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## Clutch control

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# Egg recognition and counting reduce costs of avian conspecific brood parasitism

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**Birds parasitized by interspecific brood parasites often adopt defences based on egg recognition but such behaviours are puzzlingly rare in species parasitized by members of the same species. Here I show that conspecific egg recognition is frequent, accurate and used in three defences that reduce the high costs of conspecific brood parasitism in American coots. Hosts recognized and rejected many parasitic eggs, reducing the fitness costs of parasitism by half. Recognition without rejection also occurred and some hosts banished parasitic eggs to inferior outer incubation positions. Clutch size comparisons revealed that females combine egg recognition and counting to make clutch size decisions—by counting their own eggs, while ignoring distinctive parasitic eggs, females avoid a maladaptive clutch size reduction. This is clear evidence that female birds use visual rather than tactile cues to regulate their clutch sizes, and provides a rare example of the ecological and evolutionary context of counting in animals.**

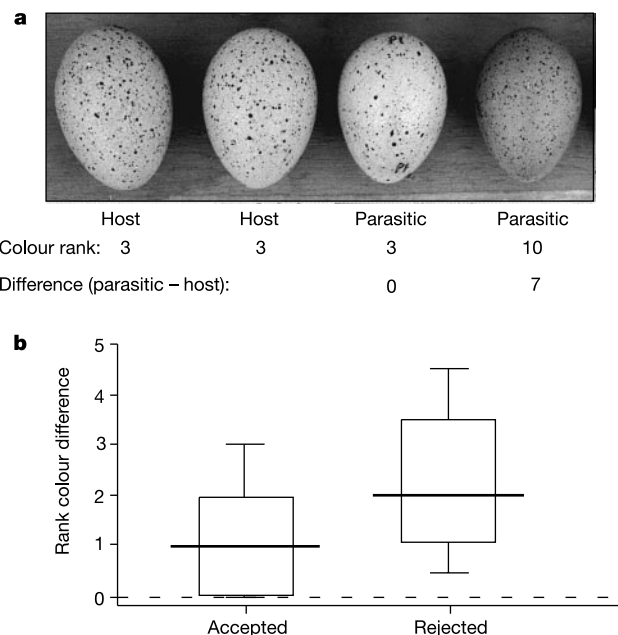
Avian brood parasitism provides a model system for studying evolutionary aspects of animal cognition because recognition mechanisms are central to host defences against parasitism, and the evolutionary costs and benefits of these mechanisms can be quantified<sup>1–7</sup>. Egg recognition and rejection is a particularly common defence in hosts parasitized by interspecific avian brood parasites<sup>2,6,7</sup>. Recent evidence reveals that brood parasitism within species is also widespread in birds<sup>7–11</sup>, but host defences based on conspecific egg recognition are surprisingly rare<sup>7,11</sup>. The reasons for this absence are unclear, but hypotheses include lower costs of parasitism for hosts of conspecific brood parasites and hence reduced natural selection for defences<sup>11</sup>, or insufficient variation in egg features among conspecific females for accurate egg recognition to be possible<sup>10</sup>.

Here I describe the results of a study of conspecific brood parasitism in the American coot (*Fulica americana*), an aquatic rail, which revealed high levels of accurate egg recognition. By examining how coots have incorporated egg recognition into a variety of defensive tactics to mitigate the costs of brood parasitism by conspecifics, I show that a full understanding of brood parasitism and host defences contributes to, and indeed integrates, three disparate disciplines—cognition, physiology and life-history evolution.

