Experimental reduction of ultraviolet wavelengths reflected from parasitic eggs affects rejection behaviour in the blackcap *Sylvia atricapilla*

Marcel Honza[1,*] and Lenka Polačiková[1,2]

[1]Institute of Vertebrate Biology, v. v. i., Academy of Sciences of the Czech Republic and [2]Institute of Botany and Zoology,
Faculty of Science, Masaryk University, Brno, Czech Republic

*Author for correspondence (e-mail: honza@brno.cas.cz)

SUMMARY

Hosts of brood parasites use a variety of cues relating to eggshell appearance of parasitic eggs, which facilitate their recognition and rejection. It has been documented that host visual perception of different colours including UV wavelengths plays an important role in this respect. In the study reported here, we aimed to test whether artificial reduction of the UV wavelengths reflected from parasitic eggshell affects rejection behaviour in the blackcap *Sylvia atricapilla*. To achieve this goal, we experimentally manipulated, with UV, part of spectra reflected from conspecific eggs and reduced it into the range of 320–350 nm. We used an ultraviolet light blocker, which did not influence the reflectance shape of other spectrum parts. We also used a group of experimental eggs coated in Vaseline, which had no effect on the spectral shape in the UV or visible ranges of the light spectrum. Additionally, we used a third experimental group of unmanipulated eggs as a control. The experimental eggs coated in the UV blocker were rejected at a higher rate than those coated in the Vaseline. Moreover, a binary logistic regression revealed that an artificial reduction of the UV wavelengths reflected from the parasitic egg significantly affected the probability of being rejected by the hosts. To our knowledge, this is the first experimental study to reveal that manipulation with UV wavelengths affects the recognition of parasitic eggs, indicating that the UV part of the spectrum has an important role in host recognition behaviour.

Key words: brood parasitism, cuckoo, blackcap, UV spectrum part, rejection behaviour, parasitic egg.

INTRODUCTION

Interspecific brood parasitism is a reproductive strategy adopted by about one percent of bird species (Payne, 1997), and consists of laying eggs in nests of unrelated species, the hosts, which incubate the eggs and feed the parasitic young (Lack, 1968). It has been documented that a successful parasitic act has a generally detrimental effect on the host's fitness because of dramatic reduction of their reproductive fitness (Davies, 2000). Many studies have shown that interaction between avian brood parasites and their hosts represent one of the best examples of coevolution (for a review, see Rothstein, 1990), which has led to a variety of adaptations and counter-adaptations on both sides, and has been described as an evolutionary arms race (Dawkins and Krebs, 1979; Davies and Brooke, 1989). For example, in the case of a host-parasite system in which the female parasite specialises on a single host species, parasitic egg mimicry is one of the outcomes of this struggle (Brooke and Davies, 1988). However, this counter-adaptation of the brood parasite must be very stressful for hosts, since egg discrimination has primarily evolved as a consequence of other selection pressures associated with nesting in dense colonies (Underwood and Sealy, 2002).

A significant effort has been devoted to studying naturally parasitized host populations to explore a role of parasitic egg mimicry (Moksnes et al., 1993; Edvardsen et al., 2001; Moskát and Honza, 2002). Similarly, many conclusions have been drawn by an experimental approach testing host responses towards both conspecific eggs (Procházka and Honza, 2003; Procházka and Honza, 2004; Lovaszi and Moskát, 2004) and an artificial model egg (Moskát and Fuisz, 1999; Honza et al., 2004). Most of these studies have tried to explain why so many different host populations accept non-mimetic eggs. This scenario could be primarily influenced by the fact that humans and birds significantly differ in their colour perception. Indeed, Honza et al. (Honza et al., 2007) in a study of song thrushes *Turdus philomelos* revealed how questionable the use of egg categories such as mimetic *versus* non-mimetic might be, since some colours of the parasitic eggs classified by humans as non-mimetic were accepted by the hosts. This discrepancy could be explained by the anatomical differences between bird and human eyes (Chen and Goldsmith, 1986; Harth et al., 1998), because birds are able to detect UV wavelengths in the range of 300–400 nm, invisible to humans (Huth and Burkhardt, 1972; Wright, 1972). Since the UV visual sensitivity plays an important role in bird recognition ability (Wright, 1972; Cherry and Bennett, 2001), interest in the role of UV visual signals has been increasing. Moreover, there is evidence about other functional significances of the UV wavelengths in mate choice, foraging and navigation (Bennett and Cuthill, 1994).

