randomly chosen host egg from each clutch to avoid pseudo replication. In order to exclude the possibility that our results arise as the consequence of a particular sampling of the host eggs, we repeated this procedure one thousand times (permutation test) and recorded the number of significant results (this applies only for the host eggs as we have only one cuckoo egg per nest). We combined the two sets of great reed warbler eggs from Hungary, where eggs were collected mainly in the 1950s and 1960s in southern Hungary and field data from Apaj from 1998 to 2004, as no difference was found when we compared these eggs' shape (MANOVA permutation test, $P < 0.05$, 16 cases out of 1000 runs).

All computations and statistical analyses were carried out within the framework of the R interactive statistical environment (R Development Core Team, 2009).

Results

Our analyses revealed that eggs of the different cuckoo genets significantly differed in shape (MANOVA Pillai = 0.388, $F_{15,387} = 3.842$, $P < 0.001$; ANOVA c_0 : $F_{5,129} = 7.641$,

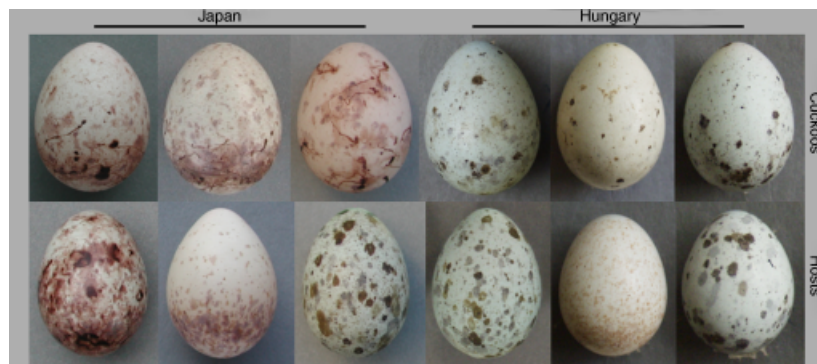


Figure 1 Cuckoo *Cuculus canorus* (top row) and host (bottom row) eggs from six populations (left to right): black-faced bunting *Emberiza spodocephala* (Japan), bull-headed shrike *Lanius bucephalus* (Japan), oriental reed warbler *Acrocephalus orientalis* (Japan), great reed warbler *Acrocephalus arundinaceus* (Hungary), robin *Erithacus rubecula* (Hungary) and marsh warbler *Acrocephalus palustris* (Hungary).

$P < 0.001$; $c1: F_{5,129} = 4.916, P < 0.001$; $c2: F_{5,129} = 0.101, P = 0.363$; Fig. 4). Our results also suggested that cuckoo eggs from the two distant geographical areas, that is, Japan and Hungary, differed significantly in terms of egg shape (MANOVA Pillai = 0.256, $F_{3,131} = 15.053, P < 0.001$; ANOVA $c0: F_{1,133} = 32.581, P < 0.001$; $c1: F_{1,133} = 12.318, P < 0.001$; $c2: F_{1,133} = 2.713, P = 0.101$; Fig. 4). Cuckoo eggs from Hungary are more elongated than those from Japan (Fig. 4). The cuckoo eggs from different hosts' nests within

these areas, however, did not differ in shape (Hungary: MANOVA Pillai = 0.088, $F_{6,148} = 1.138, P = 0.34$; ANOVA $c0: F_{2,75} = 2.25, P < 0.112$; $c1: F_{2,75} = 0.968, P < 0.384$; $c2: F_{2,75} = 0.461, P = 0.632$; Japan: MANOVA Pillai = 0.2, $F_{6,106} = 4.813, P = 0.07$; ANOVA $c0: F_{2,54} = 0.657, P < 0.522$; $c1: F_{2,54} = 4.649, P < 0.013$; $c2: F_{2,54} = 0.809, P = 0.45$).

