



# Egg Characteristics Affecting Egg Rejection **22**

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## Abstract

We have reviewed the most important results relating to particular egg characteristics responsible for recognition and subsequent rejection by hosts of brood parasites. Hosts remove a foreign egg after determining that it differs in one or more parameters. In turn, brood parasites have often evolved various mechanisms to confuse host defences and prevent egg recognition. The most conspicuous one is egg mimicry—imitation of the appearance of host eggs. We evaluate and discuss egg rejection experiments, particularly from a historical perspective, and the use of cameras in experiments. Further, we describe assessments of egg mimicry, and in particular we focus on the role played by particular characteristics in discrimination including egg colour, spottiness, chromatic versus achromatic cues, the role of UV spectra, the blunt egg pole, and the shape and volume of the parasitic egg. In addition, we discuss how research methodology and the application of experimental approaches to studying avian vision have affected studies on egg discrimination.

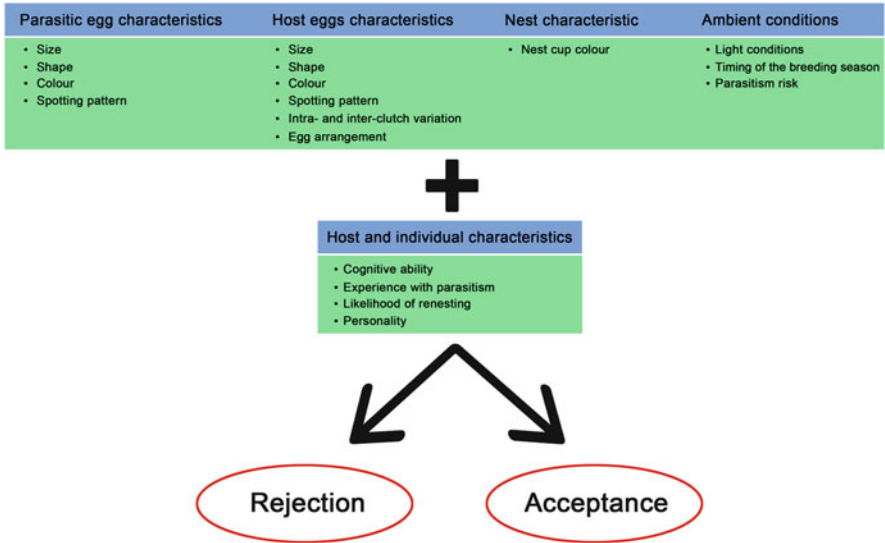
## 22.1 Introduction

A successful act of brood parasitism has a disastrous effect on host fitness because it decreases host reproduction considerably (Payne and Payne 1998; Davies 2000). However, in the face of this selection pressure, many hosts have evolved egg

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**Fig. 22.1** Cues facilitating recognition of a foreign egg by avian brood parasite hosts

discrimination, as an antiparasite defence mechanism (Davies and Brooke 1989). Strong evidence that egg recognition can function as a defence against brood parasitism is provided by studies showing that egg rejection rates correlate spatially (Soler et al. 1999a; Lindholm and Thomas 2000) or temporally (Brooke et al. 1998; Nakamura et al. 1998) with the likelihood of cuckoo parasitism.

Egg discrimination is a two-stage process comprising perceptual (egg recognition) and operational (egg rejection) components (Hauber and Sherman 2001). With regard to perception, hosts can discern a foreign egg by at least two cognitive mechanisms (Moskát and Hauber 2007; Moskát et al. 2010), namely, (1) direct comparison (Rothstein 1974; Lahti and Lahti 2002) or (2) memory (Hauber et al. 2006; Moskát and Hauber 2007; see Chap. 24 for a discussion on how different mechanisms influence egg recognition and rejection). Many cues facilitating recognition of a foreign egg play an important role in the host recognition processes (see Fig. 22.1). After assessing the level of difference between foreign and its own eggs, the host takes into account other factors such as the costs associated with egg rejection and the risk of parasitism (Davies et al. 1996; Soler et al. 2012) and may then elect to remove the foreign egg. In turn, brood parasites have often evolved various tricks to confuse hosts and prevent egg recognition. The most conspicuous is egg mimicry—imitation of the appearance of host eggs—which evolves in response to selection pressure from host ejection of brood parasite eggs (see Chap. 20).

