Biological Journal of the Linnean Society, 2007, **92**, 269–276. With 2 figures

Ultraviolet and green parts of the colour spectrum affect egg rejection in the song thrush (*Turdus philomelos*)

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Received 24 January 2006; accepted for publication 6 December 2006

Much attention has been devoted to understanding the evolution of egg mimicry in avian brood parasites. The majority of studies have been based on human perception when scoring the mimicry of the parasitic egg. Surprisingly, there has been no detailed study on the recognition and sensitivity towards differently coloured parasitic eggs. We investigated effect of different colours of the experimental eggs measured by ultraviolet (UV)-visible reflectance spectrophotometry on rejection behaviour in the song thrush (*Turdus philomelos*). We carried out a set of experiments with four blue model eggs representing mimetic eggs, whereas six other colours represented nonmimetic eggs. Our results revealed that two colours originally designed as a mimetic were rejected at a high rate, whereas one group of the nonmimetic was accepted. A multiple regression model of absolute differences between song thrush and experimental eggs on rejection rate showed that the level of mimicry in the UV and green parts of the colour spectrum significantly influenced egg rejection in the song thrush. To our knowledge, this is the first detailed study showing that different colour perception by the birds can affect their responses towards the parasitic egg. These findings suggest that the combination of UV and visible ranges of the spectra plays a major role in the evolution of discrimination processes, as well as in the evolution of the mimicry of the parasitic egg.

ADDITIONAL KEYWORDS: brood parasitism – cuckoo – egg appearance – evolution of mimicry – reflectance spectrophotometry.

INTRODUCTION

Birds possess probably the most advanced visual system of any vertebrate (Goldsmith, 1990) and therefore it is natural to expect that the colour of eggs will play a major role in avian life histories in many respects. Underwood & Sealy (2002) reviewed several functional explanations of the evolution of the striking variability in bird egg coloration. One of the exciting topics dealing with the function of egg colour is the problem related to brood parasitism, namely the host's ability to recognize an alien egg connected with its ejection.

Brood parasitism is a reproductive strategy adopted by approximately 1% of birds (Payne, 1977). Obligate brood parasites lay their eggs in the nests of other species (hosts) and these take over the care of incubation and feeding of the parasite nestlings. If successful (i.e. the host accepts the parasitic egg and successfully raises the parasitic chick), then the host breeding success is very low and close to zero (Øien *et al*., 1998). Thus, this scenario represents a strong selective agent for the hosts to evolve appropriate mechanisms to minimize the detrimental effect of parasitism. A very effective defence technique in the

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host that has been developed against the reproduction of the brood parasites is the recognition and rejection of parasitic eggs from their nest. One of the recognition cues in the species parasitized by the cuckoo is their lower intraclutch variation in egg appearance compared with those that have not been parasitized (Øien, Moksnes & Røskaft, 1995; Soler & Møller, 1996; Stokke, Moksnes & Røskaft, 2002). Such a finding has been documented also at the intraspecific level: rejecter individuals have a lower intraclutch variation in egg appearance compared with acceptor ones (Stokke *et al.*, 1999; Soler, Soler & Møller, 2000). Not only appearance, but also the contrast between the host and parasitic eggs has an effect on egg recognition (Procházka & Honza, 2003; Honza *et al.*, 2004). Because ejection of the parasitic egg represents an evolutionary force on the parasite, mimicking the host eggs can help to overcome this selective agent in the coevolutionary struggle. Many studies have been published on the response of the hosts towards differently mimetic cuckoo eggs in natural conditions (Alvarez, 1994; Edvardsen *et al.*, 2001; Rutila, Latja & Koskela, 2002; Kleven *et al.*, 2004). However, the interactions between the host and parasitic egg have been studied mainly experimentally by monitoring the responses towards nonmimetic egg (Davies & Brooke, 1989; Moksnes *et al.*, 1991b; Procházka & Honza, 2003, 2004) or differently mimetic eggs (Lotem, Nakamura & Zahavi, 1995; Honza & Moskát, 2005; Honza, Kuiper & Cherry, 2005).

