Egg discrimination by hosts and obligate brood parasites: a historical perspective and new synthesis

Spencer G. SEALY [1,✉], Todd J. UNDERWOOD [2]

[1] Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada
[2] Department of Biology, Kutztown University, Kutztown, Pennsylvania 19530, USA

Abstract With the knowledge that cuckoos and cowbirds lay their eggs parasitically, and that some hosts eject parasitic eggs, ornithologists began to ponder the question of how host females discriminate between a foreign egg and their own eggs, wondering how hosts "know" which egg to remove. Results of one of the first uncontrolled experiments were inappropriately interpreted to imply ejection was based on discordancy, with hosts simply ejecting the egg in the minority, or the "odd-looking" egg. Controlled experiments eventually revealed that hosts first learn the appearance of own their eggs and discriminate between them and any odd egg in their nest, regardless of which egg type is in the minority. Recent work has shown that discordancy may play a role in discrimination by males mated successively with females that lay polymorphic eggs. We examine the details of the early experiments, in light of recent advances in studies of egg recognition. An ability to recognize eggs also has been extended, implicitly, to include obligate brood parasites, as it underlies several hypotheses in explanation of the behavior of parasites toward their hosts. Egg recognition in parasites, however, has not been experimentally confirmed, nor has a mechanism been identified by which parasites could discriminate between their own eggs and the other eggs in a nest. We review hypotheses (parasite competition, egg removal and multiple parasitism, mafia, farming) that require the ability of obligate brood parasites to discriminate eggs at different levels and the potential mechanisms used by parasites to recognize their own eggs and suggest experiments to test for egg discrimination. An assessment of the egg recognition ability of parasites is germane to our understanding of how parasites counteract defenses of hosts.

Keywords *Cuculus canorus*, discordancy, early experiments, host egg ejection, learning, *Molothrus ater*, obligate brood parasites, template, true-egg recognition

Introduction

Since before the time of Aristotle, we have known that some species of cuckoos lay eggs in nests of other species of birds — the hosts — which incubate the parasites' eggs and rear their young as their own (Gesner,

1669; Friedmann, 1964; Payne, 1977; Davies, 2000; Schulze-Hagen et al., 2009). Imagine, as Friedmann (1964) did, the challenges faced by early naturalists in piecing together often conflicting observations of cuckoos before it was established that these species laid their eggs parasitically (Lottinger, 1775, 1795; Jenner, 1788; Rennie, 1831; Blyth, 1835; Newton, 1869; Jourdain, 1925; Friedmann, 1964; Schulze-Hagen et al., 2009). It would have been especially difficult to recognize parasitic eggs in nests in which cuckoos laid matching eggs. Even recently, it has been necessary in some cases to

hatch suspected parasitic eggs or sample blood from nestlings to confirm their identity (e.g., Chance, 1922; Stuart Baker, 1942; Becking, 1981; Yang et al., 2012). Describing the habits of nesting species was more straightforward, with adult birds attending their nests, thus providing reliable clues to the nature of their nesting habits.

Establishing that the Brown-headed Cowbird (*Molothrus ater*) of North America was a brood parasite posed a different challenge. Naturalists had been puzzled by odd-looking eggs in nests, alongside the eggs of warblers, sparrows and other species of songbirds. The challenge was to associate those eggs with the bird that laid them. It was the American ornithologist, Alexander Wilson (1766–1813), who first deduced from his own observations and those of other naturalists that it was the Brown-headed Cowbird that laid those eggs — thus identifying another species of brood parasite (Wilson, 1810, also see Brewer, 1840). It was confirmed eventually that the Brown-headed Cowbird laid a more generalized egg, spotted with shades of brown on an off-white background, rather than eggs that matched those of a particular host species, as in many cuckoos.

Over the ensuing centuries, with knowledge that cuckoos lay their eggs parasitically and some of the important hosts identified, naturalists began to debate new questions. The extent of these debates was exemplified, for example, by the plethora of anecdotal observations published in the pages of the *Magazine of Natural History* in Britain in the nineteenth century, with the slow pace of progress revealed in the titles of Edgar Chance's books, *The Cuckoo's Secret* (1922) and *The Truth About the Cuckoo* (1940). Most of the queries focused on the breeding biology of the Common Cuckoo (*Cuculus canorus*) in Europe, but other questions eventually concerned the hosts, particularly the color and patterns of their eggs (Table 1). Do hosts remove or eject the cuckoo's egg from their nests and effectively eliminate most or all of the costs of parasitism? Egg ejection requires that hosts recognize that they have been parasitized and then discriminate between the parasite's egg and their own eggs to ensure that the 'correct' egg is removed. This was especially challenging for hosts parasitized by cuckoos whose eggs were mimics of their own eggs. Similar questions were asked of the interactions between the Brown-headed Cowbird and its hosts, although with a generalized egg it seemed that it would be "easier" for hosts to recognize it.

Experimental studies over the last few centuries

(Table 1) have confirmed that many host species eject parasitic eggs. Selection for egg discrimination by birds occurs in several contexts, but it is in the responses of hosts to parasitic eggs laid in their nests that this recognition is most refined and studied (Underwood and Sealy, 2002). The knowledge of egg ejection behavior by hosts has led to a detailed understanding of counteradaptations by parasites that have produced an evolutionary arms race between hosts and parasites (Dawkins and Krebs, 1979; Rothstein, 1990; Davies, 2000). In some cases, the parasites must recognize their own eggs among clutches of hosts' eggs. Mechanisms used by hosts to discriminate foreign eggs have been examined experimentally, but not for how parasites may recognize their own eggs. In this study, we use a historical perspective to review egg discrimination by hosts and examine hypotheses that rely on the ability of obligate brood parasites to discriminate eggs at different levels. We also explore the potential mechanisms used by parasites to recognize their own eggs and suggest experiments to test for this discrimination.

Confirmation of egg ejection behavior by hosts

…I am glad to have indicated … the value of definite experiment against uncontrolled stray observation. Above all it has been fascinating again to watch natural selection at work.

Charles Swynnerton (1916)

After determining that cuckoos laid parasitically, ornithologists slowly turned their attention to the reactions of hosts to the foreign eggs after parasitism (Table 1). The assumption that hosts eject parasitic eggs was limited to observations at parasitized nests from which host or parasite eggs had disappeared. However, this did not confirm who had removed them and, whether hosts were responsible, or if so, how they recognized the foreign eggs. Experiments were required. Many naturalists pondered these interactions and either proposed or conducted experiments (see Jourdain, 1925; Schulze-Hagen et al., 2009; Sealy, 2009; Table 1). Experiments that ensued proved to be the precursors of methodology that has become the hallmark of research today in the study of the interactions between brood parasites and their hosts.

Naturalists began to realize they could simulate parasitism (e.g., Blyth, 1835) by placing eggs of other spe-

Table 1 Summary of observations by early naturalists who commented on some aspects of the coloration of hosts' and parasites' eggs, suggested or conducted experiments to describe the reactions of hosts to foreign eggs, or confirmed ejection behavior in hosts and mechanisms of recognition of parasitic eggs. Note: observers are listed in order of the dates of their published contributions.

Observer	Contribution and references
Antoine J. Lottinger (1725–1793)	France: guided by observations of previous naturalists suggesting some hosts eject cuckoo eggs, manipulated clutches by replacing entire clutches in ~ 60 nests of > 10 species of songbirds with one foreign egg. Protocol mistakenly based on widespread belief that cuckoos destroy host eggs after parasitism, thus leaving the host with only the parasite's egg; hosts generally deserted the manipulated nests, due to the reduced clutch volume (see Sealy, 1992) — Lottinger (1775, 1795)
Edward Blyth (1810–1873)	England: highlighted findings of naturalists and his own life-history observations of the cuckoo and its hosts, and suggested manipulative experiments at potential nests designed to confirm ejection of cuckoo's egg (Sealy, 2009) — Blyth (1835)
Arthur H. S. Lucas (1853–1936)	Australia: hypothesized that coloration of birds' eggs is controlled by females, under environmental influences, including food — implying that cuckoos adjust colors of their eggs to those of available hosts (see Avilés et al., 2007 for recent evidence of environmental influence on egg color). Recognized the need for experimentation in the study of brood parasitism — Lucas (1887)
Edward B. Poulton (1856–1943)	England: invoked Darwinian natural selection to counter Lucas's idea about egg coloration, but he assumed, incorrectly (see Schulze-Hagen et al., 2009), that the cuckoo carried her egg to the nest in her beak, therefore, seeing the color of her eggs before placing them into appropriate nests — Poulton (1890)
Paul Leverkühn (1867–1905)	Germany: comprehensively surveyed ideas and assessed results of experiments conducted by others on potential host species, particularly Lottinger's; conducted his own experiments, following Lottinger in switching most clutches with one foreign egg (of various species of songbird), thus recording desertion of most nests because of resulting low clutch volume; additional results provided concrete evidence of ejection of experimental eggs — Leverkühn (1891)
A. C. Eduard Baldamus (1812–1893)	Germany: along with Rey, showed that female cuckoos laid eggs of consistent patterns, just like other birds, by collecting series of eggs on individual cuckoo's restricted egg-laying ranges; recognized the existence of adaptive mimicry now known as different cuckoo gentes and that cuckoo eggs are similar in color, spot-pattern, and size to the host's eggs — Baldamus (1892)
Eugene Rey (1832–1909)	Germany: independently confirmed Baldamus's earlier finding that showed female cuckoos laid eggs of consistent patterns and parasitized one species of bird; although impressed with his vast collection of cuckoos' eggs, Jourdain (1925) criticized Rey's work because the eggs were drawn from different localities; estimated that 17–22 eggs were laid by individuals in a season, on alternate days — Rey (1892)
Václav Čapek (1862–1926)	Czech Republic: was in close contact with Rey during late 19th century. Čapek conducted similar field work as Rey but his advantage was that he collected the eggs from a restricted area and his findings of female consistency in egg appearance are free of Jourdain's early criticism. During his life he collected ~1500 cuckoo eggs, he did a much more detailed field work than Rey — Čapek (1896)
John H. Gurney (1848–1922)	England: provided evidence of cuckoo destruction of unparasitized nests with young, which would create new opportunities for parasitism; his observations also led to the suggestion that each cuckoo favored one particular host species — Gurney (1899)
Edward C. Stuart Baker (1864–1944)	India: proposed that hosts discriminate eggs that differ substantially from own eggs, leading to selection for host-egg mimicry through gradual elimination of contrasting eggs by the hosts — Stuart Baker (1913)
Charles F. M. Swynnerton (1877–1838)	Southern Africa: comprehensive review of ideas on selection on patterns of egg coloration (also reviewed by Underwood and Sealy, 2002; Kilner, 2006); experiments stimulated by Leverkühn's results, but instead usually switched one foreign egg with only one host egg and recorded ejection from 80% of nests; controlled for size by painting one egg of host's clutch (also see below) — Swynnerton (1916, 1918)
Bernhard Rensch (1900–1990)	Germany: concluded evidence was strong that selection for egg mimicry occurs through the hosts; first attempt to identify experimentally the mechanism of egg discrimination egg that leads to ejection (also see below) by ejector hosts. The addition of a striking color to one of the host's eggs led to ejection, or nest desertion in some cases; determined that ejection was by pecking, followed by ejection, by observing nests through a telescope — Rensch (1924, 1925)
Francis C. R. Jourdain (1865–1940)	England: comprehensive summary of historical ideas on the cuckoo's habits, concluding that the Common Cuckoo may be subdivided into several egg-color morphs — Jourdain (1925)
Salim Ali (1896–1987)	India: stimulated by Rensch's results, added or substituted single foreign eggs at Plain Prinia (*Prinia inornata*) nests, two during laying, one before clutch initiation (all ejected); at three Red-whiskered Bulbul (*Pycnonotus xanthorrhous*) nests (ejection of egg of different sizes and colors at one nest, other nests depredated) — Ali (1931)