The evolution of the cues influencing rejection behaviour of hosts has attracted enormous attention from many evolutionary biologists (Moskát and Fuisz, 1999; Underwood and Sealy, 2006), however, most of these studies did not take into consideration the significance of the UV wavelengths. The role of the UV wavelengths in avian brood parasite–host systems was first investigated by Cherry and Bennett (Cherry and Bennett, 2001), who identified the importance of this part of spectrum in the evolution of egg mimicry in the red-chested cuckoo, *Cuculus solitarius*. Moreover, there are other

studies demonstrating that the combination of the UV and the part of the spectrum visible to humans plays an important role in avian brood parasites–host coevolutionary system (Avilés and Møller, 2004; Avilés et al., 2006a; Polačiková et al., 2007; Underwood and Sealy, 2008).

In our study, we investigated rejection behaviour in blackcaps, *Sylvia atricapilla* Linnaeus 1758. Although, this species is rarely parasitized at present, there is evidence that blackcaps have been used as hosts by the common cuckoo *Cuculus canorus* in the past (Honza et al., 2001). Since the rejection behaviour of this species still persists, the blackcaps are considered to be current winners in the coevolutionary struggle with the cuckoo (Honza et al., 2004).

The blackcap host is a passerine species, with the ability to perceive short wavelengths including UV (Cuthill et al., 2000). Moreover, our previous study on this species (Polačiková et al., 2007) revealed that the probability of egg rejection significantly increased with decreasing brightness of host eggs at the blunt pole. In the light of this finding, we investigated an influence of reduction of UV wavelengths reflected from parasitic eggs on recognition behaviour in blackcaps. We predicted that experimental manipulation of the UV wavelengths reflected from parasitic eggshell should influence recognition behaviour of this species. We expected that the model eggs with a reduced part of the UV spectrum would be rejected from experimental nests at a different rate than those with unmanipulated UV wavelengths. In our analyses, we investigated the eggshells of both whole parasitic eggs and their blunt poles.

Fig. 1. Representative reflectance spectra of the blackcap's eggshells before (UV^0; black squares) and after (UV$^-$; grey diamonds) experimental manipulation with UV block.