## Parasitism is costly to hosts

Conspecific brood parasitism was both frequent, and costly to hosts, in the study population of coots near Riske Creek, British Columbia, Canada<sup>12,13</sup>. During the four-year study (1987–90) 13% of all eggs in the population were laid parasitically, 41% of 417 pairs were parasitized, and hosts received an average of 3.1 parasitic eggs<sup>12</sup>, a substantial number relative to the average clutch size (excluding parasitic eggs;  $8.1 \pm 0.09$  eggs,  $n = 388$ ; all values reported with means are standard errors). Indirect evidence indicates that successful parasitism was very costly to hosts owing to intense competition between host and parasitic chicks for limited parentally supplied food early in life. Chick starvation was ubiquitous during the study: 98% of all nests ( $n = 177$ ) lost at least one chick, and on average, each nest lost 52% of its chicks, primarily to starvation<sup>12</sup>. Although parasitism increased the total number of chicks that hatched at host

nests, it had no effect on the total number fledged, owing to complete compensatory chick mortality<sup>14</sup>. Together, these patterns indicate that each successful parasitic chick survives at the expense of a host chick—a one-for-one substitution<sup>14</sup>. This high cost per successful chick, combined with the high frequency of parasitism, should result in strong natural selection for effective host defences to reduce the costs of parasitism.



**Figure 1** Egg rejection on the basis of colour. **a**, Host and parasitic eggs from a single nest, illustrating variation in rank background colour (see Methods) and the difference in ranked colour between parasitic and host eggs (all host eggs in this clutch were rank 3). **b**, Rejected parasitic eggs differed more from their host eggs in rank background colour (median difference = 2.0,  $n = 28$  host–parasite dyads, see Methods) than did accepted parasitic eggs (median difference = 1.0,  $n = 55$  dyads; Mann–Whitney  $U$ -test, one-tailed  $P = 0.003$ ). Thick line on box plots, the median; box, the 25th and 75th percentiles; thin line, 10th and 90th percentiles.

# Egg recognition reduces costs of parasitic chicks

Hosts reduced potential competition from parasitic chicks by rejecting parasitic eggs from their nests before they hatched (Table 1). Overall, 57 of 133 hosts (42.9%) rejected at least one parasitic egg. Egg rejection was highly non-random, indicating a specific defence against parasitism based on egg recognition (matched-pair comparison of the proportion of host and parasitic eggs rejected at each host nest; parasitic eggs rejected at a higher rate than host eggs at 50 of 56 nests, ties excluded, sign test  $P < 0.0001$ ). Egg features such as colour and spotting patterns vary greatly among females<sup>12,13</sup> and could thus serve as cues for accurate egg recognition. Rejected parasitic eggs differed more from their host eggs in background colour than did accepted parasitic eggs (Fig. 1), strongly suggesting that hosts use visual cues to distinguish parasitic eggs from their own eggs.

For hosts, egg rejection yields a high fitness benefit yet incurs only a low cost. Hosts rejected 45% of the 208 parasitic eggs laid early enough in the host's cycle to pose a threat (that is, laid within a day of clutch completion), thereby reducing the costs of parasitism by almost half. The cost of rejection to hosts—the mistaken rejection of their own eggs ("recognition error"<sup>3</sup>)—is typically measured as the frequency of all rejected non-parasitic eggs. This may not be appropriate, however, because coots have two distinct methods of egg rejection (Table 1), only one of which appears to be directed at parasitism. Most parasitic eggs were rejected by burial, while most non-parasitic eggs were rejected by outright ejection from the nest (Table 1), which suggests that the two rejection methods solve different problems.

All eggs that were known to be cracked or rotten were ejected rather than buried (7 non-parasitic, 4 parasitic), whereas none of the many buried eggs recovered from nesting material were ever damaged or rotten. This observation suggests that ejection is used to quickly remove damaged or rotten eggs that threaten the entire clutch and is not a defence against parasitism. Moreover, ejection of non-parasitic eggs was not disproportionately common at parasitized nests, as would be expected were it a defence against parasitism (ejection at 19 parasitized and 24 unparasitized nests,  $\chi^2$  goodness-of-fit test based on a 41% parasitism rate,  $\chi^2 = 0.18$ ,  $P = 0.67$ ). Thus, the cost of rejection to hosts is probably not the frequency of all rejected non-parasitic eggs, but the frequency with which non-parasitic eggs are buried (Table 1, 9/3,062 eggs = 0.29%), a very low cost. The idea that burial and ejection solve different problems, using different cues, is supported by the observation that many species that do not recognize or reject parasitic eggs readily eject damaged eggs (whether host or parasitic)<sup>15</sup>. Thus, unlike burial, ejection does not require recognition of foreign eggs.