## 22.2 Egg Rejection Experiments

### 22.2.1 A Historical Perspective

After establishing that brood parasites lay eggs in host nests and that the egg sometimes disappears from the parasitized nests, naturalists turned their attention to answering questions about how the parasitic egg disappears and which factors caused its removal. Sealy and Underwood (2012) provide a detailed summary of observations by early naturalists who experimentally tested host responses towards real eggs originating from different species. Perhaps two names from a large number of experimenters should be highlighted: Swynnerton (1918)—who confirmed egg ejection—and Rensch (1925), who examined egg recognition by the hosts. A milestone in progress of the experimental approach is the series of papers published by Rothstein in the early 1970s (Rothstein 1974). These well and carefully designed studies based on experiments (using model eggs) provided both a baseline and inspiration for future studies. Early ones were Álvarez et al. (1976), Davies and Brooke (1988, 1989), Cruz and Wiley (1989), Higuchi (1989), Moksnes and Røskaft (1989), Soler (1990), and Sealy (1992), carried out in different areas studying different host–parasite systems. Since then, a numerous studies involving egg recognition experiments have been performed in 182 different host species (see Appendix in Soler 2014) based on different approaches using painted real, model or conspecific, or other natural parasitic eggs.

The next step involved the use of carefully designed colour manipulation of the both parasitic and host eggs: this approach has yielded new insights into underlying cognitive processes regarding discrimination of the parasitic egg (de la Colina et al. 2012). This has allowed the documentation of adaptive modulation of antiparasitic strategies through shifts in the acceptance threshold of hosts (Hauber et al. 2006) or the conditions under which hosts reduce discrimination of foreign eggs (Moskát et al. 2008a) and has demonstrated that rejection using a recognition template might be advantageous in populations with high rates of multiple parasitism (Moskát et al. 2010). A variety of other aspects of egg rejection behaviour have been tested experimentally, such as its repeatability (Honza et al. 2007a; Croston and Hauber 2014a), the costs of rejection (Martín-Vivaldi et al. 2002; Underwood and Sealy 2006a; Segura et al. 2016), responses to avian brood parasitism in sympatric and allopatric host populations (Soler and Møller 1990; Briskie et al. 1992; Soler et al. 1999b; Stokke et al. 2008; Vikan et al. 2010; Yang et al. 2014), methods of rejection of parasitic eggs (Sealy 1995; Soler et al. 2015), and timing of ejection (Požgayová et al. 2011).

Egg rejection experiments do not necessarily imply manipulation of egg colour alone. For example, tests of the “egg arrangement hypothesis” by Polačiková et al. (2013) and Hanley et al. (2015) and the evaluation of egg nest contrasts by Aidala et al. (2015) have brought new insights into additional cues driving parasitic egg rejection.

In addition, there have been many studies testing egg shape discrimination of the hosts of brood parasites using various non-egg-shaped objects, e.g. Ortega and Cruz (1988) and Moskát et al. (2003), as well as over a range of different-sized objects (Guigueno and Sealy 2009, 2012; Álvarez et al. 1976). Underwood and Sealy (2006b) concluded that rejection of odd-shaped objects most likely represents an expression of nest sanitation behaviour, where debris is removed from the nest. Egg shape recognition is predicted to be most advanced in birds which can differentiate between non-egg items in the nest and parasite or own eggs (Peer et al. 2007; Guigueno and Sealy 2009).

Igic et al. (2015) recently suggested a new method—3D printing technology—of producing experimental eggs which enables more precise manipulation of egg size and shape. Soler et al. (2015) also suggested a new method to reproduce the exact colour of both background and spot colours, in which a specialized company (Copingra Pinturas) used a laser scanner to produce paints for experimental eggs. In conclusion, there has been dramatic progress in experimental approaches over the last two decades in the use of egg rejection experiments, providing new insights into our understanding of the behaviour of hosts towards parasitic eggs.