cies that differed from a potential host's eggs into active nests, or, one or more of the species' own eggs could be painted to appear different. (Because real cuckoo eggs were in short supply, workers eventually used models cast of various materials and painted them to simulate the parasite's eggs or other desired egg types.) By the beginning of the nineteenth century, naturalists had begun to experimentally determine whether potential hosts ejected parasitic eggs (Table 1). Their results suggested implicitly that some hosts recognize and eject cuckoo eggs, as long as the cuckoo's egg differed enough in some way from their own eggs to make it identifiable. Although these experiments were generally incomplete, and lacked appropriate controls, the scene was set for others to determine which hosts actually discriminated between cuckoo eggs and, eventually, cowbird eggs, and their own eggs (e.g., Schulze-Hagen et al., 2009; Sealy, 2009; Sealy and Guigueno, 2011). The pioneering experiments conducted by Charles F. M. Swynnerton were among the first to confirm egg ejection by cuckoo hosts.

An all-round naturalist, Swynnerton worked most of his life in southern Africa. His early papers on form and color in nature, particularly of insects, led to experiments on predation by captive and wild birds, especially on butterflies, in an attempt to discover underlying mechanisms of mimicry (Cott, 1940; Marshall, 1938; Carpenter, 1941–1942). Swynnerton's background with animal colors and his experimental approach placed him in good stead to study reactions of birds to cuckoo eggs. In a remarkable series of experiments followed by insightful interpretations and new ideas, Swynnerton (1916, 1918) recorded responses of adult birds at more than 60 manipulated nests of nearly as many species of passerines, all potential cuckoo hosts, to eggs of other species placed into their nests (Fig. 1). The results were not replicated but they provided the most extensive information on ejection by hosts of foreign eggs available at the time and, thus, implicitly, of cuckoo eggs. Swynnerton (1916:557) summarized his first experiment under the heading "The selective factors in the matter of Cuckoos' eggs":

I have placed eggs not their own in the nests of a number of birds and watched the result. The first three or four, although contrasting strongly with the bird's own eggs, were accepted, and I expected a repetition of what I remembered as my boyish experience. Subsequently, though many acceptances still occurred, the majority of the changelings were

rejected, and Prof. [Alfred] Newton's explanation of the facts with regard to the eggs of the English Cuckoo —"That certain kinds of birds resent interference with their nests much less than others … but with other species it may be, nay, doubtless it is, different" —was supported.

Overall, Swynnerton's (1916, 1918) results revealed the challenge faced by cuckoos in matching eggs that vary in color and pattern of their spots and scrawls, within and among clutches, and he came up with the idea, recently expounded by Davies (2000:63), "… that the spotting patterns of passerine eggs evolved as signatures." This work stimulated the German biologist, Bernhard Rensch, to take experiments on host responses to parasitism one step farther. Rensch examined how hosts actually identify or recognize the parasite's egg.

Egg discrimination by hosts

Die Mimicry entsteht durch Selektion von Seiten der brütenden Wirtsvögel, die untergeschobene Eier von abweichender Farbe und Form entfernen.
                                        Bernhard Rensch (1924)

The ability of hosts to discriminate between the parasite's egg and their own eggs is the key to the coevolutionary arms race between many brood parasites and their hosts (Dawkins and Krebs, 1979; Rothstein, 1990; Davies and Brooke, 1998). The first attempt to identify the mechanism of egg discrimination by birds came indirectly from experiments conducted early in the 1920s by Bernhard Rensch (Fig. 2), one of the 'architects' of the new evolutionary synthesis (Mayr and Provine, 1980; Junker, 2003; Wuketits, 2006). Among his pursuits in systematics, comparative morphology, paleontology, and ethology, Rensch conducted experiments to demonstrate the effect of natural selection in different systems. As a student, he had become intrigued by observations that eggs of the Common Cuckoo often closely resemble the size, color and pattern of those of its hosts, and that some hosts reject cuckoo eggs that are unlike their own,

VII.—*Rejections by Birds of Eggs unlike their own: with Remarks on some of the Cuckoo Problems.* By C. F. M. SWYNNERTON, C.M.B.O.U.

Fig. 1 Original title of C.F.M. Swynnerton's 1918 paper, published in *Ibis,* in which his experimental results confirmed egg ejection by several species of potential cuckoo hosts in southern Africa.
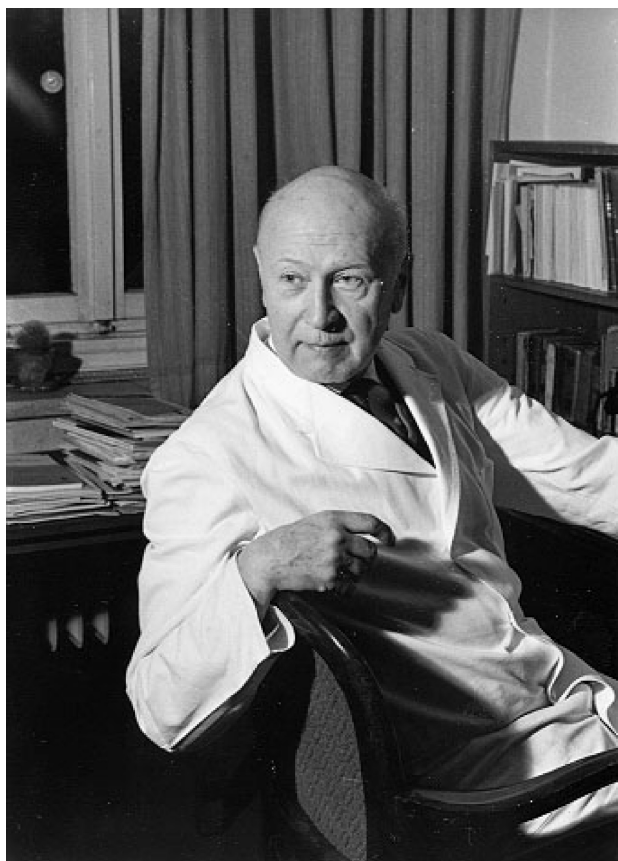
Fig. 2 Bernhard Rensch (1900–1990). (© Department of Behavioural Biology, University of Münster.)

that is, non-mimetic (e.g., Newton, 1869).

Rensch studied the results of experiments conducted by other naturalists, in particular, Paul Leverkühn (Table 1) and Swynnerton, both of whom were intrigued by the idea of egg mimicry and its origin. Rensch realized that Leverkühn had inappropriately switched entire clutches with one foreign egg, following Lottinger's lead, but he acknowledged that Swynnerton had appropriately switched one egg in the clutch with one foreign egg, thus affecting little or no change in clutch volume. Rensch (1924) synthesized information on the cuckoo's parasitic habits into five opposing hypotheses (see also Schulze-Hagen et al., 2009), but he favored only one of them, that the hosts exert the selective pressure on cuckoos to develop matching eggs, thus increasing the likelihood their eggs will be accepted. If a cuckoo's egg is a mimic of the hosts' eggs, he reasoned that changing the appearance of one or more of the eggs of the host's clutch, by painting it, thus eliminating differences in size or shape, or by inserting a differently colored egg or eggs of another species into the nest, would result in

a clutch with one or more odd-looking eggs. With the odd egg now standing out from the rest of the host's clutch, Rensch (1924) predicted that it, i.e., the discordant egg, would be ejected. His prediction was borne out at many manipulated nests and he interpreted the results accordingly, that birds recognize eggs on the basis of discordancy, thus it was unlikely that they know their own eggs.

Rensch (1925) subsequently manipulated 12 nests of eight species of passerine birds (Table 2), a small sample by today's standards, and, as in Swynnerton's experiments, there were no controls or replications of the same manipulations. Rensch created experimental eggs that differed from eggs of each species tested, either by painting them red or by replacing them with (differently appearing) eggs of another species. Because of the small sample of nests manipulated, and because the procedures and species were not consistent, all of Rensch's (1925) results are listed in Table 2. Rensch concluded from these results that there was little evidence that the birds tested recognized their own eggs. One result (number 10, Table 2), however, stood out in particular and apparently influenced Rensch's conclusion. In this case, an adult Garden Warbler (*Sylvia borin*) ejected what had become a discordant egg, even though it was the warbler's own egg. Rothstein (1970:215–220) acknowledged that this particular result suggested recognition via discordancy, but he also pointed out that the results from the tests on seven other nests (numbers 3, 4, 5, 6, 7, 9, and 11; see Table 2) suggested that the birds did recognize their own eggs because the red eggs or eggs of another species were in all cases rejected when they were either in the majority or possibly when foreign and host's eggs occurred in equal numbers (number 3). Nests depredated (numbers 1, 2, 8, and 12) before the results were obtained could not be considered in any of the interpretations. Although this experiment was incomplete, for a long time researchers perpetuated Rensch's interpretation of his results as a demonstration of ejection via discordancy (e.g., Poulsen, 1953; Welty, 1962; Hamilton and Orians, 1965; Wyllie, 1981). An additional experiment was required to identify learning by the host, in which each egg laid by a first-time breeder is replaced with a foreign egg as soon as it is laid, as closely as possible before the female can look at it. Rensch did not conduct this experiment but Stephen Rothstein did among his other far-reaching experiments on egg recognition by cowbird hosts.

By the late 1960s, compilations of knowledge and

Table 2 Protocol followed by Rensch (1925) and results of his egg-manipulations at 12 nests of eight species of songbirds, conducted in Germany from 31 May to 8 June 1924.

