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An obligate brood parasite trapped in the intraspecific arms race of its hosts

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Reciprocal selection pressures often lead to close and adaptive matching of traits in coevolved species. A failure of one species to match the evolutionary trajectories of another is often attributed to evolutionary lags[1,2] or to differing selection pressures across a geographic mosaic[3,4]. Here we show that mismatches in adaptation of interacting species—an obligate brood parasitic duck and each of its two main hosts—are best explained by the

evolutionary dynamics within the host species. Rejection of the brood parasite's eggs was common by both hosts, despite a lack of detectable cost of parasitism to the hosts. Egg rejection markedly reduced parasite fitness, but egg mimicry experiments revealed no phenotypic natural selection for more mimetic parasitic eggs. These paradoxical results were resolved by the discovery of intraspecific brood parasitism and conspecific egg rejection within the hosts themselves. The apparent arms race between species seems instead to be an incidental by-product of within-species conflict, with little recourse for evolutionary response by the parasite.

Avian obligate brood parasites depend entirely on other species to raise their offspring, often inflicting severe fitness costs on hosts. Brood parasitism provides a model system for investigating the dynamics of antagonistic coevolution, because of the reciprocally hostile relationship between parasite and host[1,2,5–8]. In some parasitic taxa, extreme fitness costs of parasitism to hosts have favoured the evolution of egg discrimination and rejection by hosts, which in turn has led to the evolution of egg mimicry and host specialization in the parasite[5–8]. The black-headed duck (*Heteronetta atricapilla*) of southern South America is unique in comparison with all other species of obligate brood parasites in that its highly precocial chicks leave the host nest within a day of hatching (Fig. 1g) and require no post-hatching parental care[9,10]. This parasite should impose few fitness costs on its hosts and, accordingly, the ecological and evolutionary dynamics of host–parasite interactions should differ markedly from those of all other brood parasites.

We conducted a large-scale observational and experimental study of host–parasite interactions in black-headed ducks during four breeding seasons on seven wetlands in the pampas of Argentina. Brood parasitism was common (29.3% of 1,927 potential host nests of 11 species parasitized). Several attributes of the brood parasitism were counter to those expected for a precocial brood parasite. First, the parasites used very few host species (Fig. 1a), and parasitized these hosts at a high frequency (Fig. 1b). Despite the diversity of species used at least occasionally as hosts in our study (11 species), 80% of the 974 duck eggs we found occurred in nests of just two species of coots (Fig. 1a, e, f), with almost half occurring in a single host, the red-gartered coot (*Fulica armillata*). Because hatching success of the duck eggs is highest with this host (Fig. 1c), an estimated 58% of all ducklings hatch from nests of this one species and 83% from both coot species combined (see Methods). Dependence on such a narrow range of hosts was unexpected because the ability to use a wide diversity of hosts has been proposed as a key factor in the evolution of obligate brood parasitism in *Heteronetta*[2,10]. Second, the parasitic eggs had low hatching success in both main hosts (Fig. 1c), despite similar incubation periods of host and parasite. Third, both main hosts showed high levels of egg rejection (Fig. 1d). A strong negative correlation between the frequency of egg rejection and the hatching success of duck eggs for each host on each wetland (Spearman rank correlation $r_s = -0.99$, $n = 8$, $P < 0.01$) indicates that egg rejection markedly decreases the reproductive success of black-headed ducks and is a main source of egg mortality.

