

Mechanism of egg recognition in defenses against conspecific brood parasitism: American coots (*Fulica americana*) know their own eggs

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Abstract Hosts of avian brood parasites use a variety of defenses based on egg recognition to reduce the costs of parasitism; the most important of which is rejecting the parasitic eggs. Two basic recognition mechanisms are possible: “true recognition”, whereby hosts recognize their own eggs irrespective of their relative frequency in the clutch, and minority recognition (or “recognition by discordancy”), whereby hosts respond to the minority egg type. The mechanism of recognition has been experimentally studied in a handful of species parasitized by interspecific brood parasites, but the mechanism used in defenses against conspecific brood parasitism is unknown. I experimentally determined the mechanism of egg recognition in American coots (*Fulica americana*), a species with high levels of conspecific brood parasitism, egg recognition, and rejection. I swapped eggs between pairs of nests to alter frequencies of host and “parasite” eggs and then used two criteria for recognition: egg rejection and nonrandom incubation positions in the clutch. Eight of 12 nests (66%) given equal frequencies of host and parasite eggs showed evidence of true recognition. In contrast, only one of eight (12.5%) nests where host eggs were in the minority showed evidence of recognition by discordancy. The nonrandom incubation positions of parasitic eggs indicates that birds sometimes recognize parasitic eggs without rejecting them and provides a means of assessing recognition on a per nest basis in species with large clutches. Adaptive recognition without rejection may

also be an important evolutionary stepping stone to the evolution of egg rejection in some taxa.

Keywords Egg recognition · Recognition mechanism · Egg rejection · Brood parasitism · American coot

Avian brood parasites lay their eggs in the nests of other birds and then leave all subsequent parental care to the recipients of the eggs, or the “hosts”. Brood parasitism occurs both between and within species, but most work has focused on the 100 species of obligate brood parasites that reproduce only by parasitizing nests of other species (Payne 1977; Rothstein 1990; Davies 2000). Most obligate brood parasites inflict severe fitness costs on their hosts, which in turn promote the evolution of host defensive tactics like egg recognition and rejection (Rothstein 1990; Davies 2000).

Analysis of the evolution of egg recognition and rejection by hosts is of particular interest because it links evolutionary biology and animal cognition (Sherman et al. 1997; Lyon 2003). Fitness costs to hosts of raising parasitic chicks often leads to natural selection for the ability to recognize and reject parasitic eggs, a defense that requires a cognitive recognition system that enables the hosts to reliably distinguish parasitic eggs from their own. As Rothstein (1975a, 1977, 1978, 1982) demonstrated with an elegant series of experiments, egg recognition systems have two key components: (1) the specific egg features used to distinguish eggs laid by different females (host vs parasite) and (2) the general mechanism or rule used to decide which eggs should be rejected. For the latter, two general mechanisms are possible. Hosts may know their own eggs and be capable of recognizing all eggs that differ sufficiently from their eggs, regardless of the frequencies of host and parasite eggs (“true egg recognition”, Rothstein 1975a). Alternatively, birds might not recognize their own eggs but simply reject any rare egg type in the clutch that

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differs sufficiently from the rest of clutch [an odd-egg-out mechanism that Rothstein (1975a) referred to as “recognition by discordancy”]. These two mechanisms can be distinguished by experimentally altering the frequencies of host and parasite eggs in a host’s clutch (Rothstein 1975a). If hosts reject parasitic eggs when given equal numbers of host and parasitic eggs, true recognition is supported. If hosts reject their own eggs when parasitic eggs are the majority types, rejection by discordancy is supported.

The mechanism of egg recognition used by avian hosts has now been examined in nine species parasitized by interspecific brood parasites, and all of these were found to show true recognition (Victoria 1972; Rothstein 1975a, 1978; Moksnes 1992; Lotem et al. 1995; Sealy and Bazin 1995; Peer and Sealy 2001; Lahti and Lahti 2002). Conspecific brood parasitism has now been documented in over 200 species of birds (Rohwer and Freeman 1989; Davies 2000; Yom Tov 2001), but conspecific egg recognition and rejection appears to be relatively rare (Andersson 1984; Lyon 2003). Accordingly, virtually nothing is known of the mechanisms of conspecific egg recognition and rejection. The mechanisms of egg recognition might be expected to differ for conspecific hosts because intraspecific variation in egg features is typically much lower than variation among species (Andersson 1984)—conspecific hosts may face a more challenging recognition task that is best achieved with different mechanisms than those used by hosts of interspecific brood parasitism.