Nest number, species	Manipulation	Result
Eggs painted red		
1, Lesser Whitethroat (*Sylvia curruca*)	31 May: 3 eggs, all painted red; 1 June: 3 red + 1 "host" egg (now painted red); 4 June: 4 red + 1 "host" egg (painted red); 7–8 June, adult incubating 7 eggs	Acceptance of clutch containing foreign (red) + "host" eggs
2, Eurasian Blackcap (*S. atricapilla*)	31 May: 5 eggs, all painted red; 1, 4, and 7 June: adult incubating	Acceptance of clutch containing only red eggs
3, Garden Warbler (*S. borin*)	31 May: 2 eggs, all painted red; 1 June: 2 red eggs + 1 host egg (red); 4, 7 and 8 June: 3 unpainted eggs, adult incubating	Ejection of red eggs when they were either outnumbered or equal to number of host eggs
4, Song Thrush (*Turdus philomelos*)	31 May: 2 eggs, both painted red; 1 June: 2 red eggs + 1 host egg (red); 4 and 7 June: nest empty, deserted	Ejection of red eggs when they were not in the minority
5, Fieldfare (*T. pilaris*)	31 May: 2 eggs, both painted red; 1 June: 2 red + 1 normal (latter painted red); 4 June: nest empty, shells below nest	Ejection of red eggs when they were not in the minority
Foreign eggs replace "host" eggs		
6, Common Linnet (*Carduelis cannabina*)	1 Jun: 3 eggs, replaced by 3 eggs of *S. borin*; 4 and 7 June: 3 foreign eggs, nest apparently deserted	Foreign eggs deserted when they were the only egg types present
7, Yellowhammer (*Emberiza citrinella*)	31 May: 3 eggs, replaced by 2 eggs of *S. curruca*; 1 June: 1 foreign egg + 1 host egg (removed); 4, 7 and 8 June: 1 host egg + 1 foreign egg, nest deserted	Ejection of 1 foreign egg that outnumbered host's own eggs, followed by desertion
8, Wren (*Troglodytes troglodytes*)	31 May: 5 host eggs replaced by 5 eggs of *S. borin*; 1 June: adult incubating; 4 June: nest damaged, eggs gone	Possible acceptance of clutch of only foreign eggs; outcome uncertain because nest depredated between days 1 and 4
9, Garden Warbler	1 June: 3 host eggs, replaced by 3 eggs of *C. cannabina*; 4 June: 2 host eggs, 3 foreign eggs gone	Ejection of foreign eggs when they were the only eggs present or were in the majority
10, Garden Warbler	1 June: 3 host eggs, replaced by 3 eggs of *S. curruca*; 4 June: 1 host egg on branch ~ 20 cm from nest + 3 foreign eggs	Ejection of own egg when outnumbered by foreign eggs
11, Lesser Whitethroat	31 May: 2 host eggs, replaced by 3 eggs of *E. citrinella*; 1 June: 3 foreign eggs + 1 host egg, replaced by 4th foreign egg; 4 June: nest empty, 1 broken foreign egg on ground	Ejection of foreign eggs when they were the only egg type present
12, Lesser Whitethroat	1 June: 3 host eggs, replaced with 3 eggs of *S. borin*; 4, 7 and 8 June: 3 foreign eggs + 2 host eggs, adult incubating	Acceptance of mixed clutch of host and foreign eggs

lists of hosts of all brood parasites, especially for the cowbirds, had become available through the comprehensive work of Herbert Friedmann and, coupled with Rensch's experiments, paved the way for Rothstein to initiate a series of insightful and carefully controlled experiments, during the late 1960s through mid-1980s (e.g., Rothstein, 1974, 1975a, 1975b, 1975c, 1978, 1982a, 1982b). He refined Rensch's experiments and provided the first definitive interpretation that Brown-headed Cowbird hosts learn their own eggs and eject

Fig. 3 Protocol for experiment to identify the basic mechanism of egg recognition, by discordancy or by true egg recognition, in an ejector host, by changing whether the host eggs, Eastern Kingbird (*Tyrannus tyrannus*), or parasite eggs, Brown-headed Cowbird, are in the minority. Top: clutch of kingbird eggs in which one host egg has been switched with one cowbird egg. Bottom: all but one of the kingbird eggs was switched with four cowbird eggs. If discrimination is by true egg recognition, only cowbird eggs would be ejected, but if discrimination is by discordancy, the egg in the minority, kingbird or cowbird, would be ejected.

those that differ in one or more parameters, rather than against any egg of a minority type. He referred to the first alternative as "true egg recognition" (TER) and to the second as "recognition on the basis of discordancy" (experiment outlined in Fig. 3). Rothstein reasoned that ejection based on TER is facilitated by hosts learning to recognize their own eggs through an imprinting-like process as they lay their first and subsequent clutches. Hosts remove the foreign egg after determining that it differs in one or more parameters such as size, color, and maculation from their own eggs or, as discovered recently, also because of differences perceived within the UV spectrum of light (Cherry and Bennett, 2001; Honza et al., 2007; but see Underwood and Sealy, 2008).

In its simplest form, birds apparently "learn" their own eggs after viewing their appearance as each is laid, probably in the first nest they attend. Innate "knowledge" of the appearance of a host's own eggs is reinforced gradually as successive eggs are laid, apparently involving re-learning during laying of first and subsequent clutches (Rothstein, 1974, 1975b, 1978; Lotem et al., 1991, 1995; Strausburger and Rothstein, 2009). This protects hosts from ejecting their own eggs in the event they become the minority, a condition that arises occasionally when clutches, particularly of cowbird hosts, receive more than one parasitic egg or in the less-likely scenario when they have been partially depredated (Rothstein, 1982a; Sealy and Lorenzana, 1998).

Rothstein's experiments paved the way for much new research that is extending his findings, aided by advances in technology. Results of experiments on Common Cuckoo hosts in Europe (Moksnes et al., 1991; Moksnes, 1992; Moskát et al., 2010) and Asia (Higuchi et al., 1998), and on hosts of the Brown-headed Cowbird in North America (e.g., Sealy and Bazin, 1995; Peer and Sealy, 2001) have supported Rothstein's hypothesis that hosts discriminate foreign eggs by TER (Underwood and Sealy, 2002), but recently an exception has been identified, involving males mated to females that lay polymorphic eggs.

Discrimination by males

Most experimental studies of egg ejection behavior reported only that foreign eggs were removed from nests, in some cases assuming that the females ejected them (e.g., Rothstein, 1975a; Davies and Brooke, 1988; Lotem et al., 1991). Whether males totally lack rejection behavior, or contribute to it in some ejector species, remains an important question critical to understanding the population genetics of the ejection trait and the likelihood of a more rapid spread among the population (Rothstein, 1975c; Kelly, 1987; Sealy and Neudorf, 1995; Lee et al., 2005; Lee, 2008). Identifying the sex responsible for egg ejection is challenging because many ejector species are not sexually dichromatic in plumage (Underwood and Sealy, 2011). Recent studies involving continuous observations from blinds and/or videotaping of nests following experimental parasitism have identified males of a few species, always in addition to females, ejecting real or model parasitic eggs, or non-mimetic eggs (Table 3). In all cases, the sexes were identifiable because of dichromatic plumage, vocalizations

Table 3 Species in which the sex of the ejector of cuckoo eggs, cowbird eggs, and various models simulating real or non-mimetic eggs were identified by direct observation and/or video-taping. Method of ejection (grasp or puncture) is given where determined, but grasp-ejection was assumed when this was not stated explicitly during ejection of models made of plaster-of Paris or other solid substances. Note: order and names of species follow Gill and Wright (2006); male and female roles in incubation are indicated.

Host species	Observed or video-taped ejections
Ejection by females only	
Eastern Kingbird (*Tyrannus tyrannus*)[a]	Manitoba: 23/23 grasp-ejections of real cowbird eggs observed (Sealy and Bazin, 1995)
Great Reed Warbler (*Acrocephalus arundinaceus*)[a]	Czech Republic: 30/30 ejections of non-mimetic eggs video-taped (Požgayová et al., 2009)
Common Blackbird (*Turdus merula*)[a]	Spain: 8/9 ejections of model eggs filmed (Soler et al., 2002)
Rufous-tailed Scrub Robin (*Cercotrichas galactotes*)[a]	Spain: 15/15 ejections of various model eggs video-taped (Palomino et al., 1998)
Common Chaffinch (*Fringilla coelebs*)[a]	Norway: 13/13 ejections filmed of real Red-wing (*Turdus iliacus*) eggs (Moksnes et al., 1994)
Great-tailed Grackle (*Quiscalus mexicanus*)[a]	Texas: 34/34 ejections of model cowbird eggs observed (Peer and Sealy, 2004; also see Rasmussen et al., 2009). Note: this species is currently not parasitized by cowbirds (Peer and Sealy, 2004)
Ejection by females and males	
Warbling Vireo (*Vireo gilvus*)[b]	Manitoba: males pecked but did not eject real cowbird eggs at two nests, no vireo eggs were damaged (Sealy, 1996): egg-pecking suggests recognition despite lack of ejection (see Rothstein, 1977; Soler et al., 2012); males video-taped grasp-ejecting 1/5 real and 1/4 model cowbird eggs (Underwood and Sealy, 2011)
Eurasian Reed Warbler (*A. scirpaceus*)[b]	England: of 17 nests that received a model egg at which pecking was observed, both sexes pecked eggs (presumably models) at 10 nests, sexes were not distinguished at five nests, and at two nests only males were seen during the observation period (Davies and Brooke, 1988)
Eurasian Blackcap (*Sylvia atricapilla*)[b]	Norway: 8/8 ejections of real eggs by females (Moksnes et al., 1994). Spain: males pecked or ejected model eggs in 6/8 nests filmed (Soler et al., 2002). Czech Republic: females significantly more likely to eject, but 14/47 (29.8%) real eggs of species other than cuckoos ejected by males; both sexes were consistent in ejector/acceptor response when re-parasitized (Honza et al., 2007)
Subalpine Warbler (*S. cantillans*)[b]	Spain: 8/8 grasp-ejections of model eggs by females filmed (Soler et al., 2002)
Vinous-throated Parrotbill (*Paradoxornis webbianus*)[a]	South Korea: first evidence for egg discrimination by discordancy, in a male host; females lay polymorphic eggs in this population, therefore, males may encounter different egg types when paired with successive mates (Lee et al., 2005; Lee, 2008; also see Liang et al., 2011)
Grey Catbird (*Dumetella carolinensis*)[a]	Pennsylvania: two eggs of Brown Thrasher (*Toxostoma rufum*) switched with two catbird eggs were ejected (A. Wilson *in* Brewer, 1840:158; also see Sealy and Neudorf, 1995). Catbirds predominantly grasp-eject but occasionally puncture-eject (Rasmussen et al., 2009)
Baltimore Oriole (*Icterus galbula*)[a]	Manitoba: breakage and piecemeal removal, or puncture-ejection, of 14/16 real cowbird eggs observed (Sealy and Neudorf, 1995)

[a] Males not known to incubate; [b] Males share incubation.

(e.g., Warbling Vireo, *Vireo gilvus*), and/or individually marked adults. That females have been confirmed as the sole ejectors in fewer species (Table 3) may reflect a bias by researchers who attempt to identify the sexes when males are also suspected of ejection. In species whose eggs are almost invariable in color and pattern through successive clutches and breeding seasons, the mechanism of egg discrimination by females and males is probably the same — true egg recognition — and males are not compelled to learn a different egg-

type if they change mates. What about host species in which females lay polymorphic eggs, as in the Vinous-throated Parrotbill (*Paradoxornis webbianus*), where a male's next mate may lay a differently colored egg? One-time learning of an egg type by the male is probably not enough.