Host eggs from different populations differed from each other in terms of egg shape (MANOVA Pillai = 0.539, $F_{15,387} = 5.655, P < 0.001$; ANOVA $c0: F_{5,129} = 12.465, P < 0.001$; $c1: F_{5,129} = 1.356, P = 0.24$; $c2: F_{5,129} = 6.186, P < 0.001$; Fig. 4), and this difference seems not to depend on a particular random sampling of the host eggs (all 1000 repetitions of the MANOVA yielded highly significant results; all $P < 0.001$). Investigating the egg shape parameters separately shows that $c0$ and $c2$ differ between hosts species significantly (in all 1000 repetition, $P < 0.008$) while the results for $c1$ are not so clear ($P < 0.05$ in only 305 cases out of 1000). As there was no common host species in the two geographical areas, we did not analyse geographical differences between the host eggs from the two areas, because the effects of species identity and geographical area cannot be separated.

We found a significant difference between cuckoo and host eggs' shape when we controlled for population effects, that is, for the host races of cuckoos (MANOVA Pillai = 0.148, $F_{3,257} = 14.997, P < 0.001$, for all 1000 repetition, $P < 0.001$;

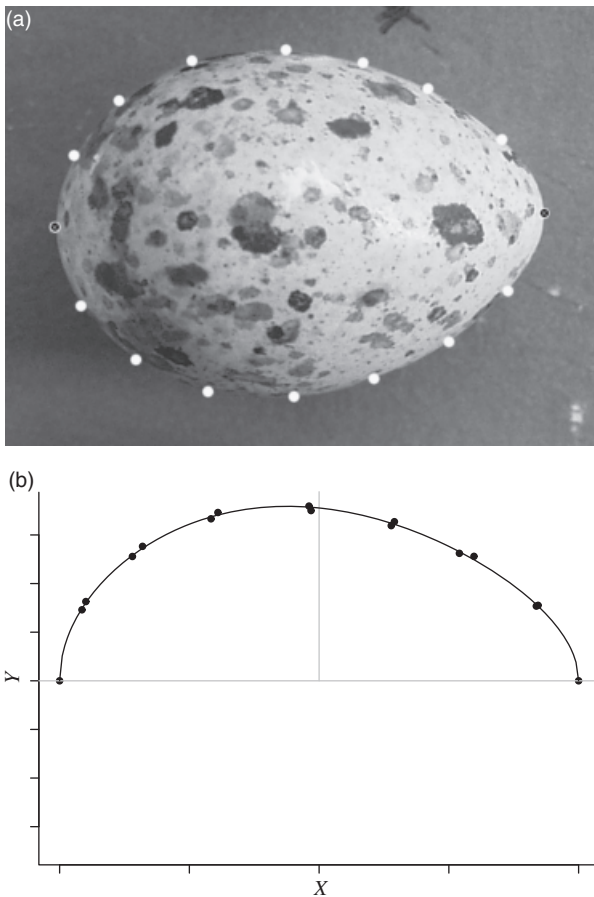


Figure 2 (a) Seven plus seven roughly equally distributed mark points along the two edges of an egg for characterizing egg shape, as demonstrated on a great reed warbler *Acrocephalus arundinaceus* egg. (b) A representation of polynomial curves fitted to the coordinates of the mark points, following Barta & Székely (1997) and Mónus & Barta (2005).

Table 1 List of host species, number of host and cuckoo *Cuculus canorus* eggs and location of samples in the present study

Host species	Number of eggs		Country
	Host	Cuckoo	
Black-faced bunting <i>Emberiza spodocephala</i> (field data)	18	6	Japan
Bull-headed shrike <i>Lanius bucephalus</i> (field data)	123	35	Japan
Oriental reed warbler <i>Acrocephalus orientalis</i> (field data)	35	16	Japan
Great reed warbler <i>Acrocephalus arundinaceus</i> (field data, museum coll)	76	25	Hungary
Robin <i>Erithacus rubecula</i> (museum coll)	110	29	Hungary
Marsh warbler <i>Acrocephalus palustris</i> (museum coll)	80	24	Hungary

The number of cuckoo eggs is equal to the number of clutches.



Figure 3 Effects of egg shape parameters ($c0$, $c1$ and $c2$) on the shape of avian eggs. Two extreme and one intermediate values per parameter. The lower the value, the darker the line.