Hosts exhibited a second, subtler defence that involved recognition without outright rejection—parasitic eggs were banished to the periphery of the clutch where incubation positions are likely to be inferior. A matched-pair comparison of the proportion of all parasitic and host egg positions that were in outer and inner positions, respectively, at each nest revealed that host eggs were in central positions proportionately more often than parasitic eggs at 22 of 25 nests (sign test  $P = 0.0002$ ; median proportion in central

positions 13.3% for parasitic eggs, 22.6% for host eggs). Because of these positional effects, parasitic eggs took longer to hatch than the corresponding host eggs laid on the same day (Fig. 2). Hosts benefit from this outcome because chick survival is strongly linked to relative hatching order<sup>12</sup>, so delaying the hatching of parasitic chicks reduces their survival and thus impact on host chicks.

These patterns indicate some level of recognition, so I wondered why the eggs were not rejected outright. One possibility is that hosts use incubation positions to deal with eggs that are distinguished as parasitic eggs with less certainty, and hence entail a higher risk of a recognition error. While positional effects are less effective than outright rejection, the cost of making a mistake and banishing a host egg to the outside is also less extreme than the outright rejection of a host egg. Regardless, the addition of egg recognition to a behaviour that is widespread in birds, shuffling eggs to ensure equitable incubation conditions, has resulted in an unusual defence against brood parasitism. Moreover, the observation that not all recognition leads to rejection means that using egg rejection as a proxy for egg recognition is not a reliable measure<sup>4</sup>.

## Why coots?

Conspecific egg recognition and rejection are known to be well developed in only three taxa: in coots and related rails<sup>13,16,17</sup>, weaverbirds (genus *Ploceus*)<sup>18</sup> and the ostrich (*Struthio camelus*)<sup>19</sup>. The evolution of defences against parasitism will depend not only on the cost of each successful parasitism but also on the frequency of such parasitism—that is, population level fitness costs. Estimates indicate that in the absence of host defences, parasitism would cause a 5.4% reduction in the total population production of non-parasitic coot chicks<sup>11</sup> (based on estimating the number of parasitic chicks that would survive in the absence of host defences (see Methods) and subtracting one host chick from the population for each surviving parasitic chick). Similar cost estimates are not available for any other conspecific parasite, but comparison with hosts parasitized by a well-known interspecific parasite, the common cuckoo (*Cuculus canorus*), is informative.

Hosts successfully parasitized by cuckoos raise no chicks of their own<sup>7</sup>, so the frequency of parasitized nests provides a maximum estimate for the population level costs that would be incurred without egg rejection (assuming that all cuckoo eggs are successful). Davies and Brooke<sup>20</sup> report parasitism frequencies for each of 14 host species in the United Kingdom, and the above fitness cost for coots equals the cost of parasitism for the most heavily parasitized cuckoo host, the reed warbler (*Acrocephalus scirpaceus*): both would lose about 5% of fitness to parasitism without defences. This is an unexpected finding, given the enormous cost to hosts of raising a cuckoo chick rather than a coot chick, but it can be attributed to the higher frequency of parasitism in coots than in cuckoo hosts. The extreme fitness costs for coots helps explain the evolution of their sophisticated battery of defences based on egg recognition.

