

Cuckoos, cowbirds and the persistence of brood parasitism

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Although Edward Jenner (1749–1823) is best remembered for experimentally inoculating his patients with cowpox as a means of preventing the smallpox and for his subsequent promulgation of antigenic vaccination, the country doctor and natural historian's first academic success, and the work that gained him the fellowship of the Royal Society of London, was a study of the common cuckoo (*Cuculus canorus*)^{1,2}. That the cuckoo is a brood parasite, laying its eggs in the nests of other species and depending on them to raise its offspring, was well known in Jenner's time. But the details of this relationship, and how it came to pass that the cuckoo nestling was the sole occupant of its foster parents' nest, was not. Jenner's crucial discovery* was that it is not the parent cuckoo or the host birds that remove the hosts' offspring from the nest, but the nestling cuckoo itself. He wrote: 'The little animal ... contrived to get the bird upon its back, and making lodgement for the burden by elevating its elbows, clambered backward with it up the side of the nest till it reached the top, where resting for a moment, it threw off its load with a jerk, and quite disengaged it from the nest. ... With these (the extremities of its wings) I have often seen it examine, as it were, an egg and nestling before it began its operations; and the nice sensibility which these parts appeared to possess seemed sufficiently to compensate the want of fight, which as yet it was destitute of.' But odder still, in view of natural selection, are Jenner's observations on the host birds' behavior (which he was able to justify in terms of natural theology); Jenner had: 'never seen an instance where the hedge-sparrow has either thrown out or injured the egg of the Cuckoo'; he reported no effort on the part of the hosts to prevent the death of their own young; and the foster parents continued to care for the grossly outsized cuckoo nestling, even when they had to perch on the young cuckoo's 'back, or half-expanded wing, to gain sufficient elevation to put the food into its mouth'².

Ornithologists since Jenner have discovered that brood parasitism in birds is widespread and phylogenetically diverse: ~1% of all species are obligatory interspecific parasites (Table 1). But the question remains as to why parasitism persists, when it seems maladaptive for hosts to care for parasitic young. Recent studies of two brood parasites

Brood parasites provide a particularly good opportunity for the study of host–parasite evolution because they directly affect the reproductive success of their hosts. Two parasitic species, the common cuckoo (*Cuculus canorus*) and the brown-headed cowbird (*Molothrus ater*), differ widely in their relationships with their hosts, yet share the attribute of having been particularly well studied by biologists. Recent work on the cuckoo and the cowbird has resulted in new answers to the question begged by all brood parasites: why do host species raise parasitic young?

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with widely differing biologies, the common cuckoo (*C. canorus*, Cuculidae; hereafter, cuckoo) and the brown-headed cowbird (*Molothrus ater*, Emberizinae; hereafter, cowbird), have provided new explanations for hosts' acceptance of parasitism.

Two ways to be a parasite *Cuckoos and their hosts*

The Old World family Cuculidae contains about 50 obligatory parasites, some of which are host generalists and some specialists⁵. The common cuckoo has an especially interesting pattern of host use: although it parasitizes over 100 species across its range, in any one locality only a few species are parasitized, and most individual female cuckoos use only one

host species⁶ (but see Ref. 7). All the female cuckoos parasitizing one host species are referred to as a gens (plural, gentes). Furthermore, some gentes lay eggs that mimic those of their host. A mechanism for the maintenance of this odd state of affairs was proposed a century ago: maternal inheritance of egg type combined with imprinting of the juvenile cuckoo on her host⁸. However, there is still no evidence to support this hypothesis^{6,9}.

The host specialization of each gens raises the possibility of an evolutionary arms race between a gens and its host. Davies and Brooke⁹ demonstrated experimentally that host species parasitized by a cuckoo gens with mimetic eggs reject nonmimetic eggs from their nests. In contrast, at least one host parasitized by a nonmimetic gens does not discriminate among different egg types. This suggests that egg mimicry by cuckoo gentes evolved in response to the host's ability to discriminate, and vice versa. In addition, the reduced discrimination shown by populations of cuckoo hosts living outside the range of the cuckoo suggests that the host's ability to discriminate is also an adaptation to parasitism. There is also evidence for a ghost of parasitism past: some potentially suitable host species that do not currently maintain a cuckoo gens are very good egg discriminators, whereas species unsuitable as cuckoo hosts are not^{9,10}. This situation is consistent with a dynamic in which cuckoos colonize a new host, thereby founding a new gens, which engages its host in an evolutionary arms race by evolving progressively more mimetic eggs, until it either switches hosts or is driven to extinction by the increasing ability of its host to recognize cuckoo eggs⁹.