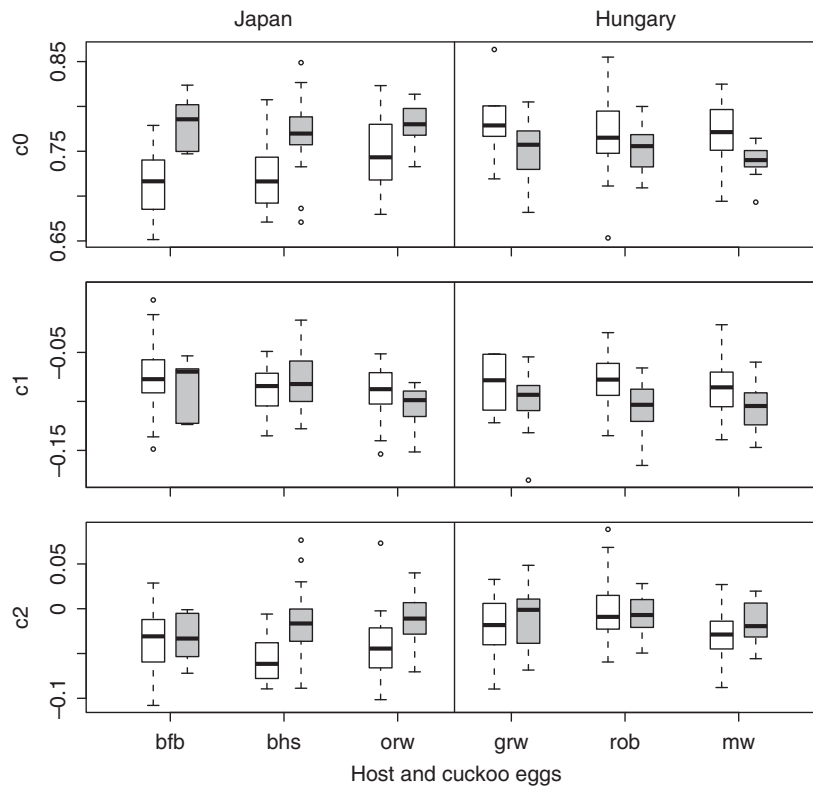


Figure 4 Box-plot diagrams of hosts' (white) and cuckoos' (grey) shape parameters (c_0 , c_1 , c_2). (Hosts: Black-faced bunting *Emberiza spodocephala* 'bfb', bull-headed shrike *Lanius bucephalus* 'bhs', oriental reed warbler *Acrocephalus orientalis* 'orw', great reed warbler *Acrocephalus arundinaceus* 'grw', robin *Erithacus rubecula* 'rob' and marsh warbler *Acrocephalus palustris* 'mw'.)

ANOVA c_0 : $F_{1,259} = 6.878$, $P = 0.009$; c_1 : $F_{1,259} = 21.246$, $P < 0.001$; c_2 : $F_{1,259} = 27.652$, $P < 0.001$; Fig. 4). The cuckoos' and hosts' eggs differ most in roundness, but this difference is opposite in the two regions. The cuckoo eggs in Japan are more rounded than their hosts while in Hungary the cuckoo eggs more elongated than their hosts.

Discussion

Our results revealed a significant difference in the shape of cuckoo eggs between Japan and Hungary, while no difference was revealed in egg shape between cuckoos parasitizing different hosts within any of these distant areas. Cuckoo parasitism in Japan may have started more recently than in Europe (Nakamura *et al.*, 1998; Takasu *et al.*, 2009), where it has a considerable history (Davies, 2000). The difference in egg shape might be the consequence of geographic isolation in the evolutionary history of cuckoos.