MATERIALS AND METHODS
Study fieldwork and experimental procedure

We monitored a population of blackcaps in a suitable habitat daily from mid April to mid June 2006 near Dolní Bojanovice (48°51′N, 17°02′E) in the Czech Republic. We searched systematically for nests during the laying period or the first days of incubation. Eggs found during incubation were floated to estimate their approximate laying date according to the methods described by Hays and LeCroy (Hays and LeCroy, 1971). All eggs were marked with small numbers on the middle part of the eggshell using waterproof ink to allow their individual identification. Experimental parasitism was carried out only when at least the fourth host egg was laid. Blackcap clutches were randomly parasitized by replacing an egg with one randomly chosen egg from an original clutch. Even though the modal clutch size in the blackcaps nest varies from four to five eggs, our previous study (Polačiková et al., 2007) on this host species documented that adding or switching host eggs in experimental nests has no effect on host response. The experimental nests were monitored daily for 5 days after manipulation. If the parasitic egg disappeared within this period but the host eggs were left unharmed in the nest, it was considered to have been rejected. Nest desertion was classified as a mode of rejection. If the parasitic egg remained unharmed in the nest, it was considered to have been accepted. Each experimental nest was parasitized only once and each experimental egg was used only in one experimental trial. Prior to each experimental procedure, we measured the reflectance spectra of both experimental and host eggs in each clutch. Two types of model eggs were used: (1) conspecific eggs coated in a UV blocker (UV$^-$), and (2) conspecific eggs coated in Vaseline™ petroleum jelly (UV^0). The UV blocker consisted of mixture of an octylmethoxysinnamate and benzophynone-3 which reduces a significant part of the UV wavelengths. The spectral reflectance curves of the experimental eggs for both treatments are shown in Fig. 1. The effect of blocker persisted for at least 48 h after coating
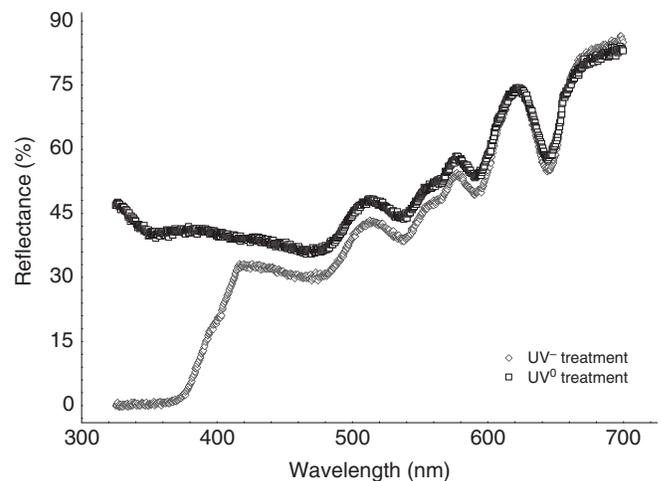
the experimental eggs, and it had no effect on curvature of the visible part of the spectrum. All experimental eggs were recoated in the test substances daily during examination of the nests. The third experimental group, consisting of conspecific eggs without any coating, was used as a control. This last group was not included in our analyses.

Measurement of the reflectance spectra

We measured the spectral reflectance of all eggs from the parasitized clutches in the range of 300–700 nm using a USB 2000 spectrophotometer (Ocean Optics, Dunedin, FL, USA). We divided each egg into three regions across its longitudinal axis: the blunt end, the middle and the sharp end. Each region was a third of the length of the egg. Three randomly located measurements on each part of the egg were taken (each covering 1 mm^2). A deuterium and halogen light source was used (DT-Mini-GS, Ocean Optics) that was shone on the eggs through a quartz optic fibre (QR400-7-UV/VIS-BX, Ocean Optics), and was reflected from the eggs at an angle of 45° to the surface. Data from the spectrophotometer were loaded into OOIBase 32 software (Ocean Optics). The measurements were relative and referred to a standard white reference (WS-2) and to darkness. Reference and calibration were made before each measurement of each clutch. Total reflectance was obtained for the UV (325–400 nm) interval, which is the invisible part of colour spectrum for humans, and a visible part of a spectrum (400–700 nm). We calculated objective variables of the colour, namely brightness (reflectance intensity), chroma (colour purity) and hue [peak wavelengths; (Endler, 1990)]. Brightness was calculated as the sum of the total reflectance values within the 325–700 nm range of wavelengths ($R_{325-700}$). Chroma for each part of the spectrum was calculated using the following reflectance ratios: $R_{325-400}/R_{325-700}$ (UV chroma), $R_{400-475}/R_{325-700}$ (blue chroma), $R_{475-550}/R_{325-700}$ (green chroma), $R_{550-625}/R_{325-700}$ (yellow chroma) and $R_{625-700}/R_{325-700}$ (red chroma). Hue was estimated by the wavelength of the maximum reflectance (R_{max}).

Since our previous study (Polačiková et al., 2007) revealed that mainly characteristics of the blunt egg pole are important for recognition behaviour in blackcaps, we calculated all colour variables reflected from both the whole egg surface and the blunt egg pole separately.