Vinous-throated Parrotbills lay blue, light blue or white eggs (Kim et al., 1995; Lee, 2008) in Korea, which complicates egg discrimination because males also eject the blue Common Cuckoo eggs. By creating clutches in which one egg was discordant within the rest of the parrotbill's clutch, Lee et al. (2005), Kim (2006), and Lee (2008) determined that females discriminate between cuckoo eggs and the variously colored host eggs based on true egg recognition. Consistently laying eggs of the same color throughout a female's lifetime facilitates memorization of her own egg color through one-time learning during her first breeding attempt and, thus, enhances the female's ability to discriminate cuckoo eggs later on (see Kilner, 2006). Males, on the other hand, eject via discordancy, following repeated bouts of learning, if they changed from year to year mates that lay different egg types (Lee, 2008). By switching eggs daily so that the host's egg became 'odd-looking', only males frequently rejected their own, discordant egg, whereas females consistently rejected foreign eggs irrespective of their relative proportion in the clutches. Liang et al. (2011) modeled this asymmetry in sex roles in egg care and recognition, supporting the idea that male recognition by learning is disadvantageous except where the host lays monomorphic eggs. Males may repeatedly learn the appearance of a partner's eggs whenever they change mates and use this new template when they discriminate parasitic eggs later on. Egg polymorphism and a sex-specific mechanism of recognition may allow hosts to respond more efficiently and stably in the co-evolutionary interaction with cuckoos (Lee, 2008; Y. Lee, B. Jang and S. G. Sealy, unpublished data).

Summary – From the results of experiments focused on female hosts, the potential mechanisms of egg discrimination may be summarized by re-stating Rothstein's hypotheses for egg ejection: 1) discordancy, i.e., ejection of an 'odd-looking' egg, and 2) true egg recognition, based on an imprinting-like process learned during the first egg-laying episode, and further bouts of reinforcement during successive breeding attempts. Empirical studies have generally supported the hypothesis of true egg recognition by learning, which likely also applies to males that eject parasitic eggs, except

in species that lay polymorphic eggs, such as Vinous-throated Parrotbill. Recognition by discordancy has been supported in that species because males may be confronted with different egg types when they change mates.

Egg discrimination by brood parasites

Far from having any "desire" to produce an egg of any particular type or colour, or to impart such "desire" to succeeding generations, I doubt very much if a cuckoo could recognize her own egg—indeed, when does she ever even see it?

Edgar Chance (1940)

That obligate parasites can recognize their own eggs must be assumed in studies of many interactions between parasites and hosts (Table 4). Egg recognition is required whether parasites are discriminating between their own and the host's eggs, or their own and eggs of other individual parasites. In theory, brood parasites "know" their own eggs, but evidence for this is not compelling and a mechanism has not been identified (e.g., Avilés et al., 2006). Results of some experiments point to an ability to recognize their eggs; the parasites may have responded to as-yet unidentified cues that facilitate distinguishing between different egg types. Obligate brood parasites, however, do not have the same opportunity to learn their own eggs. The lack of evidence for recognition of own eggs by brood parasites weakens many of the hypotheses that assume it and indicates that more research is needed to confirm recognition.

Here, we address several hypotheses and conditions (Table 4) in which parasites are assumed to possess different levels of egg discrimination when confronted with clutches of host eggs that may or may not contain their own or other parasites' eggs. Having summarized the evidence for mechanisms of egg discrimination by host species, we review those that may facilitate recognition or detectability by parasites of their own eggs and suggest experiments to confirm egg discrimination.

Parasites recognizing host eggs

Increasing the likelihood of acceptance through egg mimicry

The color and pattern of eggs of many species of brood parasites have been influenced by the discriminative be-

Table 4 Host-parasite interactions that require recognition by parasites of their own, or hosts', or other parasites' eggs

Interaction	Behavior
Acceptance of mimetic eggs	Cuckoos parasitizing nests of hosts that lay eggs most closely matching their own. Particularly important when parasitizing hosts that lay polymorphic eggs
Competition between parasites for successful parasitism	Evolution of egg mimicry selected for cryptic eggs to reduce likelihood of removal by egg-laying cuckoos
Host-egg removal and puncture	Common Cuckoos remove one host egg seconds before parasitizing the nest, whereas Brown-headed Cowbirds usually remove it after parasitism, requiring another visit to nest where they must distinguish between the host's and their own eggs
Parasitism of already-parasitized nests	Some hosts are multiply parasitized, by the same or different females (e.g., McLaren et al., 2003). To avoid parasitizing a nest already parasitized by another female, the parasite must be able to recognize the other parasite's egg(s)
Parasite retaliation ("mafia" hypothesis)	Parasites re-visit parasitized nests to confirm their egg(s) are present; if not, host clutches are destroyed in retaliation to enforce acceptance during subsequent nesting attempts. Cognitive requirement: parasites must be able to determine whether their egg(s) are still in the nest before they can determine they are missing
Creation of new opportunities for parasitism ("farming" hypothesis)	Parasites destroy nests too late to be parasitized, forcing hosts to re-nest, thus creating new opportunities for parasitism; parasites need to "know" only which nests they have parasitized, therefore, egg recognition not explicitly required

havior of hosts, in which cases selection has favored the development of mimicry and evolution of host races, or gentes (Gibbs et al., 2000). Females of several species of cuckoo lay eggs with distinctive colors and patterns in nests of hosts whose eggs match theirs most closely (Davies and Brooke, 1998), but do these cuckoos "know" their own eggs and target only hosts that lay similarly colored eggs? Davies (2000) pondered this question in a discussion of the variable eggs of three species of weavers and how such variability possibly provides a defense against parasitism by cuckoos. Weavers frequently eject experimentally introduced eggs that differ in color from their own eggs (Victoria, 1972; Lindholm, 1997; Lahti and Lahti, 2002), hence, at least some of the eggs cuckoos might lay at random would be ejected or, as Davies (2000:84) noted, "[the cuckoo] could get to know her own egg type and target those individuals in the [weaver] colony whose eggs are like her own." However, how the cuckoo would learn to recognize its own egg-type was not addressed. As a frequent parasite on weavers, female Diederick Cuckoos (*Chrysococcyx caprius*) should recognize their own eggs and target weaver nests with eggs similar in color and pattern to their own. For Common Cuckoo hosts and many other hosts that lay only one egg type, the parasite does not have to know its own egg, instead it would be sufficient to know the host's egg type. Laying polymorphic eggs would counteract this.

Parasites recognizing other parasites' eggs

Competition between parasites

Brooker and Brooker (1989, 1990) argued that egg mimicry evolved in response to selection for cryptic eggs to reduce the likelihood of other bronze-cuckoos (*Chalcites* spp.) removing them. They found "[the idea] that a female cuckoo, who probably never sees the eggs she lays and who certainly never sees all her eggs together in a clutch, should, in the few moments available to her when perched on the nest rim, be able to recognize and discriminate against the discordant egg of another cuckoo, when it is a host egg which she normally removes." They considered it likely that prior to laying, a cuckoo removes the most visible egg in the nest — a white egg in a dark, enclosed nest site, or a brightly patterned egg rather than a cryptic one. Brooker and Brooker (1990) suggested that pressure exerted by selective egg removal selected for egg crypsis. A recent study (Langmore et al., 2009) supports the idea that bronze-cuckoos lay dark colored eggs for crypsis in dark host nests, but did not differentiate whether crypsis evolved to prevent egg discrimination by hosts or other cuckoos. Thus, some cuckoo eggs appear to have evolved cryptic colors to prevent ejection, but it is not clear whether this egg discrimination is by hosts, parasites or both because these possibilities are not mutually

exclusive.

Host egg removal and egg destruction

Many brood parasites remove or puncture a host egg in association with parasitism (Wyllie, 1981; Sealy, 1992; Nakamura and Cruz, 2000). Cuckoos whose young evict nest mates should be expected to parasitize a nest only once, or, at nests already parasitized by another cuckoo, remove that cuckoo's egg before parasitizing it so its own egg will not be evicted by the other cuckoo's nestling. Cuckoos would, therefore, have to discriminate between the host's eggs and the other cuckoo's egg. Common Cuckoos remove and hold one host's egg in their bills a second or two before they lay, which assures their about-to-be-laid (possibly mimetic) egg is not mistakenly removed. Using data from Wyllie (1981), Davies and Brooke (1988) found that cuckoos parasitizing nests containing a real or model cuckoo egg showed a slight but non-significant tendency to remove a cuckoo's egg instead of a host's egg. These results were later updated but Davies (1999) still found no significant tendency for the selective removal of a real cuckoo's egg. Cuckoos only have to discriminate against an odd egg. Where cuckoo densities are low, however, nests seldom receive more than one cuckoo egg (Wyllie, 1981; Davies, 2000) and cuckoos would rarely have to choose between host and parasitic eggs. The frequency of cuckoo parasitism on the Great Reed Warbler, in Hungary, however, often exceeds 60% of nests and multiple parasitism is common (Moskát and Honza, 2002). Cuckoos often must choose either a host's or a parasite's egg to remove from the clutch during the act of parasitism. From 23 clutches containing 55 host eggs and 28 parasitic eggs, cuckoos removed 18 and 12 eggs, respectively, which did not show a significant preference for removal of a host's egg or a cuckoo's egg (Moskát and Honza, 2002).

Female Brown-headed Cowbirds frequently return to parasitized nests to remove a host's egg (Sealy, 1992), forcing the cowbird to choose between its egg and the host's egg(s), a situation that may result in mistaken removal of the cowbird's egg (Nolan, 1978). This behavior is risky and it is puzzling that most females do not remove eggs prior to or at the moment of parasitism, as cuckoos do. Perhaps it has something to do with the fact that cuckoos parasitize nests later in the day (Wyllie, 1981), whereas cowbirds parasitize them around sunrise, when it is dark (McMaster et al., 2004) and egg

discrimination, if visual, may be difficult. Cowbirds have been recorded removing mostly host eggs when they had to choose between host and cowbird eggs. They removed only host eggs from 13 nests of Kirtland's Warbler (*Setophaga kirtlandii*) where choices were made among 23 warbler eggs and 19 cowbird eggs (Mayfield, 1960). If egg removal was random, cowbirds would have taken almost as many cowbird eggs as warbler eggs and the odds against 13 consecutive correct choices by chance was about 3000 to 1. Cowbirds removed only warbler eggs where eggs of both species were present in 46 of 78 (59%) Prairie Warbler (*S. discolor*) nests (Nolan, 1978). Only host eggs were removed from at least 19 Yellow Warbler (*S. petechia*) nests where a choice had to be made (Sealy, 1992).

Cowbird eggs are about twice as large as those of the three host species considered above (Mayfield, 1960; Nolan, 1978; Sealy, 1992), but in the Ovenbird (*Seiurus aurocapilla*), where the host eggs are only slightly smaller than cowbird eggs, cowbirds were suspected of removing four cowbird eggs and about 30 host eggs (Hann, 1937). Recognition was suggested, possibly based on the slightly larger size of the cowbird eggs. Some hosts that eject cowbird eggs distinguish between them and their own eggs on the basis of a single parameter: size, ground color or spot-pattern (Rothstein, 1982b; Mason and Rothstein, 1986; Underwood and Sealy, 2006). Eggshell thickness also may be important in some situations.