Comparing egg shape in six pairs of host species and their corresponding cuckoos, our results suggest the lack of adaptation by different cuckoo genets to their specific hosts in terms of egg shape. There are two possible explanations for this finding. On the one hand, hosts' egg recognition mechanisms are not specialized on egg shape as shown in the great reed warbler (Moskát *et al.*, 2003) and also in hosts of the brown-headed cowbird *Molothrus ater* (Rothstein, 1975; Mason & Rothstein, 1986; Ortega & Cruz, 1988; Underwood & Sealy, 2006; Guigueno & Sealy, 2009). Although

some cuckoos are strictly specialized on one host population (Nakamura & Miyazawa, 1997; Honza *et al.*, 2002), others seem to be generalists (Wyllie, 1981); hence, there might be some overlap in host usage by cuckoos (e.g. Edvardsen *et al.*, 2001). Although this might act against the development of mimicry in egg shape, it cannot exploit selection for this, as mimicry in egg colour and pattern could have already been developed in many cuckoo–host relationships (Moksnes & Røskaft, 1995). On the other hand, if heat retention by eggs is the most important selection pressure, the rounded form would be the most desirable option for the shape of a cuckoo egg (Thompson, 1942; Lack, 1968; Drent, 1975; Andersson, 1978; Barta & Székely, 1997). Our results support the latter possibility, as the rounded egg shape seems to be a secondary attribute in the evolution of cuckoo eggs, which is probably more related to efficient heat transfer.

Nevertheless, there could be several other effects, which may affect the adaptations of the egg shape in cuckoos. For example, the symmetry/asymmetry of eggs may have importance in the hatchability of eggs, affected by gas exchange in the air chamber (Mao *et al.*, 2007). Another divergent selection pressure in evictor cuckoos is eggshell strength, as their eggshells are thicker than that of in non-evictor cuckoos, probably developed against host puncture attempts (Hargitai *et al.*, 2010; Spottiswoode, 2010). The puncture resistance hypothesis was also supported in *Acrocephalus* hosts in Bulgaria (Antonov *et al.*, 2006), but thicker eggshells may also protect cuckoo eggs from damage when

they are laid into host nests. García-Navas *et al.* (2011) showed in the blue tit *Cyanistes caeruleus* that supplementation of calcium-rich food resulted in thicker eggshells and shorter embryo-development. Cuckoos lay at every second day (Wyllie, 1981), by retaining their eggs in their oviducts, which results in a 31-h hatching advantage when comparing with host eggs (Birkhead *et al.*, 2010). Our results suggest that egg shape does not play an important role in cuckoo–host coevolution as other eggshell characteristics, for example, colour or pattern (Kilner, 2006; Antonov *et al.*, 2010; Spottiswoode & Stevens, 2010). Eggshell colour components show a wide variety in bird species (Cassey *et al.*, 2010), probably reflecting a long evolutionary history as they can also be found in extinct birds (Igc *et al.*, 2010). Birds have well-developed visual systems, including their sensitivity for the ultraviolet wavelengths in many species (Endler & Mielke, 2005); thus, birds are able to utilize their talent of visual recognition for using visual cues of eggshell as communication signals (Underwood & Sealy, 2002; Cassey *et al.*, 2009; Cherry & Gosler, 2010).

To summarize, our results suggest that the shape of cuckoo eggs did not adapt to host egg shape. When cuckoo eggs from Japan and Hungary were compared, the shape of cuckoo eggs showed significant differences between these geographically distant areas. We suggest further studies on the coevolution of cuckoo–host egg shape in different populations, with variation in the coevolutionary history between cuckoos and their hosts. Marchetti (2000) described a case where the size of the foreign experimental eggs affected hosts' egg discrimination ability. In such cases, we expect a more relevant effect of egg shape and a better adaptation by cuckoos to host eggs than what we have revealed between cuckoos and six populations of hosts in Japan and Hungary.

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References

- Abramoff, M.D., Magelhaes, P.J. & Ram, S.J. (2004). Image processing with ImageJ. *Biophoton. Int.* **11**, 36–42.
- Andersson, M. (1978). Optimal egg shape in waders. *Ornis. Fenn.* **55**, 105–109.