Egg rejection has arisen independently in a wide variety of birds to counter the costs of interspecific brood parasitism[1,2,5–8]; its occurrence here therefore implies some cost of parasitism to hosts. Such costs would have to be borne during incubation because the ducklings leave the nest within a day of hatching. Using both naturally and experimentally parasitized nests, we assessed costs known to be suffered by hosts of brood parasitism, including smaller host clutch size, longer incubation period, increased egg loss[11] and increased nest predation risk from the non-cryptic duck eggs[12] (Fig. 1h). We detected no costs of parasitism for red-gartered coots, whereas parasitized red-fronted coot (*F. rufifrons*) nests suffered higher egg loss rates than unparasitized nests (Table 1). Whereas many costs of parasitism are reduced by, and thus select for, egg rejection, 'unrecoverable' costs—such as incidental egg

displacement or damage by the brood parasite during parasitism—do not[13]. Further analysis of egg loss in parasitized red-fronted coot nests based on experimental egg addition and removal nests (see Methods) revealed that egg loss is associated only with the act of parasitism itself, not the presence of parasitic eggs, a cost that would not promote the evolution of egg rejection (Table 1).

We did not directly measure the energetic costs to incubating parents of caring for parasitic eggs, which could be an important fitness cost to hosts[14]. However, in the closely related American coot (*F. americana*), a species with larger clutch sizes, fat reserves actually increase throughout incubation, indicating that incubation might not be energetically costly in coots[15].

Independently of the factors selecting for egg rejection by hosts, the strong impact of egg rejection on the fitness of the black-headed duck should select for counter-adaptations such as the evolution of egg mimicry, particularly because the parasites depend on very few host species. We used field experiments with painted hen or host eggs (see Methods) to determine whether incremental improvement in egg mimicry (mimicking background colour alone or both the colour and shape of host eggs; Fig. 2a) would enhance the

acceptance rate, and hence the hatching success, of duck eggs in host nests. The degree of mimicry did not affect egg rejection rates in either host species (Fig. 2b, c); all egg treatments were rejected at similar rates and at rates within the range observed for real black-headed duck eggs.

Our results present two findings that are inconsistent with the hypothesis that interspecific interactions have driven host–parasite evolution in this system: high levels of egg rejection by the hosts in the absence of detectable costs of parasitism, and egg rejection that does not favour natural selection for egg mimicry in the brood parasite, at least over the range of egg features we examined. However, our results are consistent with an alternative hypothesis; specifically, that egg rejection evolved as a mechanism to reduce the costs of intraspecific brood parasitism within the host populations, and that rejection of duck eggs is an incidental by-product of this mechanism. A similar explanation has been proposed for egg rejection in weaverbirds (Ploceidae)[16,17], but the influence of inter-specific parasitism has not yet been assessed[2,18].

We found that intraspecific brood parasitism occurs regularly in both species of coots: females laid eggs in the nests of conspecifics, and hosts recognized and rejected some of these conspecific parasitic eggs. We studied intraspecific parasitism in red-gartered coots in 1997 and determined that at least 13% of 266 nests were parasitized by conspecifics. Retrospective analysis of our census data from previous years revealed average detectable rates of intraspecific parasitism of 4.7% in 254 red-gartered coot nests (range for individual wetlands 2.7–12.9% of nests) and 5.2% in 212 red-fronted coot nests (range for individual wetlands 2.9–7.9% of nests). These rates are considerable underestimates given that our earlier studies were not focused on detecting intraspecific parasitism (see Methods). Nine of 35 (26%) red-gartered coots rejected at least one parasitic coot egg, and 6 of 23 birds (26%) rejected conspecific eggs that we added experimentally to their nests, indicating that hosts are capable of sophisticated egg discrimination that goes well beyond distinguishing between duck and coot eggs. Red-fronted coots are also capable of recognizing and rejecting conspecific eggs: parasitic eggs were rejected at two of the nine (12%) parasitized nests.