### 22.2.2 Assessment of Egg Mimicry: From Human Vision to Model Avian Vision

Although in retrospect the method of the human scoring mimicry mostly from photographs using a three- to five-point scale (Moksnes and Røskaft 1993, 1995) seems crude, this method was successfully used in many studies on brood parasitism and certainly pushed the boundaries of our knowledge in this area. It must be noted that these studies did not take into consideration the ability of birds to detect UV wavelengths in the 300–400 nm range which is invisible to humans. In addition, eggs used in experimental studies were painted using acrylic paints, which have different spectral reflectances to natural eggshells—in particular not reflecting in the UV. Cherry and Bennett's (2001) paper, by placing emphasis on the potential role of the UV spectrum in avian egg discrimination, inspired a new wave of studies incorporating visual perception in brood parasitism research. These findings led to increased interest in studying the role of UV signals using portable spectrophotometers enabling measurements in the field; and the importance for human invisible spectra was also tested experimentally using UV blocking chemicals (see Sect. 22.3.3). Subsequent studies incorporated measurement of the UV visible range in the cuckoo (Avilés and Møller 2004; Cherry et al. 2007a) and pallid cuckoo (*Cacomantis pallidus*) hosts (Starling et al. 2006), but these studies measured the difference in reflectance between cuckoo and host eggs, ignoring how avian sensory systems process this information (Vorobyev et al. 1998; Cuthill et al. 2000). One should expect that the efficacy of a cuckoo egg in terms of matching

would be influenced by the colour of the cuckoo egg itself, in contrast to the colour of the host eggs, the environment in which matching is perceived by the host, and the perceptual abilities of the host (Endler 1990; Vorobyev et al. 1998). This approach integrates reflectance spectra of cuckoo and host eggs and light conditions in the nest vicinity with published information on photoreceptor sensitivities, photoreceptor noise, and the transmission properties of avian colour vision media (Hart et al. 2000) to calculate differences in matching in host colour space (Vorobyev et al. 1998). The model, developed for the tetrachromatic visual system of birds in its long form (Vorobyev et al. 1998), provides a way of calculating the ability of a bird to distinguish between different colours while accounting for visual pigments absorbance and oil droplet transmittance (Hart et al. 2000; Hart 2001). Avilés (2008) developed a discrimination model approach that simulates host retinal functioning; Cassey et al. (2008) used a photoreceptor noise-limited colour opponent model of host perceptual physiology to predict behavioural rates of experimental egg discrimination of cuckoo or artificial eggs. Spectrometric measures have obvious advantages over human visual estimates of egg colouration, but they have the disadvantage of not assessing the spatial attributes of egg colouration. Stoddard and Stevens (2010) therefore extended this approach and developed a new technique to evaluate spotting patterns in several hosts of the common cuckoo, using digital image analysis to measure a range of attributes including marking size, diversity in size, contrast, coverage, and dispersion. This technique uses Fourier analysis of granularity based on early-stage, low-level visual processes. A refinement of this technique which explicitly tries to quantify recognisability in a way that mimics how a bird's brain works, rather than just extracting objective measures of pattern, was published recently (Stoddard et al. 2014).

### 22.2.3 Artificial Versus Real Eggs

Generally, researchers have used either real brood parasite eggs, conspecific host eggs, or similarly sized eggs of different host species. The usefulness of real eggs can be limited because the relative influences of egg shape, size, and colour on rejection decisions cannot be easily differentiated (Antonov et al. 2009). One great advantage of real eggs is that results more accurately reflect patterns of egg rejection particularly in species that are puncture ejectors. But apart from the fact that real brood parasite eggs are often not easily available, another obvious disadvantage is the fact that eggshell colouration may change quickly with time: Moreno et al. (2011), Navarro and Lahti (2014), and Hanley et al. (2016) have provided evidence that such changes impact brood parasite host eggshell colour mimicry during the incubation stage. So far published work has mostly neglected this fact, although it could be of significance. The use of natural eggs in experiments can also result in the destruction of viable eggs, which is ethically questionable, although if abandoned

natural eggs are used (e.g. Cherry et al. 2007a), this is not problematic. A suitable alternative is the use of eggs from commercial breeds like Chinese quail (*Coturnix chinensis*) (Stokke et al. 2010) or non-fertilized eggs from exotic breeds like Bourke's parrot, (*Neophema bourkii*) (Honza et al. 2007a).