Table 1. Colour characteristics of the whole surface of the host and parasitic eggs prior to experimental reduction of the reflectance spectra

Variables	Host eggs			Parasitic eggs		
	UV$^-$	UV^0	P^*	UV$^-$	UV^0	P^*
Brightness	50454.38±116.32	47722.39±16213.22	0.59	50019.07±15042.56	49878.44±17870.95	0.98
UV chroma	0.12±0.02	0.11±0.02	0.23	0.11±0.02	0.11±0.02	0.37
Blue chroma	0.11±0.02	0.11±0.02	0.39	0.12±0.02	0.11±0.02	0.10
Green chroma	0.18±0.02	0.18±0.02	0.70	0.18±0.02	0.17±0.02	0.42
Yellow chroma	0.28±0.03	0.29±0.03	0.38	0.28±0.03	0.29±0.03	0.23
Red chroma	0.31±0.03	0.32±0.04	0.37	0.32±0.04	0.33±0.03	0.31
Hue	81.31±26.55	81.09±29.64	0.98	80.56±25.93	80.34±26.62	0.98

UV$^-$, experimental eggs coated with UV block; UV^0, experimental eggs coated with Vaseline.
*t-test, N_1=27, N_2=17.

Statistical analyses

The effect of both colour variables characterizing the parasitic egg appearance and contrast between host and parasitic eggs (both calculated for the whole egg surface and blunt egg pole separately, before and after experimental manipulation) on host's recognition ability was examined by a binomial logistic regression with backward stepwise elimination, which included experimental treatments (UV$^-$ and UV^0) as categorical variables and host response as a dependent variable (1=rejection, 2=acceptance). We started analysis by including all variables in the model, dropping non-significant steps until the last step (step 28), which was considered to be the most significant model.

RESULTS

Appearance of the host and experimental eggs

Prior to the experimental manipulation of eggshell reflectance, there was no difference between the host eggs and the parasitic eggs in the colour characteristics of the whole eggshell surface (t-test; Table 1) or of the blunt egg poles (t-test; Table 2). However, after the experimental manipulation, the brightness in UV part of the spectrum, of the eggshells coated in the UV block (UV$^-$), significantly decreased for both the whole surface (uncoated, 5759.61±1385.94 *vs* coated 3665.05±1118.78; mean ± s.d.; t-test=6.11, $N_{1,2}$=27; P<0.001) and their blunt poles (3602.46±1777.11 *vs* 2313.45±1159.89; t-test=3.16; $N_{1,2}$=27; P=0.003). The eggs coated in the Vaseline remained absolutely unchanged (for the whole eggs: 5644.56±2283.84 *vs* 5644.56±2283.84; t-test=0.00; P=1.00; for the blunt poles: 3303.59±1301.64 *vs* 3303.59±1301.64; t-test=0.00; P=1.00).

Responses towards parasitic eggs

Fig. 2 shows rejection rate of the experimental eggs in all three experimental groups. There were no differences in rejection rate between UV^0 and the control unmanipulated group (χ^2-test=0.78,

P=0.37) showing no effect of the grease surface on the bird's response. However, significantly more of the experimental eggs coated in the UV blocker (UV$^-$) were rejected than either the model eggs coated in the Vaseline (UV^0: χ^2=4.04, P=0.02). Similarly, a logistic regression revealed that the only two variables has a significant effect on the host response (rejection=1; model significance χ^2=15.7, P<0.001), the brightness of whole conspecific eggs (Wald χ^2=7.06, d.f.=1, P=0.008) and the UV brightness at blunt egg poles of experimental eggs (Wald χ^2=6.13, d.f.=1, P=0.013). The likelihood of alien egg rejection increased with increasing values of the brightness of the whole surface of experimental eggs [B=0.00±0.00 (± s.e.m.)], but with decreasing UV brightness at the blunt poles of experimental eggs [B=–0.01±0.0 (± s.e.m.)].