## Egg recognition and life-history evolution

Hosts also used recognition to deal with a previously unappreciated cost of parasitism, a maladaptive clutch-size reduction caused by misinformation provided by parasitic eggs. Coots, like many birds,

Table 1 Frequency and method of rejection of parasitic and non-parasitic eggs

Type of egg	Number of eggs		Percentage of eggs rejected	Number of eggs rejected by*		Percentage of rejections by burial
	Rejected	Not rejected		Burial	Ejection	
Parasitic	174	356	32.8%	142	32	81.6%
Non-parasitic	73	3,062	2.4%	9	65	12.2%

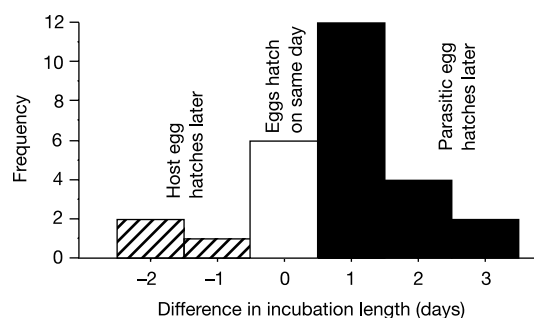
Rejected non-parasitic eggs include 38 eggs in 24 parasitized nests and 35 eggs in 25 unparasitized nests.

\*When nests are counted only once for each egg type (parasitic or not) or rejection method (burial or ejection), burial was the method used for 75.9% of 83 nests rejecting parasitic eggs, and for 12.5% of 48 nests rejecting non-parasitic eggs;  $\chi^2 = 49.0$ ,  $P < 0.0001$ .

are 'indeterminate' egg-layers that use an external cue, such as the number or surface area of eggs in the nest, to cease further development of egg follicles and thereby regulate their clutch sizes<sup>21</sup>. With this mechanism, the addition or removal of eggs early in the laying cycle alters the number of eggs present in the nest (the termination cue) relative to the number actually laid by the female up to that point, causing the female to alter the total number of eggs she lays. Thus, parasitic eggs laid early in the host's laying cycle could affect clutch-size decisions by decreasing the total number of eggs laid by the host.

Using a titration approach to identify the temporal window of sensitivity and the degree of response to the extra eggs added by parasites (see Methods), I found that hosts do alter their clutch size in response to parasitic eggs, and that the strongest effect was observed for eggs added by the host's third day of laying. I then separately examined the clutch-size responses of two classes of host nests—nests where the parasitic eggs were accepted and nests where they were rejected. The acceptors reduced their clutch size in response to early-laid parasitic eggs (Fig. 3a: slope =  $-1.06 \pm 0.24$  host eggs per parasitic egg added;  $F_{1,111} = 20.18$ ,  $P < 0.0001$ ). In contrast, the clutch sizes of hosts that rejected parasitic eggs were unaffected by the number of early-laid parasitic eggs (Fig. 3b: slope =  $-0.03 \pm 0.29$ ;  $F_{1,111} = 0.013$ ,  $P = 0.91$ ). Ignoring the number of parasitic eggs received and comparing means revealed that clutch sizes differed significantly between these two classes of nests ( $6.65 \pm 0.45$  eggs for 17 acceptors,  $8.12 \pm 0.42$  eggs for 17 rejecters;  $t = 2.41$ ,  $P = 0.02$ ).