Cowbird hosts and cowbirds

In contrast to the cuckoo, the cowbird is a generalist at the level of both the species and the individual. Compared with the ~50 species of parasitic cuckoos, there are only

*Although Aristotle had apparently concluded the same thing ('when the young bird is born it casts out of the nest those with whom it has so far lived'), the surprise with which Jenner's discovery was received suggests that this knowledge had been lost by the 18th century^{1,3,4}.

five species of parasitic cowbirds. Within this New World group, the primitive species is a host specialist and the increasingly derived species are increasingly generalist¹¹. Although this situation seems to contradict the received wisdom that host-parasite systems evolve towards increasing specialization¹¹, it might equally well be argued that the basal taxon should be the most specialized, because it has interacted with its hosts for the longest amount of time¹²; or indeed that all the taxa should be equally specialized, because when speciation occurred the species were equally old, and they have been evolving for the same amount of time since. Perhaps the apt comparison is not within, but between, parasitic lineages.

There is no evidence that the cowbird lays eggs mimetic of its hosts' eggs. However, many cowbird hosts accept these nonmimetic eggs (Fig. 1). For its part, the cowbird parasitizes some of the species that reject cowbird eggs, but avoids some of the others, making it difficult to generalize about the adaptiveness of cowbird laying behavior¹². The cowbird's host generalism and lack of egg mimesis, as well as the lack of egg-rejection behavior by many cowbird host species, suggest that if the cowbird is involved in an evolutionary arms race, it has yet to escalate. A simple, although not particularly testable, explanation for this difference between the cuckoo and the cowbird systems is that the cuckoo system is older – more than 60 million years – compared with 2.8–3.8 million years for cowbirds, assuming that the ancestral taxa were parasitic¹².

Why do hosts tolerate parasitism?

On an ecological scale, the existence of gentes means that the population dynamics of the cuckoo and its host species are likely to be coupled within each gens, because the cuckoo can only reproduce via the host, and the host's reproduction is eliminated by the cuckoo nestling. In contrast, because the cowbird is a generalist, the negative feedback between parasite and host populations is dissipated, making it unlikely that coupled oscillations in population size between the cowbird and any one host would occur. Rather, the cowbird could depress the population size of a particular host species without experiencing any concomitant reduction in its own population; hence, declining hosts can suffer unabated parasitism¹³.

On an evolutionary scale, if parasites benefit from brood parasitism and hosts are harmed by it, why do hosts tolerate parasitism? Hosts can get rid of the parasitic egg in various ways (in this review, these activities are all subsumed under the term 'rejection'), including ejecting the egg from the nest with their bill, building an additional layer of nest lining over the unwanted egg or abandoning the parasitized nest. Several hypotheses have been proposed to explain why rejection is not universal among hosts of brood parasites.

Are hosts just lagging behind?

According to the evolutionary lag hypothesis, hosts accept parasitic eggs because they have not yet evolved the ability to reject them¹⁴. Lag is an inherently unstable explanation: hosts would be better off rejecting, but at

Table 1. The obligate avian brood parasites^a

Order	Family	Subfamily ^b	Common name of group	Number of parasitic genera	Number of parasitic species
Anseriformes	Anatidae	Anatinae	Black-headed duck	1	1
Piciformes	Indicatoridae	NA	Honeyguides	4	17
Cuculiformes	Cuculidae	NA	Old World cuckoos	12	~50
	Neomorphidae	NA	New World cuckoos	2	3
Passeriformes	Passeridae	Ploceinae	Parasitic weaver	1	1
		Estrildinae	Indigobirds	1	16
	Fringillidae	Emberizinae	Cowbirds	1 or 2	5

^aData from Refs 29,36.