Nevertheless, these studies did not consider the 'bird-eyes' perspective (Cuthill & Bennet, 1993; Bennet & Cuthill, 1994; Church *et al.*, 1998). The fact that mimicry has been assessed by human observers, without consideration of the differences between human colour vision and the visual system in birds, may have lead to incorrect conclusions being drawn because colour determination based on human vision is not applicable to ultraviolet (UV)-sensitive study objects (Bennet & Cuthill, 1994; Bennett, Cuthill & Norris, 1994). Even though birds can detect wavelengths in the same range as humans (approximately 400–700 nm), most birds are also sensitive to UV wavelengths in the range 300–400 nm (Huth & Burkhardt, 1972; Wright, 1972; Bennet & Cuthill, 1994). These discrepancies from humans give the birds a potential for higher dimensions of colour space, modulated by wavelengths that humans cannot perceive (Thompson, Palacios & Varela, 1992; Bennet & Cuthill, 1994). Cuthill, Partridge & Bennett (2000) and Honkavaara *et al.* (2002) reviewed several hypotheses regarding the functional significance of avian UV vision in mate choice and foraging. However, growing interest in the function of UV vision in birds has led researchers to investigate also the role of UV reflectance in brood parasite mimicry (Cherry & Bennet, 2001; Avilés & Møller, 2003, 2004; Soler *et al.*, 2003).

In addition, all the available studies published to date have considered the degree of similarity between the coloration of brood parasitic eggs as evidence for mimicry without considering the different sensitivity towards different colours of the particular hosts. This aspect is crucial because some species can tolerate eggs appearing to humans as nonmimetic and/or some colours classified by humans as mimetic may be quickly rejected. Therefore, we conducted a series of experiments with differently coloured experimental parasitic egg representing mimetic and nonmimetic eggs as classified by humans. The major goal was to explore host sensitivity towards different colours of the parasitic eggs (measured by reflectance spectrophotometry) resulting in the different host's responses. The reflectance spectrophotometry technique allowed us to objectively determine colour parameters eliciting the rejection behaviour.

MATERIAL AND METHODS

STUDY AREAS

The study was conducted in the south-eastern Czech Republic in late April to early May 2001–05 at: Dolní Bojanovice (48°51′N, 17°02′E), Dukovany (49°05′N, 16°11′E), Brno (49°12′N, 16°37′E), Rousínov (49°12′N, 16°53′E), Studenec (49°13′N, 16°05′E), and Veverské Knínice (49°14′N, 16°24′E). Because egg rejection responses of the tested birds did not differ among years or sites, all data were pooled in the subsequent analyses.

STUDY SPECIES

The song thrush is a monogamous passerine breeding at relatively high densities in south-eastern part of the Czech Republic. The species lays bluish eggs of uniform ground colour and rejects model nonmimetic eggs (Grim & Honza, 2001). This makes it a good candidate for the present study.

EXPERIMENTAL EGGS

Conspecific eggs used for the experiment were collected from abandoned clutches. In addition to conspecific eggs, we used model eggs made of plaster and painted by various acrylic colours. Each group of eggs was painted at once using one blended colour. Colours were classified according to PANTONE formula guide coated/uncoated (Pantone Inc., 2004) and traditionally divided into two groups according to human vision: four different shades of blue represented mimetic eggs, whereas six other colours represented a group of

Table 1. PANTONE colour codes and rejection rates of experimental eggs (number of rejected eggs/total number of experiments given in parentheses)

Egg type	Code	Rejection rate (%)
Mimetic		
Blue	2915 C	76.4 (13/17)
Light blue	2975 U	33.3 (5/15)
Dark blue	300 C	55.5 (10/18)
Bluish	299 C	20.0 (3/15)
Conspecific	–	7.7 (1/13)
Nonmimetic		
Light brown	732 U	73.3 (11/15)
Dark brown	476 U	86.6 (13/15)
Orange	7507 U	92.8 (13/14)
Pink	5025 U	76.9 (10/13)
Red	1788 C	53.3 (8/15)
Green	369 C	20.0 (3/15)