In this study, I examine the mechanism of egg recognition used by American coots (*Fulica americana*) to recognize and reject the eggs of conspecific brood parasites. Conspecific brood parasitism is common in some populations of coots, and over 40% of the nests at my study site received one or more eggs from conspecific females not associated with the nest (Lyon 1993b). Hosts show high levels of accurate egg recognition and rejection of real parasitic eggs (Lyon 2003) and, to a lesser extent, conspecific eggs experimentally added to their nests (Arnold 1987).

I conducted two separate experiments to determine the mechanism of egg recognition American coots use to distinguish parasitic eggs from their own. To determine whether some coots use true recognition, I experimentally created clutches of eggs with equal numbers of host eggs and eggs from one other nest. To determine whether some coots use recognition on the basis of discordancy, a second experiment created clutches where the hosts’ own eggs were in the minority. While these mechanisms are mutually exclusive in the same individual for a given breeding attempt, they are not mutually exclusive at the population level because individuals might vary in the mechanism of recognition. I used two criteria to assay recognition: egg rejection and nonrandom egg positions. Coots show very

accurate egg rejection, and reject about 40% of parasitic eggs with very few rejections of their own eggs (Lyon 2003). Nonrandom incubation positions at nests where hosts do not reject parasitic eggs indicate that coots sometimes recognize parasitic eggs without rejecting them; some parasitic eggs are kept at the periphery of the clutch more than expected by chance (Lyon 2003) and this allows me to test for recognition on a per nest basis. Finally, some studies reveal plasticity in host egg rejection behavior—parasitic eggs added experimentally are rejected less than parasitic eggs laid by brood parasites (Davies and Brooke 1988; Moksnes et al. 1991)—so I compared the egg rejection rates observed in this experimental study to those observed at naturally parasitized nests in my broader observational study of egg rejection (Lyon 2003).

Materials and methods

Study area and animal

The experiments were part of a larger study of brood parasitism conducted from 1987 to 1990 at three sites within 60 km of each other near Riske Creek in central British Columbia, Canada (see Lyon 1993a for details). At these sites, coots are migratory and my banding studies show that adult philopatry is very rare (unpublished data) so I studied different individuals each year. Coots are monogamous and males share in all aspects of reproduction including nest-building, incubating, feeding and brooding the chicks, and defending the territory (Gullion 1953). Although both sexes incubate, it is not known whether females or both sexes recognize and reject eggs. All but one of the nests used in this study were at Kloh Lake south of Hanceville (1989–1990); one nest from a pilot study in 1988 at Riske Creek (Beecher’s Prairie) is also included.

Experimental nests

All experiments were initiated after the birds had finished laying their own clutches. Eggs were exchanged between nests at similar stages of incubation and located within a distance of at most a few territories on the same wetland. Most experiments were set up on a single day and the adults remained off their nests while I was exchanging eggs among nests. Accordingly, host and experimental eggs cooled to ambient temperature, ruling out any influence of egg temperature on host responses to parasitic eggs. In the true recognition experiments, the experimental hosts were left with five of their own eggs and given five eggs from one other female. In the recognition by discordancy experiment, all but one experimental host nest was left with two host eggs and eight eggs from one other female

(nest B21–1988 was left with two host eggs and received seven experimental parasitic eggs). To increase the chance that birds would be able to distinguish between host and experimental parasitic eggs, the donor eggs for all experimental nests were chosen to maximize the difference in appearance between the host's eggs and the experimental parasitic eggs, particularly in background color because this affects egg rejection in parasitized nests (Lyon 2003). Nests were chosen randomly, however, with respect to egg size to ensure that parasitic eggs were not consistently larger or smaller than host eggs across the experiments. I used two criteria to assay egg recognition: egg rejection and nonrandom incubation positions. Elsewhere, I show statistically that egg rejection is extremely accurate and that very few host eggs are mistakenly rejected (Lyon 2003). I therefore considered egg rejection as definitive evidence for recognition at the level of individual nests and did not determine probabilities associated with these per nest rejections. In addition, because rejection was considered as definitive evidence for recognition, I did not analyze egg positions at any nests with egg rejection.