^bNA = not applicable.

present they lack the necessary mutation, or selection has not had time to work on the genetic variation that exists. When selection is strong, evolutionary lag predicts a bimodal distribution of rejection frequencies among hosts, with each species rejecting close to 0% or 100% of parasitic eggs, because a 'rejecter allele' should quickly go to fixation once it appears. Even with strong selection, however, the rejection frequencies observed might still be a bit 'fuzzy' at both endpoints. It is often difficult to know whether a host behavior such as abandoning a parasitized nest is aimed at the parasitic egg; hence, it is easy for the occasional rejection to be attributed falsely to a species that actually accepts. At the other extreme, rejection might not go to fixation if selection for it relaxes, owing to decreased parasitism of rejecters¹⁴.

It seems likely that lag is prevalent in the cowbird system because the cowbird is a relatively recent colonist of North America (the oldest fossils are 0.5 million years old¹⁵), and because anthropogenic habitat change has given the cowbird access to new hosts during the past 300 years. The cowbird is widespread and abundant, and across large geographical areas most are parasitic for some host species¹⁶, making it likely that selection for rejection is strong. As the lag hypothesis would predict in this situation, cowbird hosts are relatively bimodal in their rejection behavior (Fig. 1).

That evolutionary lag exists in the cuckoo system has been argued by Davies and Brooke, because lag is inherent in the idea of an evolutionary arms race. Because the cuckoo is less abundant than the cowbird and the selection regimen it imposes is therefore weaker, its hosts might take longer to evolve complete rejection. The length of this time lag is suggested by the case of the dunnock (*Prunella modularis*), which has failed to evolve rejection even though it has been a host at least since the 14th century, according to Chaucer^{17,18}. Hence, the observation that more cuckoo than cowbird hosts reject an intermediate proportion of parasitic eggs (Fig. 1) can be explained by the lag hypothesis.

Does it pay to accept?

According to the cost-benefit equilibrium hypothesis (also known as the cost-benefit balance or evolutionary equilibrium hypothesis)[†], hosts accept parasitic eggs when the costs of rejection are greater than the benefits¹⁹. In its

[†]Note that all of these terms are somewhat misleading in that there is in reality no balance or equilibrium between the costs and benefits of rejection, or between the net benefit of rejection and the frequency with which a host rejects. Equilibrium, as used here, can be interpreted as the dividing line along which the net benefits of being a rejecter and an acceptor are equal; a given host will be on one side or the other of this line, and will be selected to reject or accept, accordingly.