Conspecific egg rejection is rare in birds[19] and seems difficult to evolve; its presence in the two hosts of black-headed ducks is difficult to explain other than as a defence against the costs of conspecific brood parasitism. Intraspecific brood parasitism and egg rejection are widespread in the rail family (Rallidae), including several other species of coots[19–21], none of which are parasitized by interspecific brood parasites. Detailed studies of the American coot
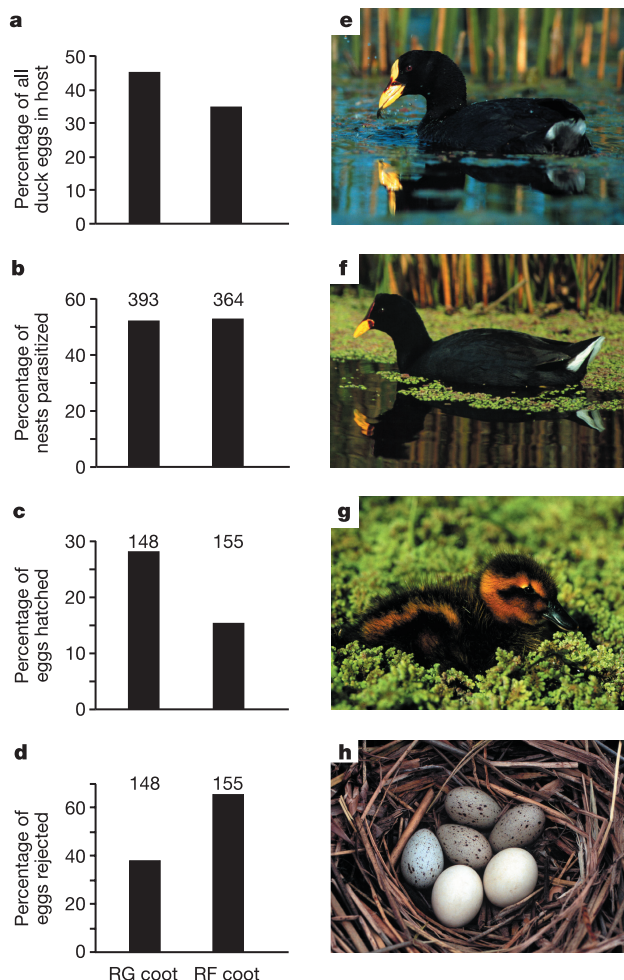
Figure 1 Frequency and attributes of parasitism in the two main hosts of the black-headed duck, the red-gartered coot (RG coot) and red-fronted coot (RF coot). **a**, Percentage of the total 974 duck eggs encountered during the study that were laid in nests of the two main hosts. **b**, Percentage of nests of each species parasitized by the ducks. **c**, Percentage of duck eggs laid in nests of each host species that hatched. **d**, Percentage of the duck eggs laid in nests of each host species that were rejected. The sample size above each bar indicates the number of nests (**b**) or eggs (**c**, **d**). **e**, Red-gartered coot. **f**, Red-fronted coot. **g**, One-day-old black-headed duckling, the age at which the ducklings become completely independent of hosts. **h**, Parasitized red-gartered coot nest with two duck eggs, showing a lack of mimicry.

Table 1 **Potential costs of parasitism by black-headed ducks on two main host species**

Parameter	Parasitized	Not parasitized	P
Red-gartered coot			
Clutch size	4.10 ± 0.09 (144)	4.11 ± 0.09 (151)	0.95*
Host incubation period (d)	22.5 ± 1.24 (11)	23.4 ± 0.65 (11)	0.50*
Nests losing host eggs (%)	16.4 (61)	11.5 (87)	0.39†
Nest predation rate (%)	27.9 (86)	26.5 (49)	0.86†
Red-fronted coot			
Clutch size	5.04 ± 0.14 (53)	5.20 ± 0.14 (56)	0.44‡
Host incubation period (d)	21.5 ± 0.89 (9)	23.1 ± 0.60 (22)	0.15*
Nests losing host eggs§ (%)	28.7 (94)	9.8 (61)	< 0.005†
Nest predation rate (%)	25.0 (44)	35.4 (48)	0.29†