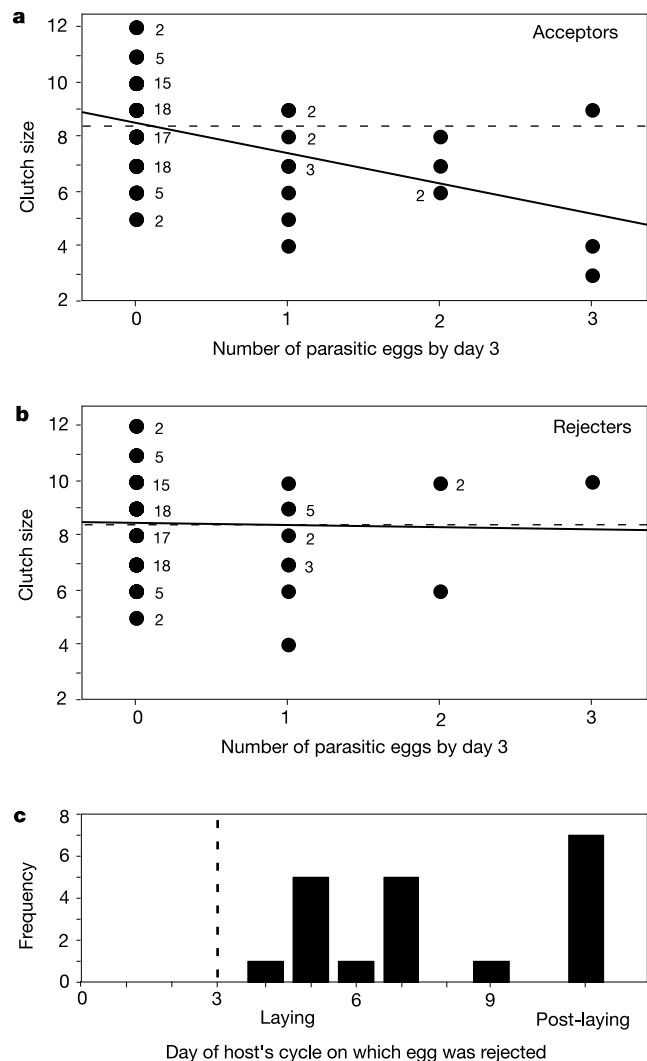
Why did early-parasitized acceptor and rejecter females differ in their clutch-size responses? The difference is not explained by inherent differences in female quality between acceptor and rejecter nests because there was no difference in the clutch sizes of rejecter and acceptors parasitized after host clutch-size decisions were made (that is, reference hosts in Fig. 3:  $8.18 \pm 2.46$  eggs for 39 acceptors,  $8.12 \pm 0.32$  eggs for 17 rejecters;  $t = 0.14$ ,  $P = 0.89$ ). The difference is also not explained by the effects of rejection itself on the total number of eggs present when hosts made their clutch-size decisions because rejecters did not reject the parasitic eggs until after they had made their clutch-size decisions (Fig. 3c). Consequently acceptor and rejecter nests had the same number of total eggs (host plus parasite) on day 3, the end of the responsive period for clutch-size adjustment ( $4.67 \pm 0.21$  eggs for acceptors,  $4.50 \pm 0.20$  eggs for rejecters;  $t = 0.57$ ,  $P = 0.57$ ), an observation that rules out the use of tactile cues to regulate clutch size<sup>21</sup>.



**Figure 2** Difference in the length of the incubation period for paired parasitic and host eggs laid in the same nest on the same day. The incubation period is the time from laying to hatching. Black bars indicate pairs of eggs where the parasitic egg took longer to hatch, striped bars where the host egg took longer, and white bars where both eggs hatched on the same day. On average, parasitic eggs hatched 0.78 days later than their corresponding host egg (matched-pair comparison of average values for each host–parasite female dyad, rather than individual pairs of eggs;  $t = 2.63$ , degrees of freedom = 16, one-tailed  $P = 0.009$ ).

## Coots can count

The different clutch-size responses of acceptors and rejecters appears to arise instead from their use of visual cues—specifically counting the number of eggs perceived as their own—to decide when to stop further development of maturing egg follicles. The perception of such visual information would have differed for acceptors and rejecters, as follows. By chance, acceptor females received parasitic eggs too similar to their own to permit recognition (or rejection, Fig. 1) so they included the parasitic eggs in their count during clutch-size assessment. The observed clutch-size reduction, 1.06 fewer host eggs per parasitic egg (Fig. 3a), does not differ significantly from a slope of  $-1.0$  ( $P > 0.05$ ), the slope expected if a host counts each parasitic egg as one of her own. At rejecter nests, in contrast, parasitic eggs were sufficiently different to be recognized (Fig. 1), and their lack of impact on clutch size (Fig. 3b) suggests that rejecter females counted only their own eggs and ignored parasitic eggs when making their clutch-size decisions.



**Figure 3** Host clutch-size response to early-laid parasitic eggs. **a, b**, Parasitic eggs includes those added during the host's responsive period (up to day 3 of laying cycle) and either accepted (**a**) or rejected (**b**) by the hosts. Solid lines, simple regression lines; dashed lines, mean clutch size for reference birds not parasitized early. Numbers indicate data points with multiple identical values. **c**, The timing of egg rejection for the nests used to examine the clutch-size responses of rejecters (shown in **b**). All eggs were rejected after the three-day window of host responsiveness (vertical dashed line) during which clutch-size decisions are made.