All eggs in each nest were given unique identification numbers with indelible felt markers at the start of the experiment so I could record the presence/absence and position of each egg on each visit. Nests were then checked every 1 or 2 days after the experiment was initiated, and on each visit I noted which eggs were in central incubation positions and whether any eggs had been rejected. Eggs were scored as being in “central” positions only if they were completely surrounded by other eggs on all sides; all other eggs were scored as occupying “outer” positions. Egg

rejection in coots is mainly by burial in the nest material, but eggs are occasionally ejected from nests outright (Lyon 2003). Eggs were scored as rejected when they were fully buried in the nest material, when at least 50% of the egg was buried in the nest material on the last visit to the nest, or if eggs disappeared completely without being buried (only one egg). Nests were followed long enough to have detected most cases of egg rejection (minimum time followed 8 days for true recognition experiment, 10 days for discordancy experiment; Tables 1 and 2). In my observational study of brood parasitism, 83% of 104 parasitic eggs monitored closely were rejected by day 10 (unpublished data).

Hosts often respond differently to real vs experimental brood parasitism—seeing a brood parasite at the nest appears to stimulate a heightened response (Davies and Brooke 1988; Moksnes et al. 1991). It is important, then, to know if experimental nests were also parasitized by real brood parasites and, if so, if this influenced patterns of rejection. I did not monitor experimental nests closely before setting up the experiment so I was unable to determine whether parasitism had previously occurred on the basis of unusual egg-laying rates (≥ 1 new egg per day; the most accurate indicator of brood parasitism). However, post hoc analysis of parasitic eggs identified by unusual laying rates revealed that egg features can be used reliably to identify parasitized nests in cases where the parasitic and host eggs differ dramatically in features like background color and spotting patterns and color (Arnold 1990; Lyon 1993b). I therefore paid particular attention to the egg features in experimental nests to see if any of the eggs

Table 1 Experimental tests of true recognition, with each nest containing five host and five parasite eggs

Nest-year	Number nest checks (total days followed)	Total eggs in central positions	Total parasitic eggs in central positions	One-tailed <i>P</i> for egg positions	Parasitic eggs rejected	Support for true recognition?	Parasitized by a real brood parasite?
K10–1989	5 (11)	11	0	<0.0001 ^a	0	Yes	No
K21–1989	5 (11)	–	–	–	3 (bury)	Yes	No
K34–1989	5 (10)	–	–	–	1 (bury)	Yes	No
K7–1990	10 (11)	18	2	0.0008 ^a	0	Yes	No
K22–1990	14 (17)	27	10	0.10	0	No	No
K25–1990	8 (9)	–	–	–	4 (bury)	Yes	Yes
K27–1990	9 (10)	–	–	–	5 (bury)	Yes	No
K28–1990	13 (14)	29	11	0.11	0	No	No
K36–1990	6 (8)	11	4	0.26	0	No	Yes
K44–1990	10 (11)	18	4	0.01 ^b	0	Yes	No
K46–1990	10 (14)	19	9	0.50	0	No	Yes
K52–1990	8 (14)	15	4	0.044	0	Yes	No

Recognition was assessed by egg rejection or egg incubation positions (number of parasitic eggs in central positions). “Total eggs in central positions” is the cumulative total number of eggs in central positions summed across all visits, while “total parasitic eggs in central positions” is the cumulative total number of parasitic eggs in central positions.

^a Remains significant after Bonferroni adjustment of alpha.

^b Not significant after Bonferroni adjustment.