Statistical tests for comparison of parasitized and unparasitized nests: *Student's *t*-test; †χ^2 test; ‡analysis of covariance to control for seasonal influence on clutch size; means are least-square means.
§We used a combination of experimental and observational nests to distinguish egg loss due to displacement or damage during the act of parasitism (a cost not affected by egg rejection) from egg loss due to the presence of duck eggs after parasitism (a cost prevented by early egg rejection). We experimentally removed duck eggs from parasitized nests to assay the former, and we experimentally added duck eggs to unparasitized nests to assay the latter. We then combined these experimental nests with the observational nests and used logistic regression to partition the two sources of egg loss statistically: the act of parasitism itself affected host egg loss (logistic regression; Wald χ^2 for parasitized versus unparasitized nests = 7.86, P = 0.005), but the presence of duck eggs did not (Wald χ^2 for the duration for which parasitic eggs are in a nest = 0.003, P = 0.96). Data are shown as means ± s.e.m. or as percentages, with the sample size in parentheses.

in North America reveal high costs of intraspecific brood parasitism to hosts and confirm that egg rejection is an evolutionary response specifically to reduce these costs[19]. Similar costs are likely to apply to the two Argentine coots, given their high chick provisioning rates (B.E.L. and J.McA.E., personal observation) and the fact that both species have highly ornamented chicks, a characteristic of extreme competition for limited food in American coots[22].

The switch of perspective from between-species to within-host dynamics can explain why the hosts reject duck eggs, even though parasitism by black-headed ducks seems not to be costly to them. It can also explain why more mimetic duck eggs are not favoured: given that hosts have been selected to distinguish their own eggs from those of other coots, the duck eggs differ too much from host eggs for incremental changes in appearance to increase their acceptance rate (Fig. 1h). Perfectly mimetic eggs would be selectively favoured over the existing white eggs, because both host species rejected conspecific parasitic eggs at a lower rate than the experimental mimicry eggs (all treatments combined; Fisher's exact $P < 0.01$ for both species) or real duck eggs ($P < 0.05$ for red-gartered coots; $P < 0.01$ for red-fronted coots). However, because incremental changes in shape and background colour do not improve the acceptance rate of duck eggs (Fig. 2), several simultaneous, independent changes in egg features would be needed to achieve such sophisticated mimicry. Furthermore, given that all members of the waterfowl order Anseriformes have immaculate eggs[23], the evolution of spotted eggs is likely to be phylogenetically
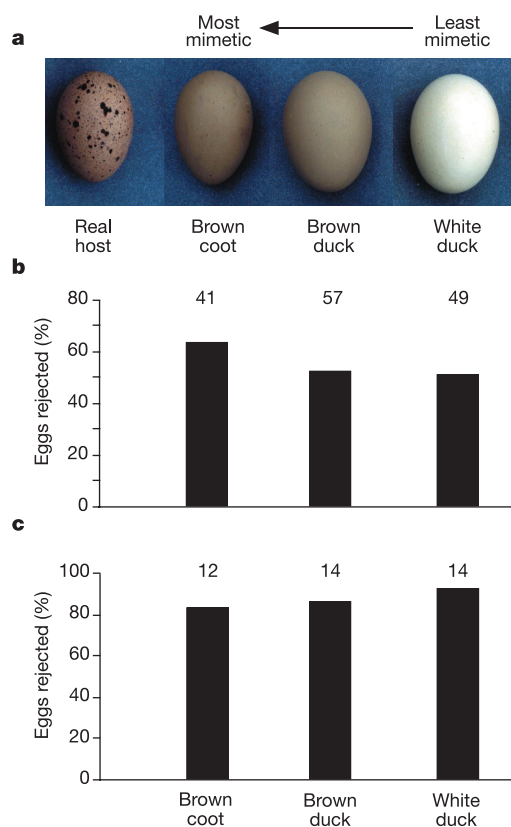

Figure 2 Results of egg mimicry experiments in the two principal hosts. **a**, Examples of a real host egg and the mimetic series of model eggs used in the experiment, arranged from most mimetic (brown coot) to least mimetic (white duck). The white duck treatment was similar in appearance and shape to real duck eggs. **b**, **c**, The degree of mimicry did not affect egg rejection rates by red-gartered coots (**b**) or by red-fronted coots (**c**). With degree of mimicry entered as a ranked variable, logistic regressions revealed no effect of mimicry rank on the proportion of eggs rejected for either red-gartered coots (Wald $\chi^2 = 0.98$, $P = 0.32$) or red-fronted coots (Wald $\chi^2 = 0.55$, $P = 0.46$). The sample size above each bar indicates the number of nests in each treatment.

constrained. Black-headed ducks seem to be trapped in the social conflict of their hosts, without recourse to evolutionary counter-adaptations, at least with regard to the possibility of reducing egg rejection rates.