The ability of females to count only their own eggs in a mixture of eggs is a remarkable feat that provides a convincing, rare example of counting in a wild animal<sup>1</sup>. This observation also has broad implications for proximate mechanisms of clutch-size regulation, and their evolutionary consequences. These clutch-size patterns provide the first convincing evidence that birds use visual cues and egg recognition to regulate their clutches, because tactile cues cannot explain the different responses of acceptors and rejecters. The widespread assumption of the ubiquity of tactile information as decision cues for indeterminate egg layers<sup>21</sup> clearly needs to be reassessed.

The different clutch-size responses to parasitic eggs at acceptor and rejecter nests (Fig. 3) also raise questions about the adaptive basis of these patterns. Theory predicts that hosts can benefit from clutch-size reductions in some situations<sup>22,23</sup>. However, none of these benefits apply to the females who rejected eggs because egg rejection nullifies any costs that would favour a smaller clutch size. For these females, avoiding an inadvertent clutch-size reduction, as they did (Fig. 3b), is the adaptive response, a response that required the evolution of a sophisticated mechanism consisting of recognizing and counting the right eggs, while discounting parasitic eggs. Further work is needed to determine if the clutch-size reductions at coot nests where eggs are accepted (Fig. 3a), and in other species in general<sup>22</sup>, is a selected, adaptive response favoured by natural selection, or an inadvertent, maladaptive artefact of the mechanism used to regulate clutch size.

Experiments have confirmed the existence of simple counting abilities in a diversity of taxa in the laboratory<sup>1,24</sup>. However, the ecological and evolutionary context of such capacities is unknown, and clear examples of counting in wild animals are virtually non-existent<sup>1,25</sup>. In American coots, egg counting is directly linked to clutch size, a key life-history trait with fitness consequences. Visual egg counting may turn out to be common in a variety of birds that use external cues to regulate their clutch size, but without the clear signal provided by brood parasitism and egg recognition it may prove difficult to detect in observational field studies. More broadly, a connection between counting abilities and reproductive investment is likely to be widespread among animals with parental care<sup>26</sup>, because fitness is tightly coupled with the number of offspring produced, and parents should benefit from mechanisms that enable them to fine-tune reproductive decisions to fitness payoffs<sup>26</sup>. Studies of reproductive decisions concerning numbers of eggs and offspring can provide fertile ground for studying counting in animals and may provide model systems for integrating animal cognition and physiological mechanisms in an ecological and evolutionary context.

## Methods

### Detecting parasitism and parasitic eggs

Depending on the year of the study, each nest was checked daily ( $n = 206$ ) or every second day ( $n = 211$ ). All new eggs were individually numbered with indelible felt pens. Parasitism was detected primarily by the appearance of more than one new egg in a 24-h period but egg features were then used to determine which of the new eggs were parasitic, and to match parasitic eggs laid by the same female (parasites often laid several eggs per host nest and many host nests were parasitized by several females<sup>13</sup>). The accuracy of these field techniques has been verified by both discriminant function analysis based on egg features<sup>13</sup> and DNA fingerprinting<sup>14</sup>.

### Egg features, incubation positions and rejection

On each nest visit all eggs were censused to determine whether new eggs had been laid or previously labelled eggs had disappeared. Eggs that disappeared were assigned to two rejection categories: (1) buried, if recovered from the nest material or last observed at least 50% buried (most buried eggs were initially observed partly buried); and (2) ejected, for all other eggs that disappeared without meeting the criteria for burial. Ejection is thus a catch-all category that may include sources of egg loss unrelated to rejection, including partial predation and accidental displacement during parasitism (parasites seem not to remove host eggs deliberately<sup>13</sup>). In several cases, ejected eggs were recovered from the water below nests.