Table 2 Experimental tests of recognition by discordancy

Nest/year	Number nest checks (total days followed)	Total central eggs	Total host eggs in center	One-tailed probability for egg positions	Host eggs rejected	Parasitic eggs rejected	Support for minority recognition?	Parasitized by real brood parasite?	Critical values for $P=0.05^b$
B21–1988	14 (17)	23	1	0.015 ^a	0	0	Yes	No	2
K4–1990	8 (10)	15	2	0.38	0	0	No	Yes	1
K5–1990	10 (12)	19	5	0.85	0	0	No	Yes	1
K6–1990	11 (12)	20	4	0.63	0	0	No	Yes	1
K23–1990	8 (11)	16	4	0.59	0	0	No	Yes	2
K39–1990	14 (17)	26	5	0.56	0	0	No	No	2
K45–1990	11 (13)	19	6	0.94	0	0	No	No	1
K48–1990	11 (13)	17	6	0.97	0	1	No	No	1

All nests contained eight parasitic and two host eggs, except B21 which had seven parasitic and two host eggs. See Table 1 for explanation of variables.

^a Not significant after Bonferroni adjustment of alpha.

^b Value for $P=0.05$ in distribution of 10,000 randomizations (number of central host eggs at the 500th ranked observation)

differed dramatically from the majority in characteristics that have been shown to be diagnostic of parasitism: background color, spot size, and spot color (Lyon 1993b). Because parasitic eggs are often quickly rejected by burial in the nest (Lyon 2003) I also searched for eggs buried down in the nest below the cup. Based on visual comparisons of eggs and the presence of buried eggs, I determined that seven of the experimental nests had been parasitized before the experiment, while the appearance of eggs in one additional nest were suggestive of parasitism, but not conclusive. At the remaining nests, the eggs within each clutch were very similar to each other with respect to the features that reliably vary among females (Lyon 1993b) and I am confident that these nests had not been parasitized. None of the nests were parasitized after the experiment began. It is critical to note, however, that an accurate understanding of the parasitic histories of the experimental nests is not essential for interpreting the outcome of the experiments.

I also compared rejection rates in the experimental nests to rejection rates at naturally parasitized nests from my entire observational study [conducted 1987–1990; (Lyon 2003)]. However, because number of parasitic eggs affects rejection rate (unpublished data) and the experiments all entailed the addition of a large number of parasitic eggs, I limited the pool of naturally parasitized nests to those that received four or more parasitic eggs.

Statistical analysis of egg positions

I used randomization tests (a separate test for each nest) to determine the one-tailed probabilities of obtaining the observed total number of parasitic or host eggs in central positions at each nest, summed across all visits. One-tailed tests were used because each of the two experiments (and mechanisms) makes a specific one-tailed prediction. For

example, in the true recognition experiment, recognition is indicated when *parasitic* eggs are observed in central positions less often than expected by chance. For the recognition by discordancy experiments, recognition is indicated when *host* eggs are observed in central positions less often than expected by chance. Central egg positions change at least daily, so observations on different days were treated as independent data points.

For each nest simulation, I replicated the number of nest checks (i.e., different days a nest was checked) and for each simulated nest check, I replicated the total number of central positions observed on the actual nest check, and then randomly assigned eggs to these central egg positions on the basis of the relative frequencies of host and parasitic eggs in the nest: 0.5 for both egg types in the true recognition nests; 0.8 for parasitic eggs and 0.2 for host eggs in the recognition by discordancy nests (except for nest B21–1988 which had seven parasitic and two host). I then tallied the cumulative total number of host or parasitic eggs observed in central positions across all nest visits. I repeated this entire process 10,000 times to obtain a distribution of the total number of parasitic or host eggs expected in central positions by chance and used the distribution to determine the one-tailed probability associated with the real data (i.e., the observed numbers of central host or parasitic eggs in the experimental nest).

Results

True egg recognition experiment

Eight of the twelve nests (66%) in the true recognition experiment showed clear evidence for true recognition (Table 1). Parasitic eggs were rejected at four of the nests,

all by burial (Table 1). Parasitic eggs were kept in outer incubation positions more often than expected by chance at four of the remaining eight nests (Table 1). No host eggs were rejected at any of the nests. Correcting error rates for table wide comparisons (Rice 1989; applied only to the eight nests without egg rejection) does not change the interpretation of the experiments (Table 1)—with adjusted alpha levels, there is still clear evidence for true recognition at six of the 12 nests (50%).