Because eggs are removed by puncture-ejection, preferential removal of host eggs by cowbirds may actually reflect differences between the resistance of cowbird eggs to puncture (Mermoz and Reboreda, 1999:880), given that the more spherical, thick-shelled cowbird eggs are stronger (Picman, 1989). This also may explain preferential puncturing (i.e., destruction) of host eggs by females of other species of cowbirds. Instead of removing eggs, Shiny Cowbirds (*M. bonariensis*) and Bronzed Cowbirds (*M. aeneus*) peck eggs in parasitized clutches, thus destroying but leaving them in the nest. In 54 nests of the Brown-and-yellow Marshbird (*Pseudoleistes virescens*), which contained host and cowbird eggs, 31% of 147 host eggs versus 12% of 111 cowbird eggs were punctured or removed by predators, which is a significant difference (Mermoz and Reboreda, 1999:880). These authors noted that "[t]his apparent 'selective' pecking would be adaptive if all the parasitic eggs were laid by the same female, and would imply that Shiny Cowbird females recognize their own eggs."

They argued, however, that recognition of the respective eggs probably was not involved, but rather more host eggs were punctured because they were less resistant to pecking by cowbirds. They also found a greater proportion of punctured host eggs in nests parasitized by more than one female, which was not expected if females recognized their own eggs. Overall, evidence suggests Brown-headed Cowbirds show some ability to preferentially remove host eggs that are not close in appearance to their own eggs, and other cowbirds show a clear preference to peck host eggs over cowbird eggs. However, these preferences may reflect either egg discrimination ability or are a byproduct of the influence of thick eggshells on puncture-ejection.

Multiple parasitism and avoidance of
already-parasitized nests

Results of molecular genetic studies of host selection have revealed that more than one egg may be laid in the same nest by the same female, or by more than one female in Great Spotted Cuckoos (*Clamator glandarius)* (Martínez et al., 1998) and Brown-headed Cowbirds (McLaren et al., 2003; Rivers et al., 2012). Parasites may avoid undue competition with their own or another parasite's offspring. Evidence for avoidance of parasitized nests, however, is controversial (Preston, 1948; Mayfield 1965; Orians et al., 1989; Ortega et al., 1994) and the "need" to avoid parasitized nests in many cases is questionable. Egg discrimination would be required at multiply parasitized nests to avoid nests already parasitized by another parasite, or to avoid removing its own egg, instead of the host's, in nests parasitized again. The only way a parasite could identify those nests would be to recognize that there is another parasite's egg in the nest and move on, or remove that egg and then lay. The relatively large hippocampus of female cowbirds (Sherry et al., 1993) facilitates remembering nests already parasitized and, depending upon the circumstance, cowbirds may lay in nests again or avoid them. Relatively large hippocampi have been found in animals that experience exceptional demands on their spatial cognition, such as food storing (Sherry et al., 1989), but also brood parasites that remember the location and status of host nests (Sherry et al., 1993, Reboreda et al., 1996; Pagel et al., 1998). Where egg-laying ranges overlap, females may not determine that a nest has been parasitized by another cowbird unless upon inspection they recognize another cowbird's egg in the nest (Orians et

al., 1989).

Using artificial cowbird eggs, Ortega et al. (1994) tested whether cowbirds avoided already-parasitized nests. Their results provided weak support for this hypothesis, but their results were not significant with small sample sizes and the experimental eggs were added to nests throughout the host's laying cycle; but by early incubation cowbirds probably have made their decisions to parasitize nests. Nevertheless, Ortega et al.'s (1994) data suggest cowbirds avoided some experimentally parasitized nests and these results initially support recognition of parasitized nests, presumably based only on the presence or absence of a cowbird egg. (It was not clear in this experiment whether a supply of alternative unparasitized nests was available for parasitism.) It would be more efficient for the cowbird to remove the cowbird egg, then parasitize the nest if it is still at the right stage. This should enhance the cowbird's reproductive success (Orians et al., 1989; but see Weatherhead, 1989) without requiring the female to find another suitable nest; regardless, the female must recognize other cowbirds' eggs.

Parasites recognizing their own eggs

"Mafia" behavior

Zahavi (1979) hypothesized that brood parasites re-visit parasitized nests to check on the progress of their eggs, and to determine whether hosts have accepted their eggs. If their eggs have been ejected, parasites retaliate by destroying the clutches, thus "punishing" hosts in an effort to elicit compliance (i.e., acceptance), at the same time re-creating opportunities for parasitism. This has become known as the "mafia" hypothesis (Soler et al., 1995; J.J. Soler et al., 1998). Under this scenario, hosts are forced to modulate their propensity to eject the parasites' eggs because of costly delays and lowered reproductive success. For this to work, however, parasites bent on retaliation would have to re-visit the well-guarded nests they have parasitized, each time assessing differences in appearance, or some other cues, of the egg types in the hosts' nests, before determining whether their own egg or eggs are missing (see also Pagel et al., 1998). Presumably, this would be even more challenging in multiply parasitized nests. Recall that true egg recognition requires that hosts assess relative differences in the appearance of different eggs in their clutches (Rothstein, 1975b). Are brood parasites capable

of such finely tuned egg discrimination?

Although evidence suggests such discrimination occurs, the ability has not been confirmed or reconciled with a mechanism that would aid the parasite in recognizing their own eggs, whether by TER, by discordancy, or by some other means. By whatever means, the caveat remains that individuals that parasitized the original clutches, and who later destroyed them because their egg or eggs were gone, were the same individuals that returned to parasitize the replacement clutches. Evidence for this behavior is scrutinized below in a cuckoo-host system and a cowbird-host system.

Results from two studies conducted in Spain on a frequently used host of the Great Spotted Cuckoo, the European Magpie (*Pica pica*), which ejects non-mimetic eggs and sometimes closely matching eggs, provide support for the mafia hypothesis (Soler et al., 1995; Soler et al., 1999). In the first study, 16 of 29 nests from which investigators removed naturally laid cuckoo eggs were destroyed, presumably by the cuckoos that had parasitized the nests in the first place; however, only 3 of 28 unmanipulated nests were destroyed (Soler et al., 1995). In one case, a female cuckoo tracked by a radio-transmitter destroyed the original clutch then pecked the model eggs, and apparently also laid the replacement egg, although this and other similar observations of the final egg laying events were not confirmed. In the second study, magpies that ejected experimentally added cuckoo eggs and whose nests were subsequently destroyed, accepted the cuckoos' eggs laid in their replacement nests (Soler et al., 1999). This suggests strongly that cuckoos do recognize their own eggs, despite laying them alongside several closely matching eggs belonging to the hosts or other cuckoos (see also Davies, 2000), assuming the discrimination is visual. Regardless, it would be tricky for cuckoos to identify nests from which their eggs have been ejected, when they no longer can compare them with the hosts' eggs, and birds in general are not considered to be able to count (Rothstein and Robinson, 1998; but see Pepperberg, 2001; Lyon, 2003; Bogale et al., 2011), although cuckoos have not been tested for this ability.

Hoover and Robinson (2007) presented the first experimental evidence for retaliatory behavior by the Brown-headed Cowbird, directed toward the cavity-nesting Prothonotary Warbler (*Protonotaria citrea*). They found that acceptors experience very little depredation (6%), whereas experimentally simulated ejectors were often depredated (56%). Furthermore, hosts that re-nested after cowbird predation had higher levels of parasitism (85% of 81 nests) than the rest of the population (36%). Individuals that actually destroyed the nests also were not identified, but when cowbirds were denied access to nests, no nests failed, which is strong evidence that the cowbirds that destroyed the original nests were the ones who parasitized the re-nests (Hoover and Robinson, 2007). A possible evolutionary effect is inherent in this scenario, because destruction of ejectors' nests results in a reduction of the number of young that are genetically ejectors, which may slow the evolution of this anti-parasite defense (Hoover and Robinson, 2007). The Prothonotary Warbler, however, accepts cowbird eggs (Hoover, 2003), thus, there would be no selection on cowbirds to destroy warbler nests because in nature their eggs would not normally disappear in this manner. If mafia behavior by cowbirds is widespread, this behavior might be manifested in the same way toward the nests of all host species instead of responding differently to particular host species.

"Farming" hosts

The farming hypothesis predicts that brood parasites destroy host nests that are discovered too late for parasitism, to force potential hosts to replace their clutches, creating new parasitism opportunities (Gehringer, 1979; Gärtner, 1981; Davies and Brooke, 1988; Arcese et al., 1996; McLaren and Sealy, 2000). Chance (1922, 1940) knowingly did this when he forced Meadow Pipits (*Anthus pratensis*) to replace nests he destroyed so that he could generate more opportunities to photograph cuckoos in the act of laying and to collect more cuckoo eggs. In this scenario, female parasites must remember only that they have or have not parasitized a particular nest, then depredate unparasitized nests; egg recognition is not necessarily involved. This hypothesis has been tested indirectly with support by statistically analyzing nest success data from parasitized versus unparasitized nests (Arcese et al., 1996; but see McLaren and Sealy, 2000), and by a removal experiment (Smith et al., 2003). Nest destruction should be relatively cost-free, therefore, a positive correlation between the size of the cowbird population and the amount of nest predation would be expected (McLaren and Sealy, 2000; see also Sealy et al., 2002). Arcese et al.'s (1996) results were consistent with this; females with overlapping territories depredated nests parasitized by other cowbirds. Gerhinger's (1979) data only suggest that the same Common Cuckoos par-

asitize the replacement clutches that hosts were forced to lay. Farming is suggested in certain circumstances and may work by egg recognition or remembering which nests have not been parasitized.

Summary – At the outset, we must acknowledge that egg recognition behavior is not just the purview of the hosts, but also the parasites, and that success of several behaviors engaged in by brood parasites hinge on their ability to discriminate between their own eggs and other eggs. Some experimental evidence points to recognition abilities, suggesting parasites may have responded to as-yet unidentified cues that facilitate egg discrimination, but no mechanism has been identified to facilitate this discrimination. Parasites have the potential to use the same egg discrimination mechanisms as hosts. Recognition by discordancy seems the most likely mechanism that could operate under many situations, especially in cowbirds who parasitize an array of hosts that may lay different egg types, as this mechanism does not rely on learning one's egg type during laying. By contrast, true egg recognition would be required in a few specific situations, such as matching mimetic eggs to hosts that lay polymorphic eggs and mafia behavior. However, obligate brood parasites do not have the same opportunity to learn their own eggs, or may never even see them, as Chance queried.

Avenues of future research

It is probable … that results of sufficient, and perhaps in some cases striking, interest are to be obtained by careful and systematic experimentation. And the field is open.