Artificial eggs are specifically useful in separating the relative influences of different phenotypic characteristics on rejection decisions (Álvarez et al. 1976; Rothstein 1982; Hauber et al. 2015; Roncalli et al. 2017 although see Lahti 2015). However, there are limitations to using artificial eggs, traditionally made of plasticine, plastic, wood, or plaster of Paris (Prather et al. 2007). For example, some researchers concede that rejection of hard-shelled eggs may underestimate rejection rate (Moksnes et al. 1991; Martín-Vivaldi et al. 2002; Prather et al. 2007), but see Honza and Moskát (2008) for opposing results. On the other hand, the softness of the material may overestimate ejection (Roncalli et al. 2017). The size of the host, which is manifest in its ability to grasp foreign eggs, plays a major role in this respect. Artificial material may also affect the mode of the responses towards such eggs, as unsuccessful attempts to puncture hard model eggs could increase the costs of rejection and/or provoke clutch desertion (Martín-Vivaldi et al. 2002).

In addition, shell thickness and strength of the parasitic egg (real or artificial) may also influence host reaction times (Antonov et al. 2008; Honza and Moskát 2008). Painting experimental or real eggs using acrylic paints, which have different spectral reflectances to natural eggshells (in particular not reflecting in the UV), is problematic as these eggs may be rejected based on features that were not experimentally manipulated or controlled (Prather et al. 2007). The advent of new acrylic paints reflecting in the UV opens new research possibilities (Šulc et al. 2016).

## 22.2.4 The Use of Cameras

The use of small cameras in well-planned experiments to minimize disturbance to breeding birds has recently become increasingly possible and should enable more detailed study of host responses towards parasitic eggs. Analyses of video recordings of experimentally parasitized nests in particular could contribute to a better understanding of cognitive processes in the context of egg discrimination.

Using cameras has enabled the discovery of birds aggressively pecking the experimental egg (Soler et al. 2002), indicating that egg recognition does not necessarily imply egg rejection. Further evidence of this was the study by Antonov et al. (2009), revealing that eastern olivaceous warblers (*Hippolais pallida*) frequently pecked real cuckoo eggs or experimental egg models but accepted almost half of them; the same behaviour exhibited by warbling vireos (*Vireo gilvus*) was recorded by Underwood and Sealy (2006a). Soler et al. (2012) suggested that pecking not followed by rejection should be considered as part of a stepwise discrimination process, in which accumulating motivation plays a key role in determining behavioural pathways shaping host response to parasitic eggs.

Furthermore, video recordings may be also useful in the detection of variation of the responses towards parasitic egg at the level of host populations, host species, or

host individuals. These techniques have confirmed that in species where both sexes incubate and spend time in the nest, both males and females eject eggs (Soler et al. 2002; Požgayová et al. 2009), whereas unsurprisingly, in species when only females incubate, only females reject parasitic eggs (Požgayová et al. 2011). Furthermore, it has been demonstrated that increased egg mass provokes the acceptance of an experimental egg that has been previously recognized, because ejection of a heavy egg may imply higher rejection costs for hosts (Ruíz-Raya et al. 2015). So video recording has in particular allowed investigation of the relationship between egg recognition and egg ejection (Antonov et al. 2009; Soler et al. 2012, 2015, 2017; Ruíz-Raya et al. 2015), its timing (Antonov et al. 2008; Požgayová et al. 2011), and the consistency in egg rejection behaviour of hosts when parasitized repeatedly within one breeding attempt (Honza et al. 2007a).

In all these studies, hosts were typically confronted with an artificial, non-mimetic foreign egg placed into their nest. Because it is time-consuming, the majority of studies were conducted for only a short time after the host was “parasitized”. Therefore, despite the difficulties involved, it would be very interesting to study the behaviour and discriminative processes towards real parasitic eggs, to try and resolve the puzzle of why some hosts delay their egg rejection decisions (Požgayová et al. 2011) or, even more important, they decide to accept a previously recognized foreign egg (Soler et al. 2017).

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## 22.3 The Role of Different Factors Affecting Discrimination

### 22.3.1 Egg Colour and Spottiness

Inspired by the early experiments of Rothstein (1982), researchers have attempted to clarify the importance of these cues in recognition. Egg colouration is clearly vitally important as even relatively small perceivable differences in eggshell colouration can result in substantial increase in host rejection rates (Honza et al. 2011; Hauber et al. 2015). Generally, experiments have shown that hosts are able to recognize parasitic eggs on the basis of colour and spotting (Table 22.1): the larger the difference in colour between parasitic egg and host eggs and the greater the difference in spottiness, the greater the probability of rejection. There are some exceptions: for example, Honza et al. (2007b) in a study of song thrushes (*Turdus philomelos*) revealed that some colours of the parasitic eggs classified by humans as non-mimetic were accepted by the hosts. Some hosts may have strong rejection biases towards specific colours. Hanley et al. (2017), working on two Turdid species, the blackbird (*Turdus merula*) and the American robin (*Turdus migratorius*), found that across a natural colour gradient, both species were more likely to accept blue-green eggs and reject brown eggs, regardless of the perceived difference between foreign eggs and their own. By contrast, their responses did not vary across an artificial (green to purple) gradient, suggesting that in Turdids, at least, egg recognition is specifically tuned to the natural gradient of eggshell colouration.