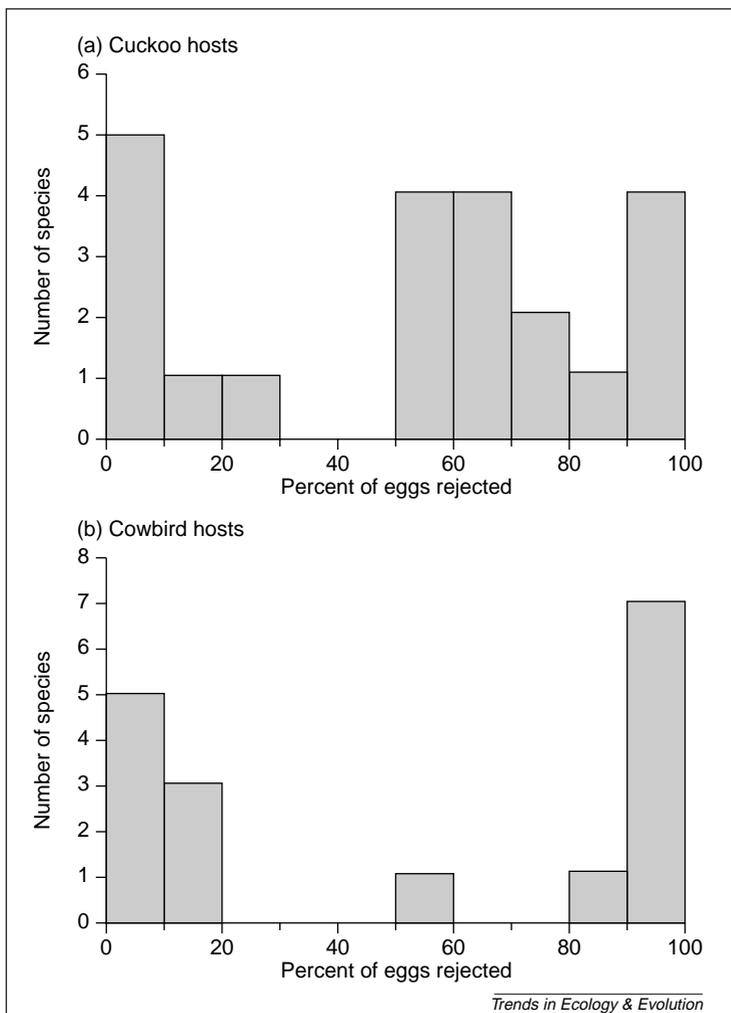


Fig. 1. Frequency of parasite egg rejection by (a) hosts of the cuckoo (*Cuculus canorus*) and (b) hosts of the cowbird (*Molothrus ater*). Cowbird hosts are more binary in their rejection behavior than are cuckoo hosts, many of which show intermediate rates of rejection. All data are from experiments in which the researcher placed 'parasitic' eggs in the nest and observed the hosts' response. Sample sizes ranged from 10 to 133 nests. Data from Refs 9, 10, 18, 20, 32, 34, 37-47.

simplest form, cost-benefit equilibrium predicts a bimodal distribution of rejection frequencies among host species, because a particular species should reject when the benefits of rejection are greater than the costs, and accept otherwise (Box 1). Clearly, there are benefits to rejecting a parasitic egg, but rejection can also be costly. First, the host might make a mistake and reject its own eggs

Box 1. The hypotheses defined

The evolutionary lag hypothesis: according to this hypothesis, it would be adaptive for hosts to reject parasitic eggs, but there has not been sufficient time for them to evolve the ability to do so. The 'lagging' element could be mutation, recombination or fixation. When selection is strong (rejecters are much more fit than acceptors), rejection behavior should go to fixation rapidly once it appears, so that host species reject either all or none of the parasitic eggs they receive. However, under weak selection, time to fixation is long and a range of rejection frequencies might be observed.

The cost-benefit equilibrium hypothesis: this proposes that it is not necessarily adaptive for hosts to reject parasitic eggs. Rather, in some cases the costs of rejection outweigh the costs of acceptance. If these costs are constant within each host species, all individuals of a species should reject 0 or 100% of parasitic eggs. However, if costs vary over time or space, or among individuals, a host species might reject some intermediate proportion of parasitic eggs.

(recognition error)^{3,20,21}. Second, the host could damage its own eggs while getting rid of the parasitic one (egg damage)^{21,22}. Third, the parasite could destroy nests from which the parasitic egg had been removed (the Mafia hypothesis^{23,24}). Costs of the last two behaviors would increase with the frequency of parasitism, but the cost of the first might not.

Jenner was the first to suggest that a cuckoo host might mistakenly reject its own eggs (recognition error). He believed that parasitism 'occasions some discomposure' on the part of the female dunnock, which 'not infrequently throws out some of her own eggs'² (but see Ref. 9). More recently, Lotem *et al.*²⁰ used field estimates of damage to the hosts' own eggs to quantify the fitness of rejecters and acceptors in terms of the probability of parasitism, and of recognition error on the part of the host. They found that when the parasitism rate is 1-5%, within the usual range for cuckoo hosts, even a recognition error rate of 3-18% is sufficient to equalize acceptor and rejecter fitness. A model for a different cuckoo host species also concluded that hosts should accept when the probability of parasitism is within a range that has been observed in the field²⁵. Therefore, acceptance can be the more fit strategy for cuckoo hosts, despite the fact that parasitism eliminates host reproduction.

Recent work has shown that rejection can also be costly owing to retribution from adult parasites who monitor host behavior. Evidence that retribution alone can make acceptance the more fit strategy comes from a study of a host of the great spotted cuckoo (*Clamator glandarius*; although a cuckoo, nestlings of this species do not eject their nestmates, making it functionally similar to the cowbird). Soler *et al.*²⁴ experimentally rejected the cuckoo egg from 29 naturally parasitized nests, and found that the number of young fledged by these 'rejecters' was fewer than that fledged by 28 naturally parasitized control nests, owing to the cuckoos' destruction of nests from which their eggs had been removed. (However, this result is not in accord with work showing that rejection behavior is increasing in this species²⁶.) More generally, parasites might simply destroy unparasitized nests; this would be a cost of rejection in those cases where rejection had occurred. There is evidence that parasitized nests are depredated less often for hosts of both cowbirds and cuckoos^{25,27}. Further work that identifies the actual nest predators is needed, however, because under the null hypothesis a negative correlation between parasitism and predation would be expected about half the time.