Arthur Lucas (1887)

1. Nest manipulations should be continued to identify the responses to parasitism of frequently and infrequently parasitized species — whether acceptance or rejection (ejection or egg burial/nest desertion). For ejector species, it is imperative also to take extra time to determine whether males also eject eggs and whether both sexes share in incubation. We have just begun to understand the role males play in egg discrimination. Results summarized in Table 2 suggest that males that also incubate tend to eject, but there are exceptions. The list of ejector species is growing, however, the role of the sexes in ejecting eggs has been described for very few species. Male ejection has implications for modeling the rate of spread of the rejector trait through a host population (Rothstein, 1975c; Sealy and Neudorf, 1995; Liang et al., 2011). We predict the mechanism for egg recognition by males of species that lay monomorphic eggs is by TER, as characteristics of eggs laid by successive mates will generally be similar, but in species that lay polymorphic eggs the mechanisms used by males is more likely to be different, probably by discordancy. Research is needed to test these predictions.

2. Determination of the moment that hosts first see and possibly imprint on their eggs, and whether brood parasites ever see their eggs, remains a gap in our knowledge. First and subsequent eggs of first-time and older layers can be better controlled in experiments conducted in the aviary, despite the trade-off against a loss of ecological validity, but experimental eggs must still be switched before females can see them. Even in an aviary, there would be seconds or minutes during which females could see their eggs before being switched. Observations and photographs of cuckoos holding hosts' egg in their bills before laying, then flying away without looking into the nests, which may happen rapidly, within seconds or minutes (Sealy et al., 1995) compared to hosts (McMaster et al., 2004), suggest many cuckoos never see their eggs. Brown-headed Cowbirds usually return to remove a host's egg, where they must discriminate between their own egg and the host's eggs (Sealy, 1992). We also must consider the possibility that a parasite may sacrifice its first egg by laying it on the ground or in an empty nest to imprint on it, although there is no evidence for this behavior.

Laying in an unparasitized nest more than once may provide an obligate parasite an opportunity to learn its own eggs, but this would be complicated by the simultaneous appearance of the host's eggs and possibly those laid by other parasites. The rapidity of the act of parasitism probably provides little opportunity for parasites to learn their eggs and those parasites that lay mimetic eggs may learn the host egg type. Individual female brood parasites tend to lay eggs that are consistent in color and maculation (Chance, 1940; Wyllie, 1981; Dufty, 1983) and, therefore, imprinting on one egg may be enough. Recognition of eggs by discordancy would be simpler and it could be innate, but this mechanism would not work in all situations.

3. The parasite competition hypothesis requires that experiments be conducted to test a cryptic egg benefit and to identify the source of selection for crypsis. This could be tested by placing a white or similarly conspicuous real or model cuckoo egg in nests of one group and

a "cryptically" colored model in nests of another group (making sure that this difference holds up in the UV spectrum in which the birds can see). Cuckoos would be expected to remove more conspicuous "eggs", whereas a similar number of models and host "eggs" would be removed in the other group. Ejections should be observed or video-recorded to determine whether the models were removed by cuckoos or the hosts. Selection for crypsis by both cuckoos and hosts is possible because these hypotheses are not mutually exclusive.

4. The preference to remove or peck host eggs over cowbird eggs should be addressed to determine whether these apparent preferences are due to egg discrimination abilities or are a byproduct of the thick eggshells and puncture ejection. Whether host eggs are pecked preferentially could be tested by monitoring two groups of nests, placing a real cowbird egg into nests of one group and a model cowbird egg made of plasticine in the other. Failed attempts to remove model eggs would be revealed by models that disappeared or were pecked by the cowbird during attempts to remove model eggs or models would be undamaged, but a host egg might be damaged or gone.

5. Egg discrimination abilities are strongly linked to mafia behavior, but research is needed to confirm this. The following experiment should generate more clear-cut results in tests for parasites suspected of engaging in mafia behavior. Switch the parasites' originally laid eggs with either an artificial egg or a real parasite's egg collected from a site beyond the parasite's egg-laying range and record whether these nests are destroyed more often than the nests where the egg was left alone (or at a similar frequency to one where the parasite's egg was removed and not replaced). A positive result would support the mafia hypothesis but still leave undetermined that it was the same female that parasitized the replacement nest that had forced the hosts to re-build in the first place.

A more invasive approach would involve tracking successive visits by parasites to particular nests using passive integrated transponders (PIT tags) with passive readers and antennae (McEwan and Joy, 2011), or radio-telemetry in the same way (Wyllie, 1981; Honza et al., 2002), as has been done on a small scale (Nakamura and Miyazawa, 1997; Soler et al., 1995). Both methods, however, would have to be accompanied by visual observations of individually marked birds entering and laying in nests, or video-taped from the side to record the marked females and also from above to view

the contents of nests to confirm the addition of the parasite's egg. A non-invasive approach that would alleviate the need for labor-intensive tracking would be to swab the exterior of the parasite's egg in the replacement nest for microsatellite maternal genotyping (Schmaltz et al., 2006). Having already swabbed the egg the parasite laid in the nest she later destroyed, both eggs could be compared to confirm that the same individual laid eggs in both nests

6. Researchers should consider the possible role of chemical cues by parasites, and possibly also hosts, to discriminate eggs, because evidence is increasing for functional olfactory systems in birds (e.g., Roper, 1999; Hagelin and Jones, 2007). Odor detection by Brown-headed Cowbirds has been confirmed (Clark and Mason, 1989). A specific odor on a cuckoo's or cowbird's egg, derived from preen gland secretions, may allow the parasite to ascertain that its egg is still in a host's nest without having to see it or any other eggs, although it is not known how long odors would remain detectable after ejection of the parasite's egg. Thus, this olfactory mechanism could allow parasites to recognize their egg is present in a nest but would not represent an ability to recognize and differentiate that egg from the host's clutch. Whittaker et al. (2009) demonstrated that female Dark-eyed Juncos (*Junco hyemalis*), whose nests and eggs were exposed to hetero- and conspecific preen gland secretions, reduced the level of incubation constancy in response to foreign secretions, though the effects were temporary and did not carry over into incubation or chick rearing. Nevertheless, this might provide a mechanism by which parasites could farm hosts or allow parasites to monitor and destroy nests from which their eggs were ejected.

7. Consideration should be given to the possibility that parasites have retained the ability to recognize their own eggs from a time in their history before they evolved the brood-parasitic mode of reproduction. Evidence exists for hosts having retained the ability to discriminate between their own eggs and parasitic eggs long after cessation of parasitism, even surviving speciation events (Davies and Brooke 1989; M. Soler et al., 1998; Underwood et al., 2004; Peer et al., 2007). But as far as the parasites are concerned, there would be the question of whether selection existed in the first place for the development of egg recognition capability prior to the evolution of brood parasitic species, because egg recognition has evolved mainly as a response to brood parasitism (Underwood and Sealy, 2002), unless birds

responded to selection to respond to eggs as signals (e.g., Moreno and Osorno, 2003; Soler at al., 2012). Davies (2000:62) argued compellingly for birds in general that egg recognition probably is not innate, noting that birds most likely must learn their eggs because "the patterns of eggs are so complex that it would be difficult, if not impossible, for there to be a completely innate program for egg recognition." He likened this to bird song, which also is characterized by complex patterns that are acquired through learning, though there may be an innate "template" that predisposes individuals to be more likely to learn their own songs.

Conclusion

Despite nearly three centuries of research on egg discrimination behavior by birds within the context of brood parasitism, many questions remain unanswered. Most in need of addressing are those pertaining to the abilities of various species of brood parasites to recognize their own eggs. We summarized the conditions where discrimination by parasites have been assumed, identified specific areas in need of research for hosts and parasites, and outlined experiments that may be used to confirm egg discrimination in parasites. The challenge is for researchers studying brood parasitism in different systems around the world to answer these outstanding questions in the near future.

References

Ali S. 1931. The origin of mimicry in cuckoo eggs. J Bombay Nat Hist Soc, 34:1067–1070.

Arcese P, Smith JNM, Hatch MI. 1996. Nest predation by cowbirds and its consequences for passerine demography. Proc Natl Acad Sci USA, 93:4608–4611.

Avilés JM, Soler JJ, Prez-Contreras T. 2006. Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. Proc R Soc Lond B, 273:2821–2829.

Avilés JM, Stokke BG, Moksnes A, Røskaft E, Åsmul M, Møller AP. 2006. Rapid increase in cuckoo egg matching in a recently parasitized Reed Warbler population. J Evol Biol, 19:1901–1910.

Avilés JM, Stokke BG, Moksnes A, Røskaft E, Møller AP. 2007. Envormental conditions influence egg color of Reed Warblers *Acrocephalus scirpaceus* and their parasite, the Common Cuckoo *Cuculus canorus*. Behav Ecol Sociobiol, 61:475–485.

Baldamus E. 1892. Das Leben der euorpäischen Kuckucke. Parey, Berlin.

Becking JH. 1981. Notes on the breeding of Indian cuckoos. J Bombay Nat Hist Soc, 78:201–231.

Blyth E. 1835. Observations on the cuckoo. Mag Nat Hist, 8:325–340.

Bogale BA, Kamata N, Mioko K, Sugita S. 2011. Quantity discrimination in Jungle Crows, *Corvus macrorhynchos*. Anim Behav, 82:635–641.

Brewer TM. 1840. Wilson's American Ornithology. Otis, Broaders, Boston.

Brooker MG, Brooker LC. 1989. The comparative breeding behaviour of two sympatric cuckoos, Horsefield's Bronze-cuckoo *Chrysococcyx basalis* and the Shining Bronze-cuckoo *C. lucidus*, in Western Australia: a new model for the evolution of egg morphology and host specificity in avian brood parasites. Ibis, 131:528–547.

Brooker LC, Brooker MG. 1990. Why are cuckoos host specific? Oikos, 57:301–309.

Čapek V. 1896. Beiträge zur Fortpflanzungsgeschichte des Kuckucks. Ornithol Jahrbuch, 7: 41–72, 102–118, 146–157, 165–183.

Carpenter GDH. 1941–42. Observations and experiments in Africa by the late C. F. M. Swynnerton on wild birds eating butterflies and the preferences shown. Proc Linn Soc Lond, 154:10–34.

Chance E[P]. 1922. The Cuckoo's Secret. Sidgwick and Jackson, London.

Chance EP. 1940. The Truth about the Cuckoo. Country Life, London.

Cherry MI, Bennett ATD. 2001. Egg colour matching in an African cuckoo, as revealed by ultraviolet-visible reflectance spectrophotometry. Proc R Soc Lond B, 268:565–571.

Clark L, Mason JR. 1989. Sensitivity of Brown-headed Cowbirds to volatiles. Condor, 91:922–932.

Cott HB. 1940. Adaptive Coloration in Animals. Oxford University Press, Oxford.

Davies NB. 1999. Cuckoos and cowbirds versus hosts: co-evolutionary lag and equilibrium. Ostrich, 70:71–79.

Davies NB. 2000. Cuckoos, Cowbirds and Other Cheats. Poyser, London.

Davies NB, Brooke MdL. 1988. Cuckoos versus Reed Warblers:

adaptations and counteradaptations. Anim Behav, 36:262–284.

Davies NB, Brooke MdL. 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.

Davies NB, Brooke MdL. 1998. Cuckoos versus hosts: experimental evidence for co-evolution. In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 59–79.

Dawkins R, Krebs JR. 1979. Arms races between and within species. Proc R Soc Lond B, 205:489–511.