**Table 22.1** Experiments exploring colour and spottiness as cue for rejection (R) of avian brood parasite eggs by hosts

	Findings	Source
Common cuckoo ( <i>Cuculus canorus</i> ) hosts		
Bush warbler ( <i>Cettia diphone</i> )	Adding spots to artificial egg reduced R by half compared to plain eggs	Higuchi (1989)
Rufous bush chat ( <i>Cercotrichas galactotes</i> )	Test with pale and contrasted models, support for colours as cue for R, two types non-mimetic eggs R: 17–20%, two types mimetic eggs R: 10–62%	Álvarez (1999)
Song thrush ( <i>Turdus philomelos</i> )	Green part of the spectrum significant for rejection (R), group of mimetic eggs R: 20–77%; group of non-mimetic eggs R: 20–93%, colour is the cue	Honza et al. (2007b)
Great reed warbler ( <i>Acrocephalus arundinaceus</i> )	Effect of experimentally decreased uniformity of eggs by adding extra spots on freshly laid egg affect R; egg with extra spots R: 60%, with no spots R: 95%	Moskát et al. (2008a)
Great reed warbler	Support for differential use of egg markers by manipulation of spottedness and colour, spot density 15–75% has no effect on R, the spots fully covered egg by dark brown R: 100%	Moskát et al. (2008b)
Great reed warbler	Several treatments with differently colouring eggs (green, orange), R is affected by overall clutch appearance	Moskát et al. (2014)
Oriental reed warbler ( <i>Acrocephalus orientalis</i> )	Own eggs were painted with extra spots, effect on higher R	Li et al. (2016)
Diederik cuckoo ( <i>Chrysococcyx caprius</i> ) hosts		
Red bishop ( <i>Euplectes oryx</i> )	Heavy maculation or darker ground colour significantly affected R	Lawes and Kirkman (1996)
Northern masked weaver ( <i>Ploceus taeniopterus</i> )	Difference in egg colour was a strong predictor for R	Jackson (1993)
Village weaver ( <i>Ploceus cucullatus</i> )	Use variable conspecific egg documented that colour and speckling contain the signature for R	Lahti and Lahti (2002)
Great spotted cuckoo ( <i>Clamator glandarius</i> ) hosts		
Black-billed magpie ( <i>Pica pica</i> )	Difference in mean colour value between model and parasite egg affected R	Soler et al. (2000)
Shiny cowbird ( <i>Molothrus bonariensis</i> ) hosts		
Brown and yellow marshbird ( <i>Pseudoleistes virescens</i> )	R is elicited by difference in colour between parasitic and host eggs	Mermoz and Reboreda (1994)
Mockingbird ( <i>Mimus saturninus</i> )	Strong R of white cowbird morph, evidence for colour discrimination	Sackmann and Reboreda (2003)

(continued)



**Table 22.1** (continued)

	Findings	Source
Mockingbird	R sharply decreased with spots and increased with brightness, R can be explained by spotting and brightness	de la Colina et al. (2012)
Rufous-bellied thrush ( <i>Turdus rufiventris</i> )	Strong R of white cowbird morph, evidence for colour discrimination	Sackmann and Rebores (2003)
Creamy-bellied thrush ( <i>Turdus amaurochalinus</i> )	White eggs R more frequently than spotted eggs when parasitism was associated with the presentation of the cowbird model, but there were no differences when the model was absent	Astie and Rebores (2005)
Red-crested cardinal ( <i>Paroaria coronata</i> )	Groups of mimetic and non-mimetic egg types, R: 6–100%, colour is the cue for R, but also width of egg	Segura et al. (2016)
Brown-headed cowbirds ( <i>Molothrus ater</i> ) hosts		
American robins ( <i>Turdus migratorius</i> )	R only those egg that differed at least two of the three tested trait	Rothstein (1982)
Gray catbirds ( <i>Dumetella carolinensis</i> )	R solely on their white ground colour	Rothstein (1982)
Warbling vireo ( <i>Vireo gilvus</i> )	Spot pattern significantly influenced the probability of R	Underwood and Sealy (2006a)
Cuckoo finch ( <i>Anomalospiza imberbis</i> ) hosts		
Tawny-flanked prinia ( <i>Prinia subflava</i> )	Important predictions for R: colour and aspects of pattern	Spottiswoode and Stevens (2010)