Unlike the cuckoo, the nestling cowbird does not eject its nestmates (for the one known exception, see Ref. 28). This means that, in principle, cowbird hosts can raise their own young along with the cowbird, lowering the cost of acceptance; although in practice, the ability to do this varies widely, and many small-bodied host species such as vireos and flycatchers lose all their young when they accept parasitism. Of 24 field studies comparing host reproduction in parasitized and unparasitized nests, 19 found that parasitism reduced host reproduction by more than 30% (Ref. 29). Interpreting these data in terms of the cost-benefit equilibrium hypothesis, however, is difficult because: (1) nests were parasitized naturally, not experimentally, so the results include possible cowbird behaviors such as parasitizing the safer nests or the more fit parents; (2) the cost of the host egg taken by the female cowbird is paid by both acceptors and rejecters, but in the present comparison, is paid only by parasitized nests; and (3) the costs of rejection were not measured.

A study that measured the costs of recognition error (although there was none) and egg damage, and also measured the cost of acceptance, found that northern orioles

(*Icterus galbula*) lost 0.26 of their own young for each cowbird egg they rejected from their nests²². The cost of raising a cowbird nestling increased with the number of oriole nestlings, such that within the range of the species' normal brood size, it was more costly to accept than to reject ($n = 10$ crossfostering experiments). Orioles are rejecters, so this study supports the cost-benefit equilibrium hypothesis. Similarly, the warbling vireo (*Vireo gilvus*) rejects cowbird eggs, and this is indeed the less costly behavior, even when only some of the possible rejection costs are measured³⁰. Further studies are needed to compare total rejection costs to the cost of acceptance for a range of cowbird host species.

As discussed so far, the cost-benefit equilibrium hypothesis assumes that the costs and benefits of rejection vary among, but not within, host species. This leads to the prediction that a particular species should be binary in its rejection behavior, which does not agree with the data for cuckoo hosts (Fig. 1). An explanation is provided by recent work showing that within one cuckoo host species, older individuals reject parasitic eggs more frequently; apparently, they can recognize deviant eggs because they have had time to learn the range of variation that exists within their own clutches^{21,31}. Therefore, the cost of rejection associated with mistakenly eliminating one's own eggs decreases over the lifetime of the individual. Rejection behavior is adaptive in old but not young birds, and the species as a whole shows an intermediate rate of rejection.

Several studies suggest that rejection can also be a conditional response to stimuli other than the parasitic egg itself. For example, yellow warblers (*Dendroica petechia*) are more likely to reject cowbird eggs when they have fewer of their own eggs in their nest³². The warblers usually reject by burying all the nest contents in a new layer of nest lining; hence, this study suggests that warblers can evaluate the changing costs of rejection (though it should be noted that the yellow warbler is the only cowbird host known to have a context-dependent strategy). Hosts can also respond to parasite density: rufous bush chats (*Cercotrichas galactotes*) are less likely to reject experimental eggs once the local cuckoos have departed for migration³³. Similarly, the frequency with which reed warblers (*Acrocephalus scirpaceus*) reject experimental eggs declines with the frequency of natural parasitism; and, in an unparasitized population, experimental eggs were not rejected at all³⁴. The authors argue that warblers assess parasitism risk – for example, by noting the presence of the vociferous male cuckoo – and adjust their behavior accordingly. This plasticity would be adaptive, given the costs of rejection and the patchiness of parasite abundance³⁴. Any of these mechanisms would cause rejection costs to vary across time or space, which could in turn explain the intermediate rejection rates observed within some host species.