Dufty AM Jr. 1983. Variation in the egg markings of the Brown-headed Cowbird. Condor, 85:109–111.

Friedmann H. 1964. The history of our knowledge of avian brood parasitism. Centaurus, 10:282–304.

Gärtner K. 1981. Das Wegnehmen von Wirtsvogeleiern durch den Kuckuck (*Cuculus canorus*). Ornithol Mitt, 33:15–131.

Gehringer F. 1979. Etude sur le pillage par le Coucou, *Cuculus canorus*, des œufs de la Rousserolle effarvatte. Nos Oiseaux, 35:1–16.

Gesner C. 1669. Vogelbuch. Wilhelm Serlins, Frankfurt-am-Main.

Gibbs HL, Sorenson MD, Marchetti K, Brooke MdL, Davies NB, Nakamura H. 2000. Genetic evidence for female host-specific races of the Common Cuckoo. Nature, 407:83–186.

Gill FB, Wright M. 2006. Birds of the World. Princeton University Press, Princeton, New Jersey, USA.

Gurney JH. 1899. The economy of the cuckoo (*Cuculus canorus*). Trans Norfolk Norwich Nat Hist Soc, 6:365–384.

Hagelin JC, Jones IL. 2007. Bird odors and other chemical substances: a defense mechanism or overlooked mode of intraspecific communication? Auk, 124:741–761.

Hamilton WJ, III, Orians GH. 1965. Evolution of brood parasitism in altricial birds. Condor, 37:361–382.

Hann HW. 1937. Life history of the oven-bird in southern Michigan. Wilson Bull, 49:145–237.

Higuchi H. 1998. Host use and egg color of Japanese cuckoos. In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 80–93.

Honza M, Požgayová M, Procházka P, Tkadlec E. 2007. Consistency in egg rejection behaviour: responses to repeated brood parasitism in the Blackcap (*Sylvia atricapilla*). Ethology, 113:344–351.

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 laying: a radiotelemetry study. Anim Behav, 64:861–868.

Hoover JP. 2003. Multiple effects of brood parasitism reduce the reproductive success of Prothonotary Warblers, *Protonaria citrea*. Anim Behav, 65:923–935.

Hoover JP, Robinson SK. 2007. Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. Proc Natl Acad Sci USA, 104:4474–4483.

Jenner E. 1788. Observations on the natural history of the cuckoo. Phil Trans R Soc Lond, 78:219–237.

Jourdain FCR. 1925. A study on parasitism in the cuckoos. Proc Zool Soc Lond, 1925:639–667.

Junker T. 2003. Ornithology and the genesis of the synthetic theory of evolution. Avian Sci, 3:65–73.

Kelly C. 1987. A model to explore the rate of spread of mimicry and rejection in hypothetical populations of cuckoos and their hosts. J Theor Biol, 125:282–299.

Kilner RM. 2006. The evolution of egg colour and patterning in birds. Biol Rev, 81:383–406.

Kim CH, Yamagishi S, Won PO. 1995. Egg-color dimorphism and breeding success of the Crow Tit (*Paradoxornis webbianus*). Auk, 112:831–839.

Kim DW. 2006. Egg discrimination ability of *Paradoxornis webbianus* and antiparasitic behavior against brood parasitism. MSc thesis, Kyunghee University, Seoul, Korea.

Lahti DC, Lahti AR. 2002. How precise is egg discrimination in weaverbirds? Anim Behav, 63:1135–1142.

Langmore NE, Stevens M, Maurer G, Kilner RM. 2009. Are dark cuckoo eggs cryptic in host nests? Anim Behav, 78:461–468.

Lee JW, Kim DW, Yoo JC. 2005. Egg rejection by both male and female Vinous-throated Parrotbill *Paradoxornis webbianus*. Integr Biosci, 9:211–213.

Lee Y. 2008. Egg discrimination by the vinous-throated parrotbill, a host of the common cuckoo that lays polychromatic eggs. MSc thesis, University of Manitoba, Winnipeg, Canada.

Leverkühn P. 1891. Fremde Eier im Nest: ein Beitrag zur Biologie der Vögel. Friedländer und Sohn, Berlin.

Liang W, Yang C, Antonov A, Fossøy F, Stokke BG, Moksnes A, Røskaft E, Shykoff JA, Møller AP, Takasu F. 2011. Sex roles in egg recognition and egg polymorphism in avian brood parasitism. Behav Ecol, 23:397–402.

Lindholm AK. 1997. Evolution of host defences against avian brood parasitism. PhD dissertation, University of Cambridge, United Kingdom.

Lotem A, Nakamura H, Zahavi A. 1991. Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav Ecol, 3:128–132.

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

Lottinger AJ. 1775. Le coucou. Discours apologétique, ou mémoire sur le coucou d'Europe. JB Hiacinthe LeClerc, Nancy, France.

Lottinger AJ. 1795. *Histoire du coucou d'Europe*. FG Levrault, Strasbourg, France.

Lucas AHS. 1887. On the production of colour in birds' eggs. Trans Proc R Soc Victoria, 24:52–60.

Lyon BE. 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. Nature, 422:495–499.

McMaster DG, Neudorf, DLH, Sealy SG, Pitcher TE. 2004. A comparative analysis of laying times in passerine birds. J Field Ornithol, 75:113–122.

Marshall GAK. 1938. [Obituary of] Mr. C.F.M. Swynnerton, C.M.G. Nature, 142:198–199.

Mayfield H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, Michigan.

Mayfield H. 1965. Chance distribution of cowbird eggs. Condor, 67:257–263.

Mayr E, Provine WB (eds). 1980. The Evolutionary Synthesis: Perspectives on the Unification of Biology. Harvard University Press, Cambridge, Massachusetts.

Martínez JG, Soler JJ, Soler M, Burke T. 1998. Spatial patterns of egg laying and multiple parasitism in a brood parasite: a non-territorial system in the Great Spotted Cuckoo (*Clamator glandarius*). Oecologia, 117:286–294.

Mason P, Rothstein SI. 1986. Coevolution and avian brood parasitism: cowbird eggs show evolutionary response to host discrimination. Evolution, 40:1207–1214.

McEwan AJ, Joy MK. 2011. Monitoring a New Zealand freshwater fish community using passive integrated transponder (PIT) technology; lessons learned and recommendations for future use. NZ Mar Freshwater Res, 45:121–133.

McLaren CM, Sealy SG. 2000. Are nest predation and brood parasitism correlated in Yellow Warblers? A test of the cowbird predation hypothesis. Auk, 117:1056–1060.

McLaren CM, Woolfenden BE, Gibbs HL, Sealy SG. 2003. Genetic and temporal patterns of multiple parasitism by Brown-headed Cowbirds (*Molothrus ater*) on Song Sparrows (*Melospiza melodia*). Can J Zool, 81:1–6.

Mermoz ME, Reboreda JC. 1999. Egg-laying behaviour by Shiny Cowbirds parasitizing Brown-and-yellow Marshbirds. Anim Behav, 58:873–882.

Moksnes A. 1992. Egg recognition in Chaffinches and Bramblings. Anim Behav, 44:993–995.

Moksnes A, Røskaft E, Braa AT. 1991. Rejection behavior by Common Cuckoo hosts towards artificial brood parasite eggs. Auk, 108:348–354.

Moksnes A, Røskaft E, Solli MM. 1994. Documenting puncture ejection of parasitic eggs by Chaffinches *Fringilla coelebs* and Blackcaps *Sylvia atricapilla*. Fauna norv. Series C, Cinclus, 17:115–118.

Moreno J, Osorno JL. 2003. Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? Ecol Lett, 6:803–806.

Moskát C, Bán M, Székley T, Komdeur J, Lucassen RWG, van Boheemen LA, Hauber ME. 2010. Discordancy or template-based recognition? Dissecting the cognitive basis of the rejection of foreign eggs in hosts of avian brood parasites. J Exp Biol, 213:1976–1983.

Moskát C, Honza, M. 2002. European Cuckoo *Cuculus canorus* parasitism and host's rejection behaviour in a heavily parasitized Great Reed Warbler *Acrocephalus arundinaceus* population. Ibis, 144:614–622.

Nakamura T, Cruz A. 2000. The ecology of egg-puncture behavior in the Shiny Cowbird in southwestern Puerto Rico. In: Smith JNM, Cook TL, Rothstein SI, Robinson SK, Sealy SG (eds) Ecology and Management of Cowbirds and Their Hosts. University of Texas Press, Austin, pp 178–186.

Nakamura H, Miyazawa Y. 1997. Movements, space use and social organization of radio-tracked Common Cuckoos during the breeding season in Japan. Jap J Ornithol, 46:23–54.

Newton A. 1869. Cuckows' eggs. Nature, 1:74–76.

Nolan V Jr. 1978. The ecology and behavior of the Prairie Warbler *Dendroica discolor*. Ornithol Monogr, No. 26.

Orians GH, Røskaft E, Beletsky LD. 1989. Do Brown-headed Cowbirds lay their eggs at random in the nests of Red-winged Blackbirds. Wilson Bull, 101:599–605.

Ortega CP, Ortega JC, Cruz A. 1994. Use of artificial Brown-headed Cowbird eggs as a potential management tool in deterring parasitism. J Wildl Manage, 58:488–492.

Pagel M, Møller AP, Pomiankowski A. 1998. Reduced parasitism by retaliatory cuckoos selects for hosts that rear cuckoo nestlings. Behav Ecol, 9:566–572.

Payne RB. 1977. The ecology of brood parasitism in birds. Annu Rev Ecol Syst, 8:1–28.

Palomino JJ, Martin-Vivaldi M, Soler M, Soler JJ. 1998. Females are responsible for ejection of cuckoo eggs in the Rufous Bush Robin. Anim Behav, 56:131–136.

Peer BD, Sealy SG. 2001. Mechanism of egg recognition in the Great-tailed Grackle (*Quiscalus mexicanus*). Bird Behav, 14:71–73.

Peer BD, Sealy SG. 2004. Fate of grackle (*Quiscalus* spp.) defenses in the absence of brood parasitism: implications for long-term parasite-host coevolution. Auk, 121:1172–1186.

Peer BD, Rothstein SI, Delaney KS, Fleischer RC. 2007. Defence behaviour against brood parasitism is deeply rooted in mainland and island scrub-jays. Anim Behav, 73:55–63.

Pepperberg IM. 2001. Avian cognitive abilities. Bird Behav, 14:51–70.

Picman J. 1989. Mechanism of puncture resistance of eggs of Brown-headed Cowbirds. Auk, 106:577–583.

Poulton EB. 1890. The colours of animals: their meaning and use, especially considered in the case of insects. Int Sci Ser, no. 68.

Poulsen H. 1953. A study of incubation responses and some other behavior patterns in birds. Vidensk Medd fra Dansk Naturh Foren, 115:1–131.

Požgayová M, Procházka P, Honza M. 2009. Sex-specific defence behavior against brood parasitism in a host with female-only incubation. Behav Processes, 81:34–38.

Preston FW. 1948. The cowbird (*M. ater*) and the cuckoo (*C. canorus*). Ecology, 29:115–116.