In addition, in some cases, the response to the same colour models is affected by the presence of a parasite (Moksnes and Røskaft 1989; Astie and Rebores 2005), so colour is not the only cue used in discrimination (Segura et al. 2016). Rather interesting is the ability of South American host species which were tested with a white egg: almost all tested species exhibited fine-tuned recognition ability of white, which is an adaptation towards brood parasitism by shiny cowbirds (Table 22.1).

### 22.3.2 The Role of Chromatic Versus Achromatic Cues in Egg Discrimination

At present, we can accurately measure the reflectance of birds' eggs and even simulate (on the basis of the sensitivity of bird cones) how reflected radiation is perceived by birds. From this information, the degree of similarity from the perspective of the host's eye can be assessed to determine the level of colour mimicry of parasitic eggs in the nest of the host. The Vorobyev-Osorio model (Vorobyev and Osorio 1998) calculates chromatic and achromatic contrasts between two coloured objects in a visual space that depends on the number of receptor types of the signal receiver in JNDs (just noticeable differences).

**Table 22.2** Experiments testing the effect of chromatic and achromatic contrasts on the probability of avian brood parasite eggs being rejected (R) by hosts

	Findings	Source
Common cuckoo ( <i>Cuculus canorus</i> ) hosts		
Chaffinch ( <i>Fringilla coelebs</i> )	Discrimination gradually increased with increasing differences in chromatic contrast	Avilés et al. (2010)
Great reed warbler ( <i>Acrocephalus arundinaceus</i> )	Cuckoo eggs were R with poorer chromatic with their eggs, but showed no similar effect for achromatic contrast	Cherry et al. (2007b)
Great reed warbler	R is based on chromatic contrast	Honza et al. (2011)
Blackcap ( <i>Sylvia atricapilla</i> )	R is based on degree of chromatic matching	Polačiková et al. (2007)
Brown-headed ( <i>Molothrus ater</i> ) hosts		
American robin ( <i>Turdus migratorius</i> )	Chromatic difference between natural and model eggs predicts R	Croston and Hauber (2014b)

Table 22.2 shows that chromatic contrast is more important in open-nesting hosts, whereas achromatic contrasts have been suggested to play a crucial role in egg discrimination of species nesting in dark nests where colour information is less important (Avilés et al. 2006; Langmore et al. 2009). This explains why achromatic contrasts do not appear to be important cues for the majority of both cuckoo and cowbird hosts.

### 22.3.3 Ultraviolet Reflectance

In the following studies in which egg appearance was measured using spectrophotometry, the importance of particular wavelengths for egg discrimination was documented in the spotless starling (*Sturnus unicolor*) (Avilés et al. 2006), great reed warbler (*Acrocephalus arundinaceus*) (Cherry et al. 2007b), song thrush (Honza et al. 2007b), blackcap (Polačiková et al. 2007), magpie (*Pica pica*) (Avilés et al. 2004; Soler et al. 2003), and several cowbird hosts (Underwood and Sealy 2008). This strongly suggests that UV vision is used in egg discrimination by birds.

Abernathy and Peer (2015) propose that hosts with brighter UV-reflecting eggs should be more likely to reject UV-blocked eggs than hosts with duller UV-reflecting eggs. Šulc et al. (2016) suggest that such signals may play a more important role when parasitic eggs are non-mimetic rather than mimetic when hosts can use additional cues, such as spotting pattern, to discriminate. Of the total 11 host species (Table 22.3) of hosts that have been tested using own or conspecific UV-blocked eggs, at least two species (blackcap; Honza and Polačiková 2008) and brown thrasher (*Toxostoma rufum*; Abernathy and Peer 2015) appear to use the UV range as the sole cue for discrimination.