DISCUSSION

Parent birds are usually able to discriminate a foreign egg in two ways: either using recognition of their own eggs, i.e. true recognition, or recognition of a discordant egg in their own clutch (Rothstein, 1982a). However, other particular cues facilitating recognition of a foreign egg play an important role in the host recognition processes. For example, Rothstein (Rothstein, 1982b) in a study of the American robin (*Turdus migratorius*) found that smaller parasitic eggs of brown-headed cowbirds, *Molothrus ater*, elicited a quicker host rejections, probably because of a combination of visual and tactile stimuli, since undersized parasitic eggs are possibly easier to reject. However, Underwood and Sealy (Underwood and Sealy, 2006) argued that warbling vireo (*Vireo gilvus*) hosts usually reject brown-headed cowbird's eggs only based on eggshell spot pattern, which indicates that heavy spottiness of the parasitic eggshells is primarily responsible for egg recognition and this host species does not need a stimulus summation (Underwood and Sealy, 2006). In the cuckoo-host system, there are only a few studies documenting which parameters of the eggshell appearance affect the recognition of the parasitic eggs (Stokke et al., 1999; Procházka and Honza,

Table 2. Colour characteristics of the blunt poles of host and parasitic eggs prior to experimental reduction of the reflectance spectra

Variables	Blunt pole of host eggs			Blunt pole of parasitic eggs		
	UV$^-$	UV^0	P^*	UV$^-$	UV^0	P^*
Brightness	32735.35±12341.89	34780.35±18879.44	0.67	32464.98±13682.90	31916.78±11722.26	0.89
UV chroma	0.11±0.03	0.11±0.02	0.47	0.11±0.03	0.11±0.02	0.70
Blue chroma	0.11±0.02	0.10±0.02	0.22	0.10±0.03	0.10±0.03	0.49
Green chroma	0.16±0.03	0.16±0.03	0.84	0.15±0.04	0.15±0.03	0.95
Yellow chroma	0.28±0.03	0.29±0.02	0.57	0.28±0.03	0.28±0.03	0.56
Red chroma	0.35±0.05	0.35±0.04	1.00	0.36±0.05	0.36±0.05	0.89
Hue	61.70±27.73	64.65±31.41	0.75	60.64±25.50	60.44±19.38	0.98

UV$^-$, experimental eggs coated with UV block; UV^0, experimental eggs coated with Vaseline.
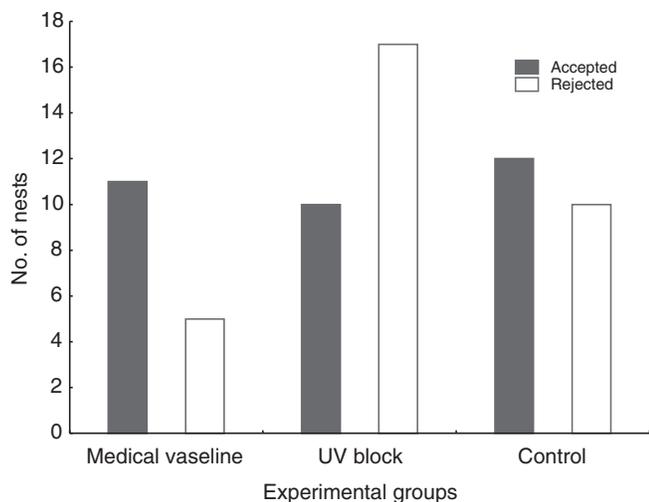*t-test, N_1=7, N_2=17.

Fig. 2. Rejection rate of the parasitic eggs in all three experimental groups.

2003; Procházka and Honza, 2004). Moreover, it is not just the colour characteristics of the whole eggshell that are important in host recognition behaviour, but also particular eggshell parts (Polačiková et al., 2007).