nonmimetic eggs (Table 1). The sample of experimental and song thrush eggs were measured (length, L; breadth, B) to the nearest 0.1 mm using callipers. Egg volume (V) was calculated using the formula $V = 0.51 \times L \times B^2$ (Hoyt, 1979). The size of experimental eggs was similar to common cuckoo eggs; the experimental egg were significantly smaller than song thrush eggs (mean ± SD = 4291.03 ± 501.51 mm^3 versus 5801.21 ± 515.63 mm^3, $N_1 = N_2 = 14$; Mann–Whitney U-test, $U = 21$, $P = 0.00$). The fact that these eggs were hard-shelled did not affect their rejection by the song thrush because this species is a grasp ejector (Moksnes, Røskaft & Braa, 1991a; M. Honza, unpubl. data based on videotaping of experimentally parasitized nests). The experimental egg was added into the nest on the day that the fourth egg was laid or during the early incubation stage. There were no differences in egg rejection between the nests experimentally parasitized during laying and during the first days of incubation ($\chi^2 = 1.33$, d.f. = 1, $P = 0.25$). Each nest was parasitized only once. Our pilot study revealed no difference in the rejection rates when the egg was added or switched with a host egg. Therefore, in the present study, we added and did not swap the eggs. The nests were monitored daily for 4 days after manipulation. If the parasitic egg disappeared within this period but the host eggs were left unharmed, it was considered to have been ejected. If the parasitic egg remained unharmed in the nest, it was considered to have been accepted. If the clutch was abandoned within the 4-day observation period, it was considered to have been deserted. Rejection includes both egg ejection and clutch desertion. Depredated clutches were excluded from the analyses.

MEASUREMENT OF THE REFLECTANCE SPECTRA

Spectral data provide an objective way to quantify colour (Endler, 1990; Cuthill *et al.*, 1999). We obtained reflectance spectra in the range 300–700 nm from each experimental egg and thrush egg using a spectrophotometer (USB2000, Ocean Optics). We measured colour in five randomly selected areas of the egg surface, each covering approximately 1 mm^2. We measured five song thrush eggs from five randomly chosen clutches and five randomly chosen experimental eggs of each colour. There was a high consistency of colour estimations in our study, and we found a high repeatability for each egg (Pearson correlation coefficient, $R > 0.94$, $P < 0.0001$); therefore we believe that these numbers were sufficient to obtain reasonable data.

The illuminant was a deuterium and halogen light source (DT-Mini-GS, Ocean Optics). The light was transferred to the eggs through a quartz optic fibre (QR400-7-UV/VIS-BX, Ocean Optics) and reached the eggs at an angle of 45°; data from the spectrometer were converted into OOIBase 32 (Ocean Optics) software. The measurements were relative and referred to the darkness and to a standard white reference (WS-2). We made a reference and dark calibration before measurement of each clutch. Total reflectance was obtained over a 100-nm part of the UV region (300–400 nm), and at 75-nm intervals in the blue (400–475 nm), green (475–550 nm), yellow (550–625 nm), and red (625–700 nm) wavelengths.

We calculated objective variables of colour (Endler, 1990). The total intensity of light reaching the bird eye from the egg (i.e. brightness) was the sum of the total reflectance values for all the UV and visible wavelength intervals ($R_{300–700}$). Values of reflectance ratios ($R_{300–400/300–700}$, $R_{400–475/300–700}$, $R_{475–550/300–700}$, $R_{550–625/300–700}$, and $R_{625–700/300–700}$) were used as estimates of 'UV chroma', 'blue chroma', 'green chroma', 'yellow chroma', and 'red chroma' (Sheldon *et al.*, 1999). The wavelength of the peak reflectance λ ($R_{\max}$) over the entire avian spectrum (300–700 nm) was used as an estimation of hue (Endler, 1990).

To estimate the degree of mimicry among host and parasite eggs, we first calculated the absolute differences of mean reflectance value in the UV, blue, green, yellow, and red wavelengths between the host and experimental egg. Mean values of these absolute differences were considered to represent the degree of mimicry between the host and parasite egg.

RESULTS

MIMETIC EGGS

Representative reflectance spectra of the eggs classified as mimetic by humans are shown in Figure 1.