**Table 22.3** Experimental tests of the role of ultraviolet reflectance in egg discrimination (R) of avian brood parasite eggs by hosts

	Type of manipulation	UV effect on R	Source
Common cuckoo ( <i>Cuculus canorus</i> ) hosts			
Blackcap ( <i>Sylvia atricapilla</i> )	UV-blocked conspecific egg	Positive	Honza and Polačiková (2008)
Reed warbler ( <i>Acrocephalus scirpaceus</i> )	Conspecific egg coated with UV <sup>-</sup>	Positive	Šulc et al. (2016)
	Non-mimetic UV <sup>+</sup> egg	Positive	Šulc et al. (2016)
	Non-mimetic UV <sup>-</sup> egg	Positive	Šulc et al. (2016)
Brown-headed cowbird ( <i>Molothrus ater</i> ) hosts			
Brown thrasher ( <i>Toxostoma rufum</i> )	UV <sup>-</sup> blocked own egg	Positive	Abernathy and Peer (2015)
American robin ( <i>Turdus migratorius</i> )	UV <sup>-</sup> blocked own egg	Positive	Abernathy and Peer (2015)
Gray catbird ( <i>Dumetella carolinensis</i> )	UV <sup>-</sup> blocked own egg	Positive	Abernathy and Peer (2015)
Northern cardinal ( <i>Cardinalis cardinalis</i> )	UV <sup>-</sup> blocked own egg	No	Abernathy and Peer (2016)
Shiny cowbird ( <i>Molothrus bonariensis</i> ) hosts			
Chalk-browed mockingbird ( <i>Mimus saturninus</i> )	UV <sup>-</sup> plaster white egg	No	De la Colina et al. (2012)
	UV <sup>+</sup> plaster white egg	No	De la Colina et al. (2012)
Great spotted cuckoo ( <i>Cuculus satoratus</i> ) hosts			
Magpie ( <i>Pica pica</i> )	UV <sup>-</sup> blocked real cuckoo egg	No	Avilés et al. (2006)
Oriental cuckoo hosts			
Yellow-bellied prinia ( <i>Prinia flaviventris</i> )	UV <sup>-</sup> blocked conspecific egg	No	Yang et al. (2014)
	UV <sup>-</sup> blocked non-mimetic egg	Positive	Yang et al. (2014)
Plain prinia ( <i>Prinia inornata</i> )	UV-blocked conspecific egg	No	Yang et al. (2014)
	UV <sup>-</sup> blocked non-mimetic egg	No	Yang et al. (2014)

### 22.3.4 Egg Pole

It is well known that maculated bird eggs have more spots at the blunt pole than at the sharp and that the overall surface area of eggshell around the blunt pole is evidently larger than around the sharp pole. Therefore, one should expect that blunt poles have the potential for greater amount of information content of eggshell signals. Polačiková et al. (2007) drew attention to this in the brood parasitism context, showing that colour characteristics of the blunt part of natural conspecific

**Table 22.4** Experiments testing the effect of egg size and shape on the probability of avian brood parasite eggs being rejected (R) by hosts

	Findings	Source
Common Cuckoo ( <i>Cuculus canorus</i> ) hosts		
Rufous bush chat ( <i>Cercotrichas galactotes</i> )	No R of giant eggs, R of both, host sized and cuckoo sized model eggs	Álvarez (2000)
Yellow-browed leaf Warbler ( <i>Phylloscopus humei</i> )	R decisions are based on the relative size of eggs in the clutch	Marchetti (2000)
Reed warbler ( <i>Acrocephalus scirpaceus</i> )	Model eggs twice as large as Cuckoo eggs were more likely to be R than normal-sized cuckoo eggs	Davies and Brooke (1988)
Reed warbler	Egg size differences apparently affect the mode and speed, but not R	Stokke et al. (2010)
Marsh warbler ( <i>Acrocephalus palustris</i> )	R was not dependent on difference in size	Antonov et al. (2006)
Great reed warbler ( <i>Acrocephalus arundinaceus</i> )	Egg shape influence R, rounder and symmetrical were R more often than more elongated model eggs	Zoelei et al. (2012)
Blackbird ( <i>Turdus merula</i> )	Size affected ejection but not nest desertion	Soler et al. (2015)
Diederik cuckoo ( <i>Chrysococcyx caprius</i> ) hosts		
Village weaver ( <i>Ploceus cucullatus</i> )	Test with conspecifics eggs showed no effect of shape and mass on R	Lahti and Lahti (2002)
Brown-headed ( <i>Molothrus ater</i> ) hosts		
American robin ( <i>Turdus migratorius</i> )	Size was the least important parameter affecting R	Rothstein (1982)
American robin ( <i>Turdus migratorius</i> )	Shape does not appear to influence egg R	Underwood and Sealy (2006a)
Gray catbird ( <i>Dumetella carolinensis</i> )	Shape does not appear to influence egg R	Underwood and Sealy (2006a)
Warbling vireo ( <i>Vireo vireo</i> )	Size did not affect probability R	Underwood and Sealy (2006b)
Yellow warbler ( <i>Setophaga petechia</i> )	Egg size was not generally used as criterion for R	Guigueno et al. (2014)
Shiny cowbird ( <i>Molothrus bonariensis</i> ) hosts		
Red-crested cardinal ( <i>Paroaria coronata</i> )	Egg width is an important cue for R	Segura et al. (2016)
Greater honeyguide ( <i>Indicator indicator</i> ) hosts	Commonest hosts did not discriminate against experimental egg that differed from their own in shape and size	Spottiswoode (2013)
Several hosts		