If hosts can recognize subtle differences between conspecific eggs, should not the strikingly different duck eggs always be rejected? An experiment conducted 30 years ago for other reasons demonstrates clearly that acceptance of non-mimetic foreign eggs can occur even where selection has acted only on host recognition and rejection of conspecific eggs. Weller added experimental white hen eggs to American coot nests in Iowa[24], a species with high frequencies of intraspecific brood parasitism and egg rejection[19]. Because this species does not suffer any interspecific brood parasitism, all aspects of egg recognition and rejection must stem from selection by intraspecific brood parasitism. As with their South American relatives, American coots rejected some, but not all, of the hen eggs added to their nests; 44% of 27 eggs added to nests on stable wetlands were accepted and incubated by the host. The striking similarity between the results of Weller's experiments and ours supports the hypothesis that rejection of duck eggs by the two South American coots is an incidental by-product of social strife within the hosts themselves.

The cognitive and ecological factors influencing the partial acceptance of duck eggs by coots remain unclear. One possibility is that young coots breeding for the first time learn to recognize their own eggs through imprinting, so that individuals parasitized during their first nesting attempt imprint on both their own and duck eggs, becoming acceptors for their entire lifetime[2,25,26]. This hypothesis is rejected by our observation that all individuals in both host species seem capable of recognizing duck eggs, even though they do not always reject them. During floods (both species) or wind-driven high waves in one open wetland (red-gartered coot), rejection rates increased to 100%. Weller found an identical pattern with American coots—in nests subjected to severe flooding, coots rejected 100% of experimental hen eggs[24].

An alternative possibility is that the costs of rejection (that is, rejection of the host's own eggs[27]) are state-dependent, such that different individuals show different degrees of rejection behaviour. Detailed study of the mechanisms of both egg recognition and rejection is now required for an understanding of how these enigmatic brood parasites are able to obtain a sufficient level of egg acceptance to persist. Indeed, rather than the generalist brood parasite once envisaged[2,10], black-headed ducks might instead be exploiting a rather narrow niche defined by the cognitive limits of their two main hosts. □

Methods

Detecting and monitoring parasitism

The biology of black-headed ducks is poorly known, and all quantitative information until now stems from Weller's pioneering single-year study more than three decades ago at some of the same sites as those we studied[10]. Our study wetlands were within 30 km west or southwest of General Lavalle, Buenos Aires province, Argentina. To detect brood parasitism we conducted systematic surveys of the marshes every two to four days on foot or by canoe. The vegetation was sparse and the large nests were conspicuous enough for us to be confident that we found almost all nests of potential host species breeding on the study area. Nests were identified to species by observing birds on or near nests, or on the basis of distinctive eggs. Parasitism was easily detected because the duck eggs differ markedly from the eggs of all of the major hosts. On each visit, all new eggs were labelled and previous eggs were censused to determine their fate: rejected, depredated, hatched or left over after host chicks hatched. Coots rejected duck eggs mainly by burying them in nesting material, but some were ejected from nests or simply disappeared. Weller[10] also observed rejection by one of the hosts, red-fronted coots.

The two species of coot are by far the most abundant birds in the study marshes, and our exhaustive searches of large tracts of marsh throughout the region did not reveal other suitable hosts that are common but not currently being parasitized. Colonial species such as brown-hooded gulls (*Larus maculipennis*) and white-faced ibis (*Plegadis chichi*) are moderately parasitized where they occur, but colonies are uncommon. Our study corroborates Weller's conclusion that black-headed ducks are obligate brood parasites[10], because our extensive surveys would have discovered duck nests had they been present.