Since Cherry and Bennett (Cherry and Bennett, 2001) revealed the importance of the part of the spectrum that is invisible to humans in host recognition of parasitic eggs, many researchers have been investigating the significance of this trait (Soler et al., 2003; Avilés and Møller, 2004; Cherry et al., 2007) (see also Moskat et al., 2008). However, to our knowledge, there is only one study, conducted by Avilés et al. (Avilés et al., 2006a), which experimentally manipulated UV reflectance to reveal the importance of this part of the spectrum in host recognition. This study investigated recognition behaviour of magpies (*Pica pica*) towards great spotted cuckoo (*Clamator glandarius*) eggs, however, their research did not reveal an effect of artificial reduction of the UV reflectance on host perception. In contrast to this result, our study revealed a positive effect of lowering UV reflectance at the blunt pole of experimental eggs on egg rejection in blackcaps. To our knowledge, this is the first experimental evidence showing that a reduction of UV wavelengths reflected from the parasitic eggshells may significantly influence host recognition behaviour.

There are several possible explanations of why our results differ from those of the Avilés et al. (Avilés et al., 2006a) study. First, corvids and small passerines may vary in their UV signal perception (Avilés et al., 2006a). Second, the logistic regression in our study revealed that it is not just UV perception that is important in recognition behaviour of blackcaps but also other parameters including host eggs characteristics. Another possibility for the differences could be the chemicals used. Our UV-blocking chemical covered a larger range of UV wavelengths than that used by Avilés et al. (Avilés et al., 2006a) and the experimental eggs coated in this UV block were darker (for comparison see Fig. 1 in both studies). Moreover, Avilés et al. (Avilés et al., 2006b) discovered that nest light properties may influence host discrimination towards parasitic eggs as the UV wavelengths reflected from the egg surface could be chosen to provide detectable cues for hosts in poorly lit environments. However, this does not apply in our case, as blackcaps usually breed in open nests. Finally, another reason for the different results could be different recognition abilities of the two tested hosts (magpies and blackcaps). Since blackcaps exhibit good recognition abilities resulting in a high rejection rate (Honza et

al., 2004; Polačiková et al., 2007), their egg recognition should favour a greater variety of different shell cues in comparison with species that exhibit lower recognition abilities. Variation in egg recognition by different hosts has been explained by different duration of co-evolution between the brood parasite and its host (Brooke and Davies, 1988; Soler and Møller, 1990). Although magpies live in sympatry with cuckoo, this species belongs to a naive host group with lower recognition abilities, that are not as sophisticated as those of blackcaps.

Our results show that not only UV wavelengths but also total brightness of experimental eggs within the 325–700 nm wavelength range significantly influenced host rejection behaviour. Our previous results on blackcaps showed that birds reject every egg that is even a little bit lighter than the host eggs and accept all eggs that are as dark as or much darker than their own host clutch. This may be connected with the spot concentration of the blackcap's eggshell (Makatsch, 1976), which might theoretically serve as a fingerprint of individual females (Kilner, 2006). Alternatively, if synthesis and allocation of pigments into the eggshell is costly (Moreno and Osorno, 2003), the darkness of the blunt end of the egg may be linked to the quality and age of the bird (Moreno et al., 2006; Siefferman et al., 2006), which can be further reflected in the host rejection response (Lotem et al., 1995).

Our findings supported the significance of ultraviolet reflectance in the egg recognition processes of hosts. However, further studies are needed to disentangle the role of functional mechanism of the UV wavelengths in egg recognition for better understanding of this co-evolutionary brood-parasitism system.

REFERENCES

Avilés, J. M. and Møller, A. P. (2004). How is host egg mimicry maintained in the cuckoo (*Cuculus canorus*)? *Biol. J. Linn. Soc. Lond.* **82**, 57-68.

Avilés, J. M., Soler, J. J., Perez-Contreras, T., Soler, M. and Møller, A. P. (2006a). Ultraviolet reflectance of great spotted cuckoo eggs and egg discrimination by magpies. *Behav. Ecol.* **17**, 310-314.

Avilés, J. M., Soler, J. J. and Perez-Contreras, T. (2006b). Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. *Proc. R. Soc. Lond. B, Biol. Sci.* **273**, 2821-2829.