- Antonov, A., Stokke, B.G., Moksnes, A., Kleven, O., Honza, M. & Røskaft, E. (2006). Eggshell strength of an obligate brood parasite: a test of the puncture resistance hypothesis. *Behav. Ecol. Sociobiol.* **60**, 11–18.
- Antonov, A., Stokke, B.G., Vikan, J.R., Fosøy, F., Ranke, P.S., Røskaft, E., Moksnes, A., Møller, A.P. & Shykoff, J.A. (2010). Egg phenotype differentiation in sympatric cuckoo *Cuculus canorus* gentes. *J. Evol. Biol.* **23**, 1170–1182.
- Avilés, J.M. (2008). Egg colour mimicry in the common cuckoo *Cuculus canorus* as revealed by modelling host retinal function. *Proc. Roy. Soc. Lond. Ser. B* **275**, 2345–2352.
- Avilés, J.M. & Møller, A.P. (2003). Meadow pipit (*Anthus pratensis*) egg appearance in cuckoo (*Cuculus canorus*) sympatric and allopatric populations. *Biol. J. Linn. Soc.* **79**, 543–549.
- Avilés, J.M. & Møller, A.P. (2004). How is host egg mimicry maintained in the cuckoo (*Cuculus canorus*)? *Biol. J. Linn. Soc.* **82**, 57–68.
- Avilés, J.M., Vikan, J.R., Fosøy, F., Antonov, A., Moksnes, A., Røskaft, E. & Stokke, B.G. (2010). Avian colour perception predicts behavioural responses to experimental brood parasitism in chaffinches. *J. Evol. Biol.* **23**, 293–301.
- Baker, E.C.S. (1942). *Cuckoo problems*. London: Witherby.
- Barta, Z. & Székely, T. (1997). The optimal shape of avian eggs. *Funct. Ecol.* **11**, 656–662.
- Birkhead, T.R., Hemmings, N., Spottiswoode, C.N., Mikulica, O., Moskát, C., Bán, M. & Schulze-Hagen, K. (2010). Internal incubation and early hatching in brood parasitic birds. *Proc. Roy. Soc. Lond. Ser. B*. (Online DOI: 10.1098/rspb.2010.1504).
- Cassey, P., Ewen, J.G., Marshall, N.J., Vorobyev, M., Blackburn, T.M. & Hauber, M.E. (2009). Are avian eggshell colours effective intraspecific communication signals in the Muscivora? A perceptual modelling approach. *Ibis* **151**, 689–698.
- Cassey, P., Honza, M., Grim, T. & Hauber, M.E. (2008). The modelling of avian visual perception predicts behavioural rejection responses to foreign egg colours. *Biol. Lett.* **4**, 515–517.
- Cassey, P., Portugal, S.J., Maurer, G., Ewen, J.G., Boulton, R.L., Hauber, M.E. & Blackburn, T.M. (2010). Variability in avian eggshell colour: a comparative study of museum eggshells. *PLoS ONE* **5**, e12054.
- Cherry, M.I. & Bennett, A.T.D. (2001). Egg colour matching in an African cuckoo as revealed by ultraviolet-visible reflectance spectrophotometry. *Proc. Roy. Soc. Lond. Ser. B* **268**, 565–571.
- Cherry, M.I., Bennett, A.T.D. & Moskát, C. (2007). Host intra-clutch variation, cuckoo egg matching and egg rejection by great reed warblers. *Naturwissenschaften* **94**, 441–447.
- Cherry, M.I. & Gosler, A.G. (2010). Avian eggshell coloration: new perspectives on adaptive explanations. *Biol. J. Linn. Soc.* **100**, 753–762.