To determine whether coots non-randomly keep parasitic eggs to the periphery of the clutch during incubation, on each nest visit the position of each host and parasitic egg was scored as either 'central' (egg completely surrounded by other eggs) or 'outer' (egg

lacked neighbouring eggs on at least one side). Coots shuffle egg positions at least daily so eggs were not constrained to particular positions. For each nest I then pooled positions from all visits and determined the proportion of host and parasite egg positions that were central and outer, and then did a matched-pair comparison for all nests comparing the proportion of parasitic and host egg positions at each nest that were in outer positions.

To determine whether egg features affected egg rejection, I scored the background colour of eggs on a ranked darkness scale that ranged from 1 (white) to 10 (dark brown; see Fig. 1) by comparing them in the field to a reference collection of ten real coot eggs. Most nests in the analysis are represented by a single host-parasite dyad (61 nests), but for the nine hosts parasitized by several parasites, contrasts were included for each of the host-parasite dyads at the nests. Five of the nine nests parasitized by several females rejected eggs from some of the parasites but not others, indicating that rejection among different dyads involving the same host is independent. For each host-parasite contrast, I computed the difference between the mean background egg rank of the parasitic eggs and each of the host eggs, and then used the smallest value as the index of difference between the host and parasite. A host-parasite dyad was scored as 'reject' if at least one parasitic egg was rejected, but in fact rejection was all or none for most dyads. I also omitted acceptors that received parasitic eggs late in incubation (day 7 or later) because there may have been insufficient time for the birds to reject eggs. In all statistical comparisons, data points were nests or females, not individual eggs.

### Fitness costs of parasitism

To estimate the number of parasitic chicks that would survive in the absence of egg rejection, each rejected parasitic egg laid in a successful host nest was assigned a survival probability based on its predicted position in the hatching order (based on laying order) using an empirically derived relationship for survival probability relative to hatching order<sup>12</sup>.

### Clutch-size comparisons

To determine the temporal window over which hosts adjusted their clutch sizes in response to parasitism, I conducted a series of linear regressions, each comparing host clutch size (dependent variable) with the number of parasitic eggs received by a specific cut-off day in the host's laying cycle (independent variable; assessed day 3, 4 and 5 of host's cycle, respectively). To avoid spurious effects due to female quality, only parasitized birds were used in these analyses, and 82 birds not parasitized early (that is, parasitized on day 6 or later) served as the reference group (that is, 0 parasitic eggs by day 3) for determining a clutch-size response of early-parasitized birds. Clutch size showed the strongest decline with number of parasitic eggs received by the host's third day of laying (slope for day 3 regression =  $-0.63 (\pm 0.20)$ ,  $P = 0.002$ ,  $n = 21$  nests parasitized by day 3; slope for day 4 regression =  $-0.39 (\pm 0.15)$ ,  $P = 0.014$ ,  $n = 31$  nests parasitized by day 4; slope for day 5 regression =  $-0.29 (\pm 0.13)$ ,  $P = 0.046$ ,  $n = 45$  nests parasitized by day 5. I therefore chose day 3 as the cut-off point for separately examining the clutch-size responses of females who accepted or rejected parasitic eggs. For simplicity, I refer to these females as 'acceptors' and 'rejecters', respectively, but this grouping applies only to their one nest I examined and does not assume that they always reject or accept. In fact, egg rejection appears to be largely due to the chance difference between host and parasitic eggs.

The clutch-size comparisons provide indirect evidence for counting, but there is disagreement among cognitive psychologists over what the term 'counting' actually means<sup>1,24,26</sup>. I adopt the terminology of Gallistel<sup>24</sup> who suggests that counting includes any "discriminations based on the numerosity of a set". Thus, 'counting' here indicates that birds are making decisions based on the number of eggs in their nests, not that they are performing addition or subtraction.