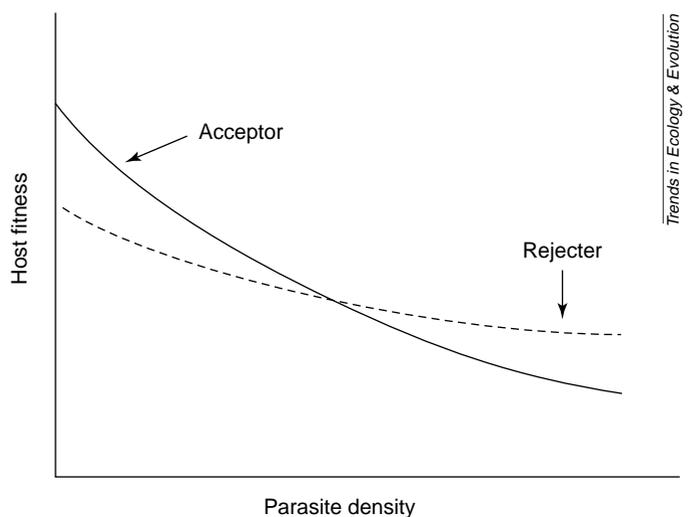
In summary, both the evolutionary lag and the cost-benefit equilibrium hypotheses seem to explain the acceptance of parasitic eggs by hosts of the cuckoo and hosts of the cowbird. Both hypotheses can, in principle, explain the variation in rejection frequency among the hosts of a single parasite: lag, because host species might have been exposed to parasitism for different lengths of time or parasitized at different rates, or simply because the 'rejecter mutant' appeared in some host species and not others; and equilibrium, because host species differ in their acceptance and rejection costs. Regarding the observed bimodal rejection response of cowbird hosts, relative to cuckoo hosts, the lag hypothesis predicts this difference because selection is stronger in the cowbird system. The equilibrium hypothesis can also explain this pattern if, as the evidence suggests, more cuckoo than

Box 2. A third explanation?

A mathematical model that can explain the acceptance of parasitic eggs by the host of a specialist brood parasite was proposed by Takasu *et al.*⁴⁸, and extrapolated to the case of a generalist parasite by Takasu⁴⁹. The model is novel because it includes both population dynamics and the evolution of a rejecter allele in the host population. However, it does not allow for evolution on the part of the parasite.

The model assumes that both rejection and acceptance entail costs, and that the cost of acceptance increases with the frequency of parasitism. The essence of the model is captured by the figure below (Modified from Ref. 48), which shows how the fitness of egg-rejecting and egg-accepting hosts might change with parasite density. In the absence of parasitism, acceptors have the highest fitness because rejecters run the risk of erroneously rejecting their own eggs. However, as parasitism increases, acceptor fitness declines more rapidly. In the original figure⁴⁸, rejecter fitness did not vary with parasite density. Here, it decreases to reflect the increasing costs of damage to the host's own eggs and of retribution from the parasite.

If these last two costs were large enough, acceptor fitness could be greater than rejecter fitness, even at high parasite densities, as demonstrated empirically by Soler *et al.*²⁴; in this case, the lines in the figure would never cross.



(Online: Fig. 1)

In Takasu's model of a specialist parasite, both population size and rejection frequency can oscillate: a large cuckoo population means the parasitism rate is high, which reduces the size of the host population and increases selection for rejection; both of these changes reduce the cuckoo population, which in turn lowers the parasitism rate; as a result, the host population grows and selection for rejection relaxes, and so on. Although the exclusion of parasite evolution limits the model's applicability, it still provides a useful way to see how intermediate rejection rates might arise within a host species as a result of frequency-dependent fitness between acceptor and rejecter genotypes.

cowbird hosts have contingent responses to parasitism – although why this should be the case is not entirely clear. However, the two hypotheses do diverge in one prediction. For a species that accepts, evolutionary lag predicts that the lifetime fitness of a rejecter individual would be greater than that of an acceptor individual, whereas under cost-benefit equilibrium the opposite would be expected (an analogous but opposite prediction could be made for species that reject). This prediction has not yet been tested.