Bennett, A. T. D. and Cuthill, I. C. (1994). Ultraviolet vision in birds: what is the function? *Vision Res.* **34**, 1471-1478.

Brooke, M. de L. and Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by host. *Nature* **335**, 630-632.

Chen, D. M. and Goldsmith, T. H. (1986). Four spectral classes of cone in the retinas of birds. *J. Comp. Physiol. A* **159**, 473-479.

Cherry, M. I. and Bennett, A. T. D. (2001). Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. *Proc. R. Soc. Lond. B, Biol. Sci.* **268**, 565-571.

Cherry, M. I., Bennett, A. T. D. and Moskát, C. (2007). Host intra-clutch variation, cuckoo egg matching and egg rejection by great reed warblers. *Naturwissenschaften* **94**, 441-447.

Cuthill, I. C., Partridge, J. C. and Bennett, A. T. D. (2000). Avian UV vision and sexual selection. In *Animal Signals: Signalling and Signal Design in Animal Communication* (ed. Y. Espmark, T. Amundsen and G. Rosenqvist), pp. 61-82. Norway: Tapir Publisher.

Davies, N. B. (2000). *Cuckoos, Cowbirds and Other Cheats*. London: T and A D Poyser.

Davies, N. B. and Brooke, M. de L. (1989). An experimental study of co-evolution between the cuckoo *Cuculus canorus*, and its hosts. I. Host egg discrimination. *J. Anim. Ecol.* **58**, 207-224.

Dawkins, R. and Krebs, J. R. (1979). Arms races between and within species. *Proc. R. Soc. Lond. B, Biol. Sci.* **205**, 489-511.

Edvardsen, E., Moksnes, A., Røskaft, E., Øien, I. J. and Honza, M. (2001). Egg mimicry in cuckoos parasitizing four sympatric species of *Acrocephalus* warblers. *Condor* **103**, 829-837.

Endler, J. A. (1990). On the measurement and classification of color in studies of animal recognition. *Biol. J. Linn. Soc. Lond.* **41**, 315-352.

Harth, N. S., Partridge, J. C. and Cuthill, I. C. (1998). Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). *J. Exp. Biol.* **201**, 1433-1446.

Hays, H. and LeCroy, M. (1971). Field criteria for determining incubation stages in eggs of the common tern. *Wilson Bull.* **83**, 425-429.

Honza, M., Polačiková, L. and Procházka, P. (2007). UV and green parts of the colour spectra affect egg rejection in the song thrush (*Turdus philomelos*). *Biol. J. Linn. Soc. Lond.* **92**, 269-276.

Honza, M., Moksnes, A., Røskaft, E. and Stokke, B. G. (2001). How are different common cuckoo morphs maintained? An evaluation of different hypotheses. *Ardea* **89**, 341-352.

Honza, M., Procházka, P., Stokke, B. G., Moksnes, A., Røskaft, E., Čapek, M., Jr and Mrlík, V. (2004). Are blackcaps current winners in the evolutionary struggle against the common cuckoo? *J. Ethol.* **22**, 175-180.

Huth, H. H. and Burkhardt, D. (1972). Der spectrale Sehbereich eines Violettohr-Kolibris. *Naturwissenschaften* **59**, 650.

Kilner, R. M. (2006). The evolution of egg colour and patterning in birds. *Biol. Rev. Camb. Philos. Soc.* **81**, 383-406.

Lack, D. (1968). *Ecological Adaptations for Breeding in Birds.* London: Methuen.

Lotem, A., Nakamura, H. and Zahavi, A. (1995). Constraints on egg discrimination and cuckoo-host co-evolution. *Anim. Behav.* **49**, 1185-1209.

Lovaszi, P. and Moskát, C. (2004). Break-down of arms race between the red-backed shrike (*Lanius collurio*) and common cuckoo (*Cuculus canorus*). *Behaviour* **141**, 245-262.

Makatsch, W. (1976). *Die Eier der Vögel Europas.* Radebeul: Neumann.