We estimated the relative importance of the two main hosts to overall duckling production by multiplying the total number of duck eggs laid in nests of each host species

by the hatching success for each host, and then calculated the fraction of all ducklings hatching in nests of each host.

Assessing costs to hosts

When assessing whether the presence of duck eggs increased the risk of nest predation for hosts, we excluded parasitized nests in which all duck eggs were rejected. Nests were considered preyed on if all eggs disappeared before they were due to hatch or if we had clear evidence for predation (broken eggs). Clutch size varies considerably between individual hosts, so we assessed hatching success in terms of the number of host eggs that failed to hatch at each nest; this measure includes eggs that disappeared, were rejected or were left over after the rest hatched. Leftover or rejected host eggs were rare, so we primarily measured egg loss. Our more detailed analysis of egg loss in red-fronted coots included experimental nests from which real parasitic eggs were removed quickly after laying ($n = 25$) or in which parasitic duck eggs were experimentally added to unparasitized nests ($n = 22$); these two types of experimental nest enabled us to decouple egg loss due to the act of parasitism itself (damage or removal by parasite) from egg loss due to the presence of duck eggs itself, such as damage to host eggs with subsequent removal by hosts[19]. The latter cost favours egg rejection; the former does not.

Mimicry experiments

The white, oval-shaped duck eggs differ from the host eggs in three key visual features—rounder shape, paler background colour and lack of spots (Figs 1h and 2a). We painted domestic chicken eggs and real host eggs to create a series of three egg treatments that increasingly resembled host eggs—the least mimetic 'white duck' eggs (experimental versions of real duck eggs) had the wrong shape, background colour and lacked spots, whereas the most mimetic 'brown coot' eggs lacked only spots (Fig. 2a). Egg colour and shape vary in real duck eggs (although to a much smaller degree), so these should be feasible evolutionary steps towards mimicry. To avoid a confounding effect of size, we used painted red-gartered coot eggs for the 'brown coot' treatment for both hosts, because this species overlaps in size with the duck eggs. For the 'brown duck' and 'white duck' treatments we used chicken eggs whose length and width both overlapped with those of real duck eggs. We added the experimental eggs to host nests in the laying or early incubation stages and we determined their fates in subsequent visits. Eggs were scored as rejected if found buried in the nest or if observed at least half buried on the final nest visit for nests that hatched or were preyed on before rejection was complete. Non-rejected eggs were scored as accepted only if the nest remained active long enough for rejection to have occurred (at least 10 days for both species).

Intraspecific brood parasitism

In 1997 our studies were conducted primarily on open wetlands where red-fronted coots were absent, so our detailed analysis of intraspecific brood parasitism is restricted to red-gartered coots. Nests were checked every two to four days, which will underestimate parasitism on the basis of unusual egg-laying rates (two or more new eggs per day)[28], so we focused on variation in egg features, a reliable method when used conservatively[29]. Our retrospective assessment of intraspecific brood parasitism from the earlier field seasons, where we did not specifically focus on detecting intraspecific brood parasitism, will greatly underestimate the actual rate of intraspecific brood parasitism: nest checks were relatively infrequent and we would have noticed only the most extreme cases of variation in egg features to detect parasitism[28–30].

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Spatial patterns in species distributions reveal biodiversity change

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Interpretation of global biodiversity change is hampered by a lack of information on the historical status of most species in most parts of the world[1–5]. Here we show that declines and increases can be deduced from current species distributions alone, using spatial patterns of occupancy combined with distribution size. Declining species show sparse, fragmented distributions for their distribution size, reflecting the extinction process; expanding species show denser, more aggregated distributions, reflecting colonization. Past distribution size changes for British butterflies were deduced successfully from current distributions, and former distributions had some power to predict future change. What is more, the relationship between distribution pattern and change in British butterflies