Recognition by discordancy experiment

I found evidence for recognition by discordancy at one of the eight nests (Table 2; 12.5%), based on nonrandom egg positions. No host eggs were rejected at any of the discordancy experiment nests. If probabilities are corrected for table-wide comparisons (Rice 1989; eight statistical comparisons), the single nest with nonrandom egg positions is no longer significant.

The low number of host eggs in the discordancy experiments may yield low statistical power, or even insufficient power for even the most extreme observations possible to be statistically significant with the observed sample size of egg positions. A comparison of the critical values at each nest—i.e., the number of host eggs in central positions at the 500th smallest value in each ranked distribution of 10,000 randomizations, or $P=0.05$ —is greater than zero for all nests (Table 2). Thus, this experiment had sufficient sample size to detect significant nonrandom patterns of egg positions at all nests had the birds used recognition by discordancy.

Although this experiment was designed to test for recognition by discordancy, a parasitic egg was rejected at one nest (Table 2, nest K48), providing additional evidence for true recognition. The rejected parasitic egg was dented, then subsequently ejected, and egg positions also tended to deviate from random at this nest (Table 2), but in the opposite direction predicted by discordancy (i.e., host eggs tended to be in central positions more than expected by chance).

Comparison of rejection rates in experimental and observational nests

Fewer experimental hosts rejected eggs than did hosts in the previous observational study: 27 of 37 (72.9%) hosts naturally parasitized with four or more eggs rejected at least one parasitic egg compared to 5 of 20 (25%) experimental hosts (Tables 1 and 2 combined; $\chi^2=10.30$, $df=1$, $P=0.0013$). If we exclude the discordancy experiment from this comparison (with the assumption that these birds may have been too overwhelmed by the high frequency of parasitic eggs to reject eggs), the rejection rates are still significantly lower for

the true recognition experiment compared to natural parasitism [4 of 12 hosts (33%); $\chi^2=4.57$, $df=1$, $P=0.032$].

There was no indication that real parasitism of the experimental nests influenced egg rejection, although sample sizes are too small to permit statistical analysis. Parasitic eggs were rejected at one of three naturally parasitized nests in the true recognition experiment, the identical proportion observed for the entire experiment (Table 1). None of the four naturally parasitized nests in the discordancy experiment rejected eggs (Table 2).

Discussion

My experiments provide convincing evidence that egg recognition in American coots is based on true recognition, not recognition by discordancy. Two thirds of the experimental birds given equal frequencies of host and parasitic eggs showed clear evidence of recognition, while only one of the nests where hosts were left with a minority of their own eggs supported recognition by discordancy. However, even this limited support for minority recognition disappears if error rates are adjusted to account for table-wide comparisons (Rice 1989).

Most previous work on the mechanism of egg recognition in the context of brood parasitism focused on species parasitized by interspecific brood parasites such as cuckoos and cowbirds (Table 3). Although two studies of village weaverbirds reveal that weavers show true recognition when conspecific eggs are added to their nests (Victoria 1972; Lahti and Lahti 2002), there is disagreement over the importance of conspecific or interspecific brood parasitism to the evolution of egg recognition and rejection because weavers suffer both forms of parasitism (Payne 1967; Freeman 1988; Jackson 1992; Davies 2000; Lahti and Lahti 2002; Underwood and Sealy 2002). It is also worth noting that these weavers show extraordinary levels of egg variation among females, levels equal to the interspecific variation faced by hosts parasitized by nonmimetic interspecific brood parasites. Similarly, although bramblings and chaffinches show true recognition of conspecific eggs that differ sufficiently from their own, it is clear that the selective agent involved is parasitism by cuckoos because conspecific parasitism does not occur (Moksnes 1992). In this case, the ability to recognize conspecific eggs is clearly an incidental outcome of an interspecific coevolutionary arms race that has led to ever more sophisticated egg mimicry by the cuckoo and concomitantly ever more sophisticated egg rejection by the hosts.