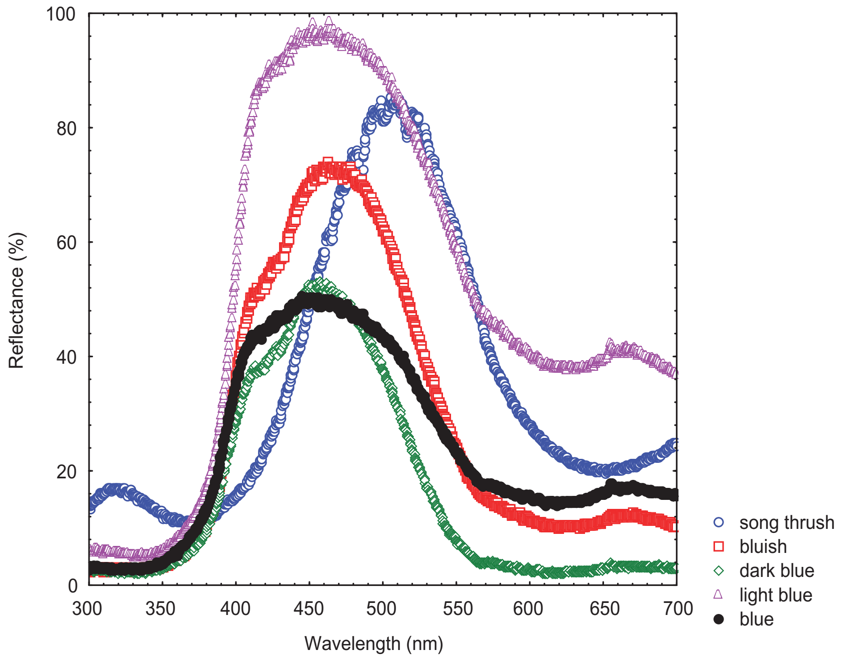

Figure 1. Representative reflectance spectra of the colours of the mimetic and song thrush eggs. Symbols are the means from five measurements of five randomly chosen eggs.

Table 2. Mean absolute differences (level of mimicry) between song thrush and experimental eggs

	Ultraviolet	Blue	Green	Yellow	Red
Green	11.32 ± 3.07	36.38 ± 2.53	52.39 ± 11.46	22.20 ± 3.35	15.47 ± 2.79
Light brown	10.81 ± 4.47	31.97 ± 3.71	67.87 ± 11.44	20.42 ± 6.49	4.63 ± 4.20
Dark brown	10.00 ± 3.92	32.46 ± 3.13	70.05 ± 11.98	26.99 ± 4.69	11.85 ± 4.10
Orange	1.41 ± 0.49	15.04 ± 6.09	17.01 ± 11.66	46.50 ± 11.73	66.35 ± 13.62
Pink	2.42 ± 3.83	37.07 ± 1.69	13.64 ± 8.36	38.16 ± 5.55	55.39 ± 5.51
Red	11.51 ± 4.54	37.94 ± 2.74	76.52 ± 10.99	7.11 ± 5.14	60.61 ± 5.53
Blue	5.29 ± 4.18	9.51 ± 6.47	38.94 ± 13.26	19.15 ± 4.76	5.34 ± 3.82
Light blue	4.38 ± 4.47	50.52 ± 9.49	10.89 ± 7.38	8.85 ± 6.24	17.94 ± 5.52
Bluish	6.29 ± 4.12	22.10 ± 3.54	25.51 ± 11.84	22.09 ± 4.64	10.10 ± 3.84
Dark blue	7.15 ± 4.46	5.43 ± 2.34	48.08 ± 10.13	32.33 ± 4.88	18.40 ± 4.20

Data are means ± SD.

Conspecific eggs were accepted in 92.3% (12/13) of cases. On the other hand, there were great differences in the rejection rates (20–76.4%) within the mimetic eggs ($\chi^2 = 11.94$, d.f. = 3, $P = 0.008$). Surprisingly, tested birds rejected two colours (blue and dark blue; Table 1) at a high rate.

NON-MIMETIC EGGS

Figure 2 shows representative spectral reflectance for the colours of experimental eggs classified as non-mimetic. Song thrushes discriminated against the majority of the nonmimetic eggs (Table 1); however, they tolerated green eggs, resulting in a mere 20% rejection rate.