- Davies, N.B. (2000). *Cuckoos, cowbirds and other cheats*. London: T. A. & D. Poyser.
- 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 coevolution between the cuckoo *Cuculus canorus* and its hosts. II. Host egg markings, chick discrimination and general discussion. *J. Anim. Ecol.* **58**, 225–236.
- Dawkins, N.B. & Krebs, J.R. (1979). Arms races between and within species. *Proc. Roy. Soc. Lond. Ser. B* **205**, 489–511.
- Drent, R. (1975). Incubation. In *Avian biology*, vol. 5: 333–420. Farner, D.S., King, J.R. & Parkes, K.C. (Eds). New York: Academic Press.
- Edvardsen, E., Moksnes, A., Røskaft, E., Øien, I.J. & Honza, M. (2001). Egg mimicry in cuckoos parasitizing four sympatric species of *Acrocephalus* warblers. *Condor* **103**, 829–837.
- Endler, J.A. & Mielke, P.W. (2005). Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* **86**, 405–431.
- García-Navas, V., Sanz, J.J., Merino, S., Martínez-de la Puente, J., Lobato, E., del Cerro, S., Rivero, J., de Castaneda, R.R. & Moreno, J. (2011). Experimental evidence for the role of calcium in eggshell pigmentation pattern and breeding performance in Blue Tits *Cyanistes caeruleus*. *J. Ornithol.* **152**, 71–82.
- Guigueno, M.F. & Sealy, S.G. (2009). Nest sanitation plays a role in egg burial of yellow warblers. *Ethology* **115**, 247–256.
- Hargitai, R., Moskát, C., Bán, M., Gil, D., López-Rull, I. & Solymos, E. (2010). Eggshell characteristics and yolk composition in the common cuckoo *Cuculus canorus*: are they adapted to brood parasitism? *J. Avian Biol.* **41**, 177–185.
- Hauber, M.E., Moskát, C. & Bán, M. (2006). Experimental shift in hosts' acceptance threshold of inaccurate-mimic brood parasite eggs. *Biol. Lett.* **2**, 177–180.
- Honza, M., Poláčiková, L. & Procházka, P. (2007). Ultraviolet and green parts of the colour spectrum affect egg rejection in the song thrush (*Turdus philomelos*). *Biol. J. Linn. Soc.* **92**, 269–276.
- 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.
- Igic, B., Greenwood, D.R., Palmer, D.J., Cassey, P., Gill, B.J., Grim, T., Brennan, P.L.R., Bassett, S.M., Battley, P.F. & Hauber, M.E. (2010). Detecting pigments from colourful eggshells of extinct birds. *Chemoecology* **20**, 43–48.
- Kilner, R.M. (2005). The evolution of virulence in brood parasites. *Ornithol. Sci.* **4**, 55–64.
- Kilner, R.M. (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. *Philos. Trans. Roy. Soc. Lond. B* **362**, 1873–1886.
- Lack, D. (1968). *Ecological adaptations for breeding in birds*. London: Methuen.
- Lahti, D.C. & Lahti, A.R. (2002). How precise is egg discrimination in weaverbirds? *Anim. Behav.* **63**, 1135–1142.
- Landstrom, M.T., Heinsohn, R. & Langmore, N.E. (2010). Clutch variation and egg rejection in three hosts of the pallid cuckoo, *Cuculus pallidus*. *Behaviour* **147**, 19–36.
- Langmore, N.E., Hunt, S. & Kilner, R.M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* **422**, 157–160.
- López-de-Hierro, M.D.G. & Moreno-Rueda, G. (2010). Egg-spot pattern rather than egg colour affects conspecific egg rejection in the house sparrow (*Passer domesticus*). *Behav. Ecol. Sociobiol.* **64**, 317–324.
- Mao, K.-M., Murakami, A., Iwasawa, A. & Yoshizaki, N. (2007). The asymmetry of avian egg-shape: an adaptation for reproduction on dry land. *J. Anat.* **210**, 741–748.
- Marchetti, K. (2000). Egg rejection in a passerine bird: size does matter. *Anim. Behav.* **59**, 877–883.
- Mason, P. & Rothstein, S.I. (1986). Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. *Evolution* **40**, 1207–1214.
- Moksnes, A. & Røskaft, 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.* **236**, 625–648.
- Moksnes, A., Røskaft, E., Braa, A.T., Korsnes, L., Lampe, H.M. & Pedersen, H.C. (1991). Behavioural responses of potential hosts towards artificial cuckoo eggs and dummies. *Behaviour* **116**, 64–89.
- Mónus, F. & Barta, Z. (2005). Repeatability analysis of egg shape in a wild tree sparrow (*Passer montanus*) population: a sensitive method for egg shape description. *Acta. Zool. Acad. Sci. Hung.* **51**, 151–162.
- Moskát, C., Avilés, J.M., Bán, M., Hargitai, R. & Zölei, A. (2008a). Experimental support for the use of egg uniformity in parasite egg discrimination by cuckoo hosts. *Behav. Ecol. Sociobiol.* **62**, 1885–1890.
- Moskát, C., Székely, T., Cuthill, I.C. & Kisbenedek, T. (2008b). Hosts' responses to parasitic eggs: which cues elicit hosts' egg discrimination? *Ethology* **114**, 186–194.
- Moskát, C., Székely, T., Kisbenedek, T., Karcza, Z. & Bártol, I. (2003). The importance of nest cleaning in egg rejection behaviour of great reed warblers *Acrocephalus arundinaceus*. *J. Avian Biol.* **34**, 16–19.
- Nakamura, H., Kubota, S. & Suzuki, R. (1998). Coevolution among the common cuckoo and their major hosts in Japan. In *Parasitic birds and their hosts*: 94–112. Rothstein, S.I. & Robinson, S.K. (Eds). New York: Oxford University Press.
- Nakamura, H. & Miyazawa, Y. (1997). Movements, space use, and social organization of radio-tracked common cuckoos during the breeding season in Japan. *Jpn. J. Ornithol.* **46**, 23–54.
- Ortega, C.P. & Cruz, A. (1988). Mechanisms of egg acceptance by marsh-dwelling blackbirds. *Condor* **90**, 349–358.