American coots thus provide the first unequivocal evidence that true recognition can arise where the evolution of egg recognition is driven entirely by conspecific brood parasitism. The distinction between forms of brood para-

Table 3 Summary of previous studies of egg recognition mechanisms in birds, including the context in which recognition is used by the species (brood parasitism or colonial breeding), the type of experimental egg used, which mechanisms were tested (equal frequency host and parasite vs reversed frequency with host in minority), by what criteria recognition was assessed, and which mechanisms were supported

Species	Context	Eggs used: interspecific or conspecific	Mechanism tested	Criterion used ^a	Mechanism shown	Study
American robin (<i>Turdus migratorius</i>)	Interspecific parasitism	Interspecific	Both	Reject	True	Rothstein 1975a
Gray catbird (<i>Dumetella caroliniensis</i>)	Interspecific parasitism	Interspecific	Both	Reject	True	Rothstein 1975a
Northern oriole (<i>Icterus galbula</i>)	Interspecific parasitism	Interspecific	Both	Reject	True	Rothstein 1978
Great reed warbler (<i>Acrocephalus arundinaceus</i>)	Interspecific parasitism	Conspecific	Both	Reject	True	Lotem et al. 1995
Village weaver (<i>Ploceus cucullatus</i>)	Interspecific or conspecific parasitism?	Conspecific	Both	Reject	True	Victoria 1972; Lahti and Lahti 2002
Chaffinch (<i>Fringilla coelebs</i>)	Interspecific parasitism	Conspecific	Both ^a	Reject	True	Moksnes 1992
Brambling (<i>Fringilla montifringilla</i>)	Interspecific parasitism	Conspecific	Both ^a	Reject	True	Moksnes 1992
Great-tailed grackle (<i>Quiscalus mexicanus</i>)	Interspecific parasitism	Interspecific	Both	Reject	True	Peer and Sealy 2001
Eastern kingbird (<i>Tyrannus tyrannus</i>)	Interspecific parasitism	Interspecific	Both	Reject	True	Sealy and Bazin 1995
Red-winged blackbird (<i>Agelaius phoeniceus</i>)	None	Interspecific	True ^b	Desertion	True	McCabe and Hale 1960
American coot (<i>Fulica americana</i>)	Conspecific parasitism	Conspecific	Both	Reject, egg positions	True	This study
Common murre (<i>Uria aalge</i>)	Colonial breeding	Conspecific	True	Egg retrieval	True	Tschanz 1968
Thick-billed murre (<i>Uria lomvia</i>)	Colonial breeding	Conspecific	True	Egg retrieval	True	Gaston et al. 1993
Royal tern (<i>Sterna maxima</i>)	Colonial breeding	Conspecific	True	Nest choice	True	Buckley and Buckley 1972
Caspian tern (<i>Sterna caspia</i>)	Colonial breeding	Conspecific	True	Nest choice	True	Shugart 1987
Elegant tern (<i>Sterna elegans</i>)	Colonial breeding	Conspecific	True	Nest choice	True	Schaffner 1990
Red-tailed tropicbird (<i>Phaethon rubricauda</i>)	Colonial breeding	Conspecific	True	Egg retrieval	True	Howell and Bartholomew 1969

^a Reversed egg frequency experiments that supported true recognition because birds rejected parasitic eggs.

^b Complete replacement of host eggs with eggs of other species.

sitism is important because in the early stages of coevolution in interspecific brood parasitism—i.e., before the evolution of egg mimicry by the parasite—recognition of parasitic eggs will involve far more obvious recognition cues than would be required for recognizing eggs of conspecifics (see Rothstein 1982). My results show that true recognition is a viable recognition mechanism even where the initial evolution of recognition requires the very fine-scaled recognition cues needed to distinguish among the eggs of conspecifics.

Recognition mechanisms have now been experimentally investigated in seventeen species, ten in the context of

brood parasitism, six in high-density colonially nesting seabirds where confusion over egg identity could arise, and one instance as an incidental outcome of swapping eggs among species for population establishment (Table 3). True recognition was demonstrated in all seventeen species. In contrast, there is no compelling evidence for any species that recognition by discordancy is an important mechanism of recognition (Table 3). However, the relative number of parasitic eggs has been shown to affect how rapidly birds reject eggs in some host species (Rothstein 1975a).