LEVEL OF MIMICRY AND THE RESPONSES TOWARDS EXPERIMENTAL EGG

Multiple regression of absolute differences between song thrush and experimental eggs (Table 2) on the rejection rate showed that the level of mimicry in the UV and green parts of the colour spectrum significantly influenced egg rejection in the song thrush

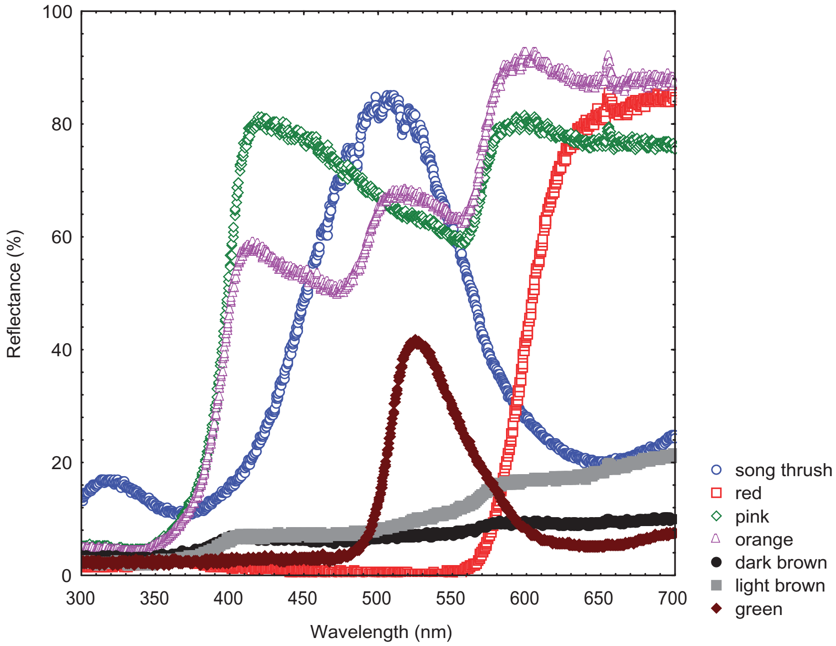

Figure 2. Representative reflectance spectra of the nonmimetic and song thrush eggs. Symbols are means from five measurements of five randomly chosen eggs.

Table 3. Summary of multiple regression (backward stepwise model building in GRM module of STATISTICA; StatSoft Inc.) of absolute differences between song thrush and experimental eggs on rejection rate [$R = 0.850$, $R^2 = 0.722$, adjusted $R^2 = 0.643$, $F_{2,7} = 9.09$, $P = 0.011$, standard error (SE) of estimate = 16.04]

	Parameter	SE	*t*	*P*	β	SE
Intercept	84.95	12.67	6.70	0.000		
Ultraviolet	–16.90	3.99	–4.24	0.004	–2.18	0.51
Green	2.29	0.56	4.09	0.005	2.10	0.51

($R = 0.850$, $R^2 = 0.722$, adjusted $R^2 = 0.643$, $F_{2,7} = 9.09$, P = 0.011, SE of estimate: 16.04; Table 3).

DISCUSSION

The recognition and rejection of the parasitic egg represent very efficient counterdefences against brood parasitism to overcome its detrimental effect on host fitness. Many studies have demonstrated that rejecter species recognize a parasitic egg by true recognition as documented by experiments on host species of various brood parasites that rejected alien eggs (Victoria, 1972; Rothstein, 1975, 1977; Moksnes, 1992). Moreover, studies conducted with experimental brood parasite eggs have shown that, when added to host nests, mimetic eggs were rejected significantly less frequently than nonmimetic eggs (Moksnes, 1992; Moskát & Fuisz, 1999). Some studies revealed a fine-tuned discrimination towards even differently mimetic eggs (Honza & Moskát, 2005; Honza *et al.*, 2005). It must be stressed, however, that these findings were based upon human vision. If this human approach is correct, then one should expect that the birds should respond towards both mimetic and nonmimetic eggs consistently (i.e. mimetic eggs should be accepted and nonmimetic eggs should be rejected). By contrast, in the present study, we found that the birds behaved inconsistently within both groups classified as mimetic/nonmimetic according to human perception. One can criticize our approach in that we used such colourful eggs, but bright blue or emerald green eggs, and also yellowish and red eggs, are laid by many species (Underwood & Sealy, 2002; Moreno *et al.*, 2005).

Moksnes & Røskaft (1995) classified museum egg collections of European passerine clutches based on human vision and found at least 15 different cuckoo egg-morphs in Europe, but none of these cuckoo eggs matched the eggs of the song thrush in appearance. Previous studies (Davies & Brooke, 1989; Moksnes *et al.*, 1991b; Grim & Honza, 2001) showed that song thrushes reject experimental eggs mimicking those of several cuckoo gentes at different rates (58.5%, 80.0%, and 58.3%, respectively).