Rasmussen JL, Sealy SG, Underwood TJ. 2009. Video recording reveals the method of ejection of Brown headed Cowbird eggs and no cost in American Robins and Gray Catbirds. Condor, 111:570–574.

Reboreda JC, Clayton NS, Kacelnik A. 1996. Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. Neuroreport, 7:505–508.

Rennie J. 1831. The Architecture of Birds. Charles Knight, London.

Rensch B. 1924. Zur Entstehung der Mimikry der Kuckuckseier. J Ornithol, 72:461–472.

Rensch B. 1925. Verhalten von Singvögeln bei Aenderung des Geleges. Ornithol Monatschr, 33:169–173.

Rey E. 1892. Altes und Neues aus dem Haushalte des Kuckucks. Freese, Leipzig.

Rivers JW, Young S, Gonzalez EG, Horton B, Lock J, Fleischer RC. 2012. High levels of relatedness between Brown-headed Cowbird (*Molothrus ater*) nestmates in a heavily parasitized host community. Auk, 129:623–631.

Roper TJ. 1999. Olfaction in birds. Adv Stud Behav, 28:247–332.

Rothstein SI. 1970. An experimental investigation of the defenses of the hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*). PhD dissertation, Yale University, New Haven, Connecticut.

Rothstein SI. 1974. Mechanisms of avian egg recognition: possible learned and innate factors. Auk, 91:796–807.

Rothstein SI. 1975a. An experimental and teleonomic investigation of avian brood parasitism. Condor, 77:250–271.

Rothstein SI. 1975b. Mechanisms of avian egg-recognition: do birds know their own eggs? Anim Behav, 23:268–278.

Rothstein SI. 1975c. Evolutionary rates and host defenses against avian brood parasitism. Am Nat, 109:161–176.

Rothstein SI. 1977. Cowbird parasitism and egg recognition of the Northern Oriole. Wilson Bull, 89:21–32.

Rothstein SI. 1978. Mechanisms of avian egg-recognition: additional evidence for learned components. Anim Behav, 26:671–677.

Rothstein SI. 1982a. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. Am Zool, 22:547–560.

Rothstein SI. 1982b. Mechanisms of avian egg recognition: which parameters elicit responses by ejecter species? Behav Ecol Soiciobiol, 11:229–239.

Rothstein SI. 1990. A model system for coevolution: avian brood parasitism. Annu Rev Ecol Syst, 21:481–508.

Rothstein SI, Robinson SK. 1998. The evolution and ecology of avian brood parasitism. In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 3–56.

Schmaltz G, Somers CM, Sharma P, Quinn JS. 2006. Non-destructive sampling of maternal DNA from the external shell of bird eggs. Conserv Genet, 7:543–549.

Schulze-Hagen K, Stokke BG, Birkhead TR. 2009. Reproductive biology of the European Cuckoo *Cuculus canorus*: early insights, persistent errors and the acquisition of knowledge. J Ornithol, 150:1–16.

Sealy SG. 1992. Removal of Yellow Warbler eggs in association with cowbird parasitism. Condor, 94:40–54.

Sealy SG. 1996. Evolution of host defenses against brood parasitism: implications for puncture-ejection by a small passerine. Auk, 113:346–355.

Sealy SG. 2009. Cuckoos and their fosterers: uncovering details of Edward Blyth's field experiments. Arch Nat Hist, 36:129–135.

Sealy SG, Bazin RC. 1995. Low frequency of observed cowbird parasitism on Eastern Kingbirds: host rejection, effective nest defense, or parasite avoidance? Behav Ecol, 6:140–145.

Sealy SG, Guigueno MF. 2011. Cuckoo chicks evicting their nest mates: coincidental observations by Edward Jenner in England and Antoine Joseph Lottinger in France. Arch Nat Hist, 38:220–228.

Sealy SG, Lorenzana JC. 1998. Yellow Warblers (*Dendroica petechia*) do not recognize their own eggs. Bird Behav, 12:57–66.

Sealy SG, Neudorf DL. 1995. Male Northern Orioles eject cowbird eggs: Implications for the evolution of rejection behavior. Condor, 369–375.

Sealy SG, McMaster DG, Peer BD. 2002. Tactics of obligate brood parasites to secure suitable incubators. In: Deeming DC (ed) Avian Incubation: Behaviour, Environment, and Evolution. Oxford University Press, Oxford, pp 254–269.

Sealy SG, Neudorf DL, Hill DP. 1995. Rapid laying by Brown-headed Cowbirds and other parasitic birds. Ibis, 137:76–84.

Sherry DF, Vaccarino AL, Buckenham K, Herz RS. 1989. The hippocampal complex of food-storing birds. Brain Behav Evol, 34:308–317.

Sherry DF, Forbes ML, Khurgel M, Ivy GO. 1993. Females have a larger hippocampus than males in the brood-parasitic Brown-headed Cowbird. Proc Natl Acad Sci USA, 90:7839–7843.

Smith JNM, Taitt MJ, Zanette L, Myers-Smith IH. 2003. How do Brown-headed Cowbirds (*Molothrus ater*) cause nest failure in Song Sparrows (*Melospiza melodia*)? A removal experiment. Auk, 120:772–783.

Soler JJ, Møller AP, Soler M. 1998. Mafia behavior and the evolution of facultative virulence. J Theor Biol, 191:267–277.

Soler JJ, Sorci G, Soler M, Møller AP. 1999. Change in host rejection behavior mediated by the predatory behavior of its brood parasite. Behav Ecol, 10:275–180.

Soler M, Soler JJ, Martínez JG. 1998. Duration of sympatry and coevolution between the Great Spotted Cuckoo (*Clamator glandarius*) and its primary host, the Magpie (*Pica pica*). In: Rothstein SI, Robinson SK (eds) Parasitic Birds and Their Hosts: Studies in Coevolution. Oxford University Press, Oxford, pp 113–142.

Soler M, Fernández-Morante, Espinosa F, Martín-Vivaldi M. 2012. Pecking but accepting the parasitic eggs may not reflect ejection failure: the role of motivation. Ethology, 118:662–672.

Soler M, Martín-Vivaldi M, Pérez-Contreras T. 2002. Identification of the sex that is responsible for recognition and the method of ejection of parasite eggs in some potential Common Cuckoo hosts. Ethology, 108:1093–1101.

Soler M, Soler JJ, Martínez JG. 1997. Great Spotted Cuckoos improve their reproductive success by damaging magpie host eggs. Anim Behav, 54:1227–1233.

Soler M, Soler JJ, Martínez JG, Møller AP. 1995. Magpie host manipulation by Great Spotted Cuckoos: evidence for an avian mafia? Evolution, 49:770–775.

Strausberger BM, Rothstein SI. 2009. Parasitic cowbirds may defeat defense by causing rejecters to misimprint of cowbird eggs. Behav Ecol, 20:691–699.

Stuart Baker EC. 1913. The evolution of adaptation in parasitic cuckoos' eggs. Ibis, Series 10, 1:384–398.

Stuart Baker EC. 1942. Cuckoo Problems. Witherby, London.

Swynnerton CFM. 1916. On the coloration of the mouths and eggs of birds. — II. On the coloration of eggs. Ibis, Series 10, 4:529–606.

Swynnerton CFM. 1918. Rejections by birds of eggs unlike their own: with remarks on some of the cuckoo problems. Ibis, Series 10, 6:127–154.

Underwood TJ, Sealy SG. 2002. Adaptive significance of egg coloration. In: Deeming DC (ed) Avian Incubation: Behaviour, Environment, and Evolution. Oxford University Press, Oxford, pp 280–298.

Underwood TJ, Sealy SG. 2006. Parameters of Brown-headed Cowbird *Molothrus ater* egg recognition and ejection in Warbling Vireos *Vireo gilvus*. J Avian Biol, 37:457–466.

Underwood TJ, Sealy SG. 2008. UV reflectance of eggs of Brown-headed Cowbirds (*Molothrus ater*) and acceptor and rejecter hosts. J Ornithol, 149:313–321.

Underwood TJ, Sealy SG. 2011. Behavior of Warbling Vireos ejecting real and artificial cowbird eggs. Wilson J Ornithol, 123:395–400.

Underwood TJ, Sealy SG, McLaren CM. 2004. Experiments on egg discrimination in two North American corvids: further evidence for retention of egg rejection. Can J Zool, 82:1399–1407.

Victoria JK. 1972: Clutch characteristics and egg discriminative ability of the African Village Weaverbird *Ploceus cucullatus*. Ibis, 114:367–376.

Weatherhead PJ. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbird. Auk, 106:358–366.

Welty JC. 1962. The life of birds. WB Saunders, Philadelphia, Pennsylvania.

Whittaker DJD, Reichard DG, Dapper AL, Ketterson ED. 2009. Behavioral responses of nesting female Dark-eyed Juncos *Junco hyemalis* to hetero- and conspecific passerine preen oils. J Avian Biol, 40:579–583.

Wilson A. 1810. American Ornithology. Vol. 2. Bradford and Inskeep, Philadelphia, Pennsylvania, USA.

Wuketits FM. 2006. Bernhard Rensch, German evolutionist. Biol Theory, 1:410–413.

Wyllie I. 1981. The Cuckoo. Universe, New York.

Yang C, Cai Y, Liang W. 2012. Species identification of sympatric cuckoo nestlings in a multiple-cuckoo system, China. Chinese Birds, 3:108–112.

Zahavi A. 1979. Parasitism and nest predation in parasitic cuckoos. Am Nat, 113:157–159.

专性寄生繁殖的鸟类及其宿主的卵识别：文献综述与新的整合

Spencer G. SEALY [1], Todd J. UNDERWOOD [2]

（1 加拿大曼尼托巴大学生物学系；2 美国宾州库兹敦大学生物学系）

摘要：杜鹃和牛鹂为寄生性繁殖鸟类，把卵产于宿主的巢中，而一些宿主能够扔掉寄生卵。宿主如何识别寄生卵和自己的卵，然后扔掉？最初的实验由于未设对照组，错误地认为宿主是采取"不一致性识别"，即扔其中占少数或"较异常"的卵。后来的实验证明，宿主首先通过印记自己的卵，然后识别和扔掉与该记忆模板不同的卵，而无论该卵是少数还是多数。最新的研究表明，对于能产多种颜色卵的宿主而言，由于雄鸟在同一繁殖季可能与产不同颜色卵的雌鸟配对，因而非记忆的"不一致性识别"在雄鸟的卵识别中扮演着重要角色。本文综述了卵识别研究的早期工作和最新进展，包括新技术的应用。卵识别实际上对寄生者和宿主都重要，但寄生者如何识别自己的卵和宿主的卵，却很少有人研究。对诸如寄生者竞争、多寄生性扔卵、黑手党效应、寄养等假说，均需要了解寄生者的卵识别机制，为此我们给出了具体的研究建议。对寄生者卵识别能力的研究，有助于了解寄生性繁殖的鸟类如何反过来应对宿主的反寄生策略。

关键词：*Cuculus canorus*，不一致性识别，早期实验，宿主扔卵行为，学习，*Molothrus ater*，专性寄生，记忆模板，真识别