Why is true recognition so prevalent in birds? Two possible reasons have been proposed in the context of

brood parasitism (Rothstein 1975a) and a third reason applies to the colonial seabirds. First, true recognition might be easier to evolve because it requires a single component, recognition, whereas discordancy requires two components, recognition plus the ability to assess frequencies of eggs and determine which type is the minority. Second, true recognition is immune from incorrect rejection decisions that would occur when nests contain more parasitic eggs than hosts. The former idea seems to be more likely than the latter because there are probably few instances where hosts end up with more parasitic eggs than their own. Third, for colonial seabirds with a single egg, true recognition is the only possible mechanism.

Logistic implications of recognition without rejection

The nonrandom incubation positions of parasitic eggs observed in this study (Table 1) and in a previous nonexperimental study (Lyon 2003) indicate that some coots recognize conspecific parasitic eggs without rejecting them—clearly, a lack of egg rejection does not always indicate an inability to recognize the eggs (see also Soler et al. 2000). Similar egg position effects have been examined in four previous studies of brood parasitism in waterfowl, one on conspecific parasitism (Eadie 1989) and three on interspecific parasitism (Mallory and Weatherhead 1993; Sorenson 1997; Dugger et al. 1999). Only one of these studies found that parasitic eggs were nonrandomly kept to the periphery of the clutch (Mallory and Weatherhead 1993).

Nonrandom egg positions thus provide a second criterion for egg recognition that is independent of the standard one used in recognition studies, egg rejection. This turned out to be particularly important in this experimental study because of the low rejection rates of experimental eggs relative to rejection rates of real parasitic eggs. Accordingly, the use of egg positions greatly increased my ability to detect egg recognition, with half of the detected cases of recognition in the true recognition experiment based on this criterion (Table 1).

Another benefit to the use of egg positions to assay recognition is that recognition can be statistically tested on a per nest basis, something not possible with egg rejection. While the two mechanisms of recognition—true recognition and discordancy—are mutually exclusive in the same individual at a given nest, different individuals could use different mechanisms or individuals could vary with age. An ability to test for recognition on a per nest basis allows us to test this possibility. A limitation of the egg position criterion, however, is that statistical power may be somewhat lower for tests of recognition by discordance than true recognition, due to the differences between the two types of experiments in the frequencies of parasite vs host eggs. Additionally, the use of egg positions as a test of

recognition will likely be limited to species with large clutch sizes where there are clear central and peripheral egg positions. Notably, all studies to date that have examined egg position effects have been in species with large clutches.

Evolutionary implications of recognition without rejection

The occurrence of recognition without rejection indicates that factors other than recognition also play a role in determining whether eggs are rejected. Factors that have been shown to influence such plasticity in egg rejection behavior include seasonal, annual, and geographic variation in the presences of brood parasites or frequency of brood parasitism (Alvarez 1996; Brooke et al. 1998; Lindholm 2000), whether hosts observe the brood parasite at their nest (Davies and Brooke 1988; Moksnes et al. 1991), retaliatory behavior by the brood parasites in the form of host egg destruction (Soler et al. 1999), or even variation within the same host individual (Soler et al. 2000). In most of these cases, it appears as though at least some of the plasticity in egg rejection is adaptive, whereby hosts adjust the costs and benefits of rejection behavior to variation in the risks or costs of brood parasitism (Davies et al. 1996).

Given that coots often recognize eggs without rejecting them, it is worth considering why the eggs are not rejected. A likely explanation is that the two behaviors—banishing vs rejecting eggs—comprise a graded response that is a nuanced version of the adaptive plasticity described above. Thus, the costs and benefits of the two responses might differ, with rejection being the most appropriate response in some contexts, and banishment being appropriate in others. In terms of benefits, banishing parasitic eggs to outer incubation positions is a less extreme host defense than outright rejection because the parasitic eggs can still hatch, but it nonetheless reduces the impact of parasitic eggs on host fitness. Keeping parasitic eggs to the periphery of host clutches exposes them to cooler incubation conditions, on average, and they consequently have slower development than host eggs laid at the same time (Lyon 2003). Because later-hatched chicks suffer dramatically reduced survival (Lyon 1993a), delayed hatching of parasitic chicks decreases that probability that the parasites will survive, a benefit to hosts because each parasitic chick that survives does so at the expense of a host chick (Lyon et al. 2002). Previously, I reported a hatching delay of 0.7 days for parasitic eggs relative to host eggs laid on the same day in the same nest (Lyon 2003), but this value is an underestimate of the impact of banishing on parasitic eggs because its a population estimate based on all nests, including those with and without positional effects. For the small number of nests ($n=6$) where I was able to detect nonrandom egg positions on a per nest basis, the delay in hatching for parasitic eggs was 1.25 days,