These studies, however, used different colours but did not evaluate the coloration objectively. We used a range of colours and assessed the appearance of eggs using reflectance spectrophotometry. One should expect higher consistency in the responses towards nonmimetic eggs. Indeed, the majority of our differently coloured nonmimetic eggs were rejected at high rates (54–94%). However, this species was very tolerant towards green eggs and these were accepted at a similar rate as the conspecific. By contrast to the splitting of the experimental eggs into two groups using human vision, the song thrushes surprisingly rejected only two colours of mimetic eggs (dark blue and blue) at rates of 55.5% and 76.4%, respectively.

Although Davies & Brooke (1989) considered their model eggs of the redstart cuckoo gens as nonmimetic, this egg model had the lowest rejection rate (27.3%). This model represented immaculate pale blue eggs and we assume that song thrushes could have considered this egg type to be the most similar in coloration to their own eggs (mimetic egg). By contrast, the reed warbler type, represented by a greenish egg with green and brown speckling, was rejected at a rate of 100%. This example illustrates how questionable the usage of categories such as mimetic versus nonmimetic might be (for a detailed discussion of this issue, see Grim, 2005).

The colour of the object depends on the relative amounts of different wavelengths of light it reflects, emits or transmits (Cuthill *et al.*, 2000). Colour is a psychophysical property (Thompson *et al.*, 1992). To see the colour, it is essential to have photoreceptors sensitive to diverse wavelengths of light and, simultaneously, to be able to compare the photoreceptors outputs (Cuthill *et al.*, 2000). Birds are at least tetrachromats compared with the existing trichromatal vision in humans (Bennet & Cuthill, 1994); each type of cone is maximally sensitive to different wavelengths (Chen & Goldsmith, 1986). The sensation of colour does not result from the action of cone types in isolation, but from the neural comparison of their outputs (Cuthill *et al.*, 2000). Because colour perception is created by a combination of certain wavelengths, a simple dissimilarity from human vision provides birds with a potential for higher dimensions of colour space, adjusted by wavelengths that humans cannot perceive (Bennett & Cuthill, 1994).

Our results showed that a combination of UV and green wavelengths plays a role in the process of egg discrimination in the song thrush. Higher rejection rates were shown for models of greater contrasts with song thrush eggs in the green spectrum, although this was only in conjunction with UV wavelengths. The fact that hosts do not use only the reflectance of UV light, as Cherry & Bennett (2001) demonstrated, but also its combination with the human visible part of the spectrum, is of particular importance.

It is not surprising that UV is important in the recognition of parasitic eggs by the song thrush because Hart *et al.* (2000) showed that a closely related species, the blackbird, is also sensitive in the UV waveband. Cherry & Bennett (2001) demonstrated the importance of UV wavelengths for the discrimination of cuckoo egg by the Cape robin (*Cossypha caffra*). Similarly, but with respect to intraclutch variation, Avilés & Møller (2003) confirmed that an allopatric population of meadow pipits (*Anthus pratensis*) shows greater variation within clutches in egg appearance of the UV part of the spectrum than a population sympatric with the common cuckoo *Cuculus canorus*. They concluded that the methods of assessment of egg appearance within clutches based on human vision might not be sufficiently sensitive to assess variation in certain colour components that may be crucial for host discrimination of the parasitic egg.

We also demonstrated the importance of green wavelengths for song thrush egg discrimination. The importance of the green spectrum has been suggested by Avilés *et al.* (2004) who documented that acceptor magpies (*Pica pica*) of the great spotted cuckoo (*Clamator glandarius*) model egg had a lower intraclutch variation in egg appearance compared with rejecters in green chroma only.

The results of our study provide strong evidence indicating that not only UV, but also its combination with visible parts of the colour spectrum, is very important in egg recognition. This challenging result contributes to a better understanding of evolution of host egg discrimination and, consequently, of egg mimicry evolution.

ACKNOWLEDGEMENTS

We are deeply indebted to B. G. Stokke for his advice with spectrometric measurements of egg reflectance. T. Albrecht, M. Čapek, T. Grim, V. Mrlík, M. Polačik, M. Požgayová, and J. Rybaříková assisted in the field. M. Požgayová and S. Švédová helped with making the model eggs. The study was supported by GAAV (grant no. A600930605) and MSM (grant no. LC06073).

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