- Polačiková, L. & Grim, T. (2010). Blunt egg pole holds cues for alien egg discrimination: experimental evidence. *J. Avian Biol.* **41**, 111–116.
- R Development Core Team. (2009). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. ISBN 3-900051-07-0. Vienna: R Development Core Team. Available at <http://www.R-project.org>.
- Rothstein, S.I. (1975). Mechanisms of avian egg recognition: do birds know their own eggs? *Anim. Behav.* **23**, 268–278.
- Spottiswoode, C.N. (2010). The evolution of host-specific variation in cuckoo eggshell strength. *J. Evol. Biol.* **23**, 1792–1799.
- Spottiswoode, C.N. & Stevens, M. (2010). Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc. Natl. Acad. Sci. USA* **107**, 8672–8676.
- Stoddard, M.C. & Stevens, M. (2010). Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc. Roy. Soc. Lond. Ser. B* **277**, 1387–1393.
- Stokke, B.G., Moksnes, A., Røskaft, E., Rudolfson, G. & Honza, M. (1999). Rejection of artificial cuckoo (*Cuculus canorus*) eggs in relation to variation in egg appearance among reed warblers (*Acrocephalus scirpaceus*). *Proc. Roy. Soc. Lond. B* **266**, 1483–1488.
- Takasu, F., Moskát, C., Munoz, A.R., Imanishi, S. & Nakamura, H. (2009). Adaptations in the common cuckoo (*Cuculus canorus*) to host eggs in a multiple-hosts system of brood parasitism. *Biol. J. Linn. Soc.* **98**, 291–300.
- Thompson, D.W. (1942). *On growth and form*. Cambridge: Cambridge University Press.
- Todd, P.H. & Smart, I.H.M. (1984). The shape of birds' eggs. *J. Theor. Biol.* **106**, 239–243.
- Underwood, T.J. & Sealy, S.G. (2002). Adaptive significance of egg coloration. In *Avian incubation*: 280–298. Deeming, D.C. (Ed). Oxford: Oxford University Press.
- Underwood, T.J. & Sealy, S.G. (2006). Influence of shape on egg discrimination in American robins and gray catbirds. *Ethology* **112**, 164–173.
- Vikan, J.R., Stokke, B.G., Fossey, F., Jackson, C., Huhta, E., Rutila, J., Moksnes, A. & Røskaft, E. (2009). Fixed rejection responses to single and multiple experimental parasitism in two *Fringilla* hosts of the common cuckoo. *Ethology* **115**, 840–850.
- Wyllie, I. (1981). *The cuckoo*. London: Batsford.