Conclusions and prospects

Biologists have offered several explanations for why host birds accept the eggs of brood parasites. The evolutionary lag hypothesis, which emerged from the first systematic study of parasite-egg rejection¹⁴, is supported by studies of both cowbirds and cuckoos. However, it is difficult to say what sort of experimental test would provide

conclusive evidence for this hypothesis; what needs to be demonstrated is the lack of genetic variation. In contrast, for host species that accept parasitic eggs, the cost-benefit equilibrium hypothesis would be unequivocally supported if the lifetime fitness of acceptors was greater than that of rejecters, and the reverse was true for species that reject parasitic eggs. Unfortunately it is difficult, if not impossible, to measure the costs of rejection for species that do not reject: there is simply no way to know how many of its own eggs a host would throw out or damage in the act of rejection. But the cost of acceptance can be measured for rejecter species by introducing a parasitic nestling to the nest, because hosts do not reject nestlings.

The lag and equilibrium hypotheses are best differentiated where selection is strong, owing to a large difference between the costs of rejection and acceptance. When selection is weak, the predictions of the equilibrium hypothesis become less clear, and lag makes no particular prediction about rejection frequency because the time to fixation is long. Therefore, further field studies of the strongly selected cowbird system would be useful. In addition, although numerous studies have measured some of the costs of rejection for cowbird hosts, no study has yet compared the total rejection cost to the cost of acceptance, which is what is required to test the cost-benefit equilibrium hypothesis. Theoretically, the role of frequency-dependent fitness between acceptors and rejecter types within a host species could use further modeling efforts, which included evolution on the part of the parasite as well as all the known costs of rejection (Box 2).

One might even argue that the evolutionary lag and cost-benefit equilibrium hypotheses could apply to the same situation, but at different scales. For example, acceptance might be less costly than rejection for species whose own intraclutch variation exceeds the host-parasite variation; but that is only because selection has not yet homogenized the host's eggs. More generally, when the costs of rejection outweigh the benefits so that the equilibrium hypothesis explains host acceptance, it could equally well be argued that lag is responsible because selection has not yet reduced rejection costs. Although we have come a long way in the 2300 years since Aristotle's observation that the cuckoo: 'makes no nest, but deposits its eggs in an alien nest'³⁵, the search continues for a single, parsimonious explanation for the varieties of parasitic experience.

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Early development and fitness in birds and mammals

Jan Lindström

It is obvious that adverse environmental conditions might have immediate effects, such as lowered survival or fecundity, on animal performance. This is a well documented fact in ecological literature. However, the long-term fitness consequences of the conditions experienced during early development have been documented only recently, even though nutritional programming has been known in developmental biology for over 100 years¹. Even more recently, studies concerning the effects that environmentally caused differences in individuals have on population dynamics and life-history evolution have begun to surface. Here, I focus on four topics: (1) What kind of consequences are a result of adverse conditions during development? (2) How can the various causes of differences in phenotype be disentangled? (3) Given the stochastic nature of environmental disturbances and the potentially long-term effects of these, especially in long-lived animals, what are the likely consequences for population dynamics? (4) As the quality of offspring affects the fitness of parents, how should the parents' life-history decisions respond to the likely prospects of their offspring? Thus, the topic of this review complements two recent *TREE* reviews by Sæther², and Mousseau and Fox³. My aim is to draw these topics closer together and review recent developments in this

Conditions experienced during early development affect survival and reproductive performance in many bird and mammal species. Factors affecting early development can therefore have an important influence both on the optimization of life histories and on population dynamics. The understanding of these evolutionary and dynamic consequences is just starting to emerge.

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expanding field. I have chosen to focus on mammals and birds as most of the individual-based long-term studies have been conducted on species within these groups, especially those that also collected data on population dynamics. However, the ideas discussed here are not restricted to these taxa. To the contrary, both empirical evidence as well as experimental results exist, for example, for lizards and snakes, showing long-term effects of environmental conditions on phenotype and subsequent performance^{4–6}.

Long-term consequences of early development

Early development is the period from conception to developmental maturity⁷. Although this is a very broad definition, it is usually found that the earlier an individual's development is disturbed, the stronger are the effects^{1,7}. Adverse conditions during early development affect growth^{7–9} and a range of related properties, including metabolism¹, immunocompetence^{9,10} and later, sexual attractiveness in adulthood^{11,12}. In humans, for example, low birth weight can be associated with an increased risk of developing impaired glucose tolerance¹³; without proper medical treatment this is often a lethal condition. In addition to lowered survival, this could lead to fecundity costs. For example, maternal diabetes can severely harm foetal development