Moksnes, A., Røskaft, E., Bičík, V., Honza, M. and Øien, I. J. (1993). Cuckoo *Cuculus canorus* parasitism on *Acrocephalus* warblers in Southern Moravia in the Czech Republic. *J. Ornithol.* **134**, 425-434.

Moreno, J. and Osorno, J. L. (2003). Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecol. Lett.* **6**, 803-806.

Moreno, J., Lobato, E., Morales, J., Merino, S., Tomas, G., Martinez-de la Puente, J., Sanz, J. J., Mateo, R. and Soler, J. J. (2006). Experimental evidence that egg color indicates female condition at laying in a songbird. *Behav. Ecol.* **17**, 651-655.

Moskat, C. and Fuisz, T. I. (1999). Reactions of red-backed shrikes *Lanius collurio* to artificial cuckoo *Cuculus canorus* eggs. *J. Avian Biol.* **30**, 175-181.

Moskát, C. and Honza, M. (2002). European cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized great reed warbler *Acrocephalus arundinaceus* population. *Ibis (Lond. 1859)* **144**, 614-622.

Moskat, C., Szekely, T., Cuthill, I. C. and Kisbenedek. T. (2008). Host's responses to parasitic eggs: which cues elicit host's egg discrimination? *Ethology* **114**, 186-194.

Payne, R. B. (1997). Avian brood parasitism. In *Host-parasite Evolution: General Principles and Avian Models.* (ed. D. H. Clayton and J. Moore), pp. 338-369. Oxford: Oxford University Press.

Polačiková, L., Honza, M., Procházka, P., Topercer, J. and Stokke, B. G. (2007). Colour characteristics of the blunt part of blackcap (*Sylvia atricapilla*) eggs: possible cues for egg recognition. *Anim. Behav.* **74**, 419-427.

Procházka, P. and Honza, M. (2003). Do common whitethroats (*Sylvia communis*) discriminate against alien eggs? *J. Ornithol.* **144**, 354-363.

Procházka, P. and Honza, M. (2004). Egg discrimination in the yellowhammer. *Condor* **106**, 405-409.

Rothstein, S. I. (1982a). 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. (1982b). Mechanisms of avian egg recognition: which parameters elicit responses by rejecter species? *Behav. Ecol. Sociobiol. (Print)* **11**, 229-239.

Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Syst.* **21**, 481-501.

Siefferman, L., Navara, K. J. and Hill, G. E. (2006). Egg coloration is correlated with female condition in eastern bluebirds (*Sialia sialis*). *Behav. Ecol. Sociobiol. (Print)* **59**, 651-656.

Soler, J. J. and Møller, A. P. (1990). Duration of sympatry and coevolution between the great spotted cuckoo and its magpie host. *Nature* **343**, 748-750.

Soler, J. J., Avilés, J. M., Soler, M. and Moller, A. P. (2003). Evolution of host egg mimicry in a brood parasite, the great spotted cuckoo. *Biol. J. Linn. Soc. Lond.* **79**, 551-563.

Stokke, B. G., Moksnes, A., Røskaft, E., Rudolfsen, G. and 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, Biol. Sci.* **266**, 1483-1488.

Underwood, T. J. and Sealy, S. G. (2002). Adaptive significance of egg coloration. In *Avian Incubation, Behaviour, Environment and Evolution* (ed. D. C. Deeming), pp. 280-298. Oxford: Oxford University Press.

Underwood, T. J. and Sealy, S. G. (2006). Parameters of brown-headed cowbird *Molothrus ater* egg discrimination in warbling vireos *Vireo gilvus. J. Avian Biol.* **37**, 457-466.

Underwood, T. J. and Sealy. S. G. (2008). UV reflectance of eggs of brown-headed cowbirds (Molothrus ater) and accepter and rejecter hosts. *J. Ornithol.* DOI 10.1007/s.10336-007-0272-8.

Wright, A. A. (1972). Psychometric and psychophysical hue discrimination functions for the pigeon. *Vision Res.* **12**, 1447-1764.