eggs experimentally added to blackcap nests may play a major role in the recognition of parasitic egg. Further studies by Polačiková et al. (2010), Polačiková and Grim (2010), and Zoelei et al. (2012) have revealed that host species rejected eggs manipulated at the blunt pole at significantly higher rates than eggs manipulated at sharp poles, indicating that they perceive critical recognition cues at the blunt pole. Polačiková and Grim (2010) regard the presence of egg recognition cues at the blunt egg pole as a general phenomenon in birds parasitized by interspecific parasites. To confirm this, it is necessary to study the effects of the appearance of the blunt egg pole of real parasitic eggs.

### 22.3.5 Egg Volume and Shape

Rigorous research studying the effects of the volume and shape of parasitic eggs with respect to rejection started in the early 1980s by Rothstein (1982) and has continued since then (Table 22.4). A variety of experimental methods have been used: conspecific eggs (Lahti and Lahti 2002; Underwood and Sealy 2006a), oversized eggs (Davies and Brooke 1988; Álvarez 2000), model eggs (Marchetti 2000; Antonov et al. 2006), and, in a single study, real parasitic eggs (Segura et al. 2016). With the exception of two studies (Marchetti 2000; Guigueno et al. 2014), results showed that egg size and/or shape were not generally used as a rejection cue.

#### Concluding Remarks and Future Directions

It is evident that the past decade has brought considerable progress in elucidating the particular cues that birds use during the process of discriminating parasitic eggs. Evaluation of egg colouration has improved considerably with the advent of spectrophotometric techniques allowing objective quantification of colour, including the UV-reflectant range that is invisible to humans. The use of video cameras has proven very useful in studying discriminatory processes, and further applications of this methodology should allow for better designed experiments related to discrimination.

We have a relatively good knowledge of the characteristics of parasitic eggs responsible for recognition, and subsequent rejection, in cuckoo and cowbird hosts. Our review suggests that some aspects of egg appearance could be more important for hosts than others. Individual cues could also interact with each other and play different roles in different circumstances, for example, UV signals could be more important in the recognition of non-mimetic eggs rather than mimetic. As the majority of published studies have focused on individual cues, we encourage the study of combined cues potentially responsible for rejection. This is because selection has shaped egg size, shape, colour, luminance, and patterns, and these cues together could contribute to egg detection and rejection behaviour. Future research should also explore different

(continued)

functions of eggshell components, e.g. shape, size, colour, and spottedness in egg discrimination in less well-known brood parasitic systems.

There is an apparent lack of knowledge on whether birds can recognize the shape of a natural parasitic egg. More studies are therefore needed with natural parasitic eggs to identify whether shape and volume are valid cues for egg recognition. In addition, further research is needed to clarify how hosts use the information content of the eggshell around the blunt pole across all brood parasitism systems, testing potential hosts in natural conditions.

Future work should also focus on improving visual models by incorporating physiologically appropriate, individual specific cone densities/absorbance spectra, as well as nest site-specific egg, nest lining, and ambient light availability data. In the future, new techniques such as 3D printing should provide opportunities for more extensive experimentation on the potential biological or evolutionary significance of size and shape variation of foreign eggs in rejection decisions.

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