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1. Shettleworth, S. J. *Cognition, Evolution and Behavior* (Oxford Univ. Press, Oxford, 1998).
2. Rothstein, S. I. A model system for coevolution: avian brood parasitism. *Annu. Rev. Ecol. Syst.* **21**, 481–508 (1990).
3. Sherman, P. W., Reeve, H. K. & Pfennig, D. W. in *Behavioural Ecology: An Evolutionary Approach* (eds Krebs, J. R. & Davies, N. B.) 69–98 (Blackwell, Oxford, 1997).
4. Rothstein, S. I. Successes and failures in avian egg and nestling recognition with comments on the utility of optimality reasoning. *Am. Zool.* **22**, 547–560 (1982).
5. Davies, N. B., Brooke, M. de L. & Kacelnik, A. Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proc. R. Soc. Lond. B* **263**, 925–931 (1996).
6. Brooke, M. de L. & Davies, N. B. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335**, 630–632 (1988).
7. Davies, N. B. *Cuckoos, Cowbirds and Other Cheats* (Poyser, London, 2000).
8. Rohwer, F. C. & Freeman, S. The distribution of conspecific nest parasitism in birds. *Can. J. Zool.* **67**, 239–253 (1989).
9. Eadie, J. M., Sherman, P. & Semel, B. in *Behavioral Ecology and Conservation Biology* (ed. Caro, T.) 306–340 (Oxford Univ. Press, Oxford, 1998).
10. Andersson, M. in *Producers and Scroungers* (ed. Barnard, C. J.) 195–228 (Croom Helm, London, 1984).
11. Lyon, B. E. *The Ecology and Evolution of Conspecific Brood Parasitism in American Coots* (Fulica americana) Thesis, Princeton Univ. (1992).
12. Lyon, B. E. Brood parasitism as a flexible female reproductive tactic in American coots. *Anim. Behav.* **46**, 911–928 (1993).
13. Lyon, B. E. Tactics of parasitic American coots: host choice and the pattern of egg dispersion among host nests. *Behav. Ecol. Sociobiol.* **33**, 87–100 (1993).
14. Lyon, B. E., Hochachka, W. M. & Eadie, J. M. Paternity-parasitism trade-offs: a model and test of host-parasite cooperation in an avian conspecific brood parasite. *Evolution* **56**, 1253–1266 (2002).
15. Kemeel, R. E. & Rothstein, S. I. Mechanisms of avian egg recognition: adaptive responses to eggs with broken shells. *Anim. Behav.* **36**, 175–183 (1988).
16. Jamieson, I. G., McRae, S. B., Simmons, R. E. & Trewby, M. High rates of conspecific brood parasitism

- and egg rejection in coots and moorhens in ephemeral wetlands in Namibia. *Auk* **117**, 250–255 (2000).
17. Arnold, T. W. Conspecific egg discrimination in American coots. *Condor* **89**, 675–676 (1987).
18. Jackson, W. M. in *Parasitic Birds and Their Hosts* (eds Rothstein, S. I. & Robinson, S. K.) 406–416 (Oxford Univ. Press, Oxford, 1998).
19. Bertram, B. C. R. *The Ostrich Communal Nesting System* 109–120 (Princeton Univ. Press, Princeton, 1992).
20. Davies, N. B. & Brooke, M. de L. An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. II host egg markings, chick discrimination and general discussion. *J. Anim. Ecol.* **58**, 225–236 (1989).
21. Haywood, S. Sensory and hormonal control of clutch size in birds. *Q. Rev. Biol.* **68**, 33–60 (1993).
22. Andersson, M. & Eriksson, M. Nest parasitism in goldeneyes *Bucephala clangula*: some evolutionary aspects. *Am. Nat.* **120**, 1–16 (1982).
23. Lyon, B. E. Optimal clutch size and conspecific brood parasitism. *Nature* **392**, 380–383 (1998).
24. Gallistel, C. R. Counting versus subitizing versus the sense of number. *Behav. Brain Sci.* **11**, 585–586 (1988).

25. Hauser, M. D. What do animals think about numbers. *Am. Sci.* **88**, 144–151 (2000).
26. Seibt, U. Are animals naturally attuned to number? *Behav. Brain Sci.* **11**, 597–598 (1988).

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