a delay that would reduce the survival of parasitic chicks by 10 to 20%, depending on when the egg was laid in the host's laying cycle.

Several factors could potentially influence the relative benefits of rejection vs banishment for American coots, including the degree to which host and parasite eggs differ and can be reliably distinguished by the host, variation in host age, or variation in cues that indicate that parasitism has occurred, such as catching the parasitic female in the act of parasitism. One of these factors may also explain why experimental eggs were rejected at a lower rate than real parasitic eggs in the present study. Naturally parasitized birds may catch the parasitic female in the act of parasitism (McRae 1996)—a stimulus that causes an increased rejection response—whereas birds in my experiment would have lacked this stimulus entirely. This effect has been demonstrated experimentally by observing increased rejection rates of experimental parasitic eggs when the hosts are also presented with a taxidermic mount of a brood parasite (Davies and Brooke 1988; Moksnes et al. 1991).

Recognition without rejection may have implications for the evolution of a complex, multicomponent defense like egg rejection, at least for species with sufficiently large clutch sizes and/or incubation behaviors for nonrandom incubation to be an effective defense. As Rothstein (1978) first pointed out, egg rejection is comprised of two distinct behavioral components: a recognition system that enables the bird to distinguish among the eggs of different females and the rejection behavior itself. However, if both components are necessary for successful nonrandom rejection of parasitic eggs, how does the system ever evolve? It is extremely unlikely that both components arise simultaneously and it seems equally improbable that egg rejection without recognition would be adaptive in many circumstances. Instead, the most likely evolutionary sequence is that recognition evolves first, in a context unconnected to egg rejection, and once birds are capable of distinguishing between host and parasite eggs, the evolution of nonrandom egg rejection based on this recognition is then possible.

Banishing parasitic eggs to the outside of clutches demonstrates a context in which recognition without rejection is adaptive and provides a plausible stepping stone to the evolution of egg rejection based on recognition. The evolution of banishing behavior itself should be fairly simple as it would result from the coupling of egg recognition and the random shuffling of egg positions to control for spatial variation in incubation conditions—a behavior that requires no egg recognition and appears to be widespread in many birds (Huggins 1941; Kessler 1960; Drent 1975). This evolutionary scenario is most feasible for species with large clutches like rails, grouse, and waterfowl, where there are clear central and peripheral incubation positions. However, nonrandom incubation behavior, with

consequences similar to banishment, is feasible in at least some species with small clutch sizes, indicating that stepping stone scenario is not necessarily exclusive to taxa with large clutch sizes. For example, brown-hooded gulls (*Larus maculipennis*) in Argentina have clutches of two or three eggs, yet some incubating birds are able exclude eggs of the parasitic black-headed duck (*Heteronetta atricapilla*) from their brood patches and prevent them from hatching, even though the duck eggs are never rejected from the nest bowl (Lyon and Eadie, unpublished data). It is intriguing to note that some individual gulls reject duck eggs from their nest outright—this species would be ideal for examining the factors that determine whether hosts adopt nonrandom incubation behavior or egg rejection to deal with parasitic eggs.

Even though recognition without rejection can clearly occur in some taxa with small clutches, it is unlikely that stepping-stone scenario proposed in this study will account for the evolution of egg rejection in all species. An alternative evolutionary route to egg rejection, suggested by Rothstein (1975b), is that egg rejection arose from nest sanitation behavior, whereby birds remove foreign objects from their nests. Distinguishing between these two alternatives will be challenging, but worthwhile.

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