

Why is mimicry in cuckoo eggs sometimes so poor?

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I propose that the existence of imperfect adaptations (e.g. egg mimicry) in brood parasites and their hosts (e.g. discrimination abilities) could reflect age-dependent territory and nest-site selection patterns of the host. Studies of various passerines indicate that (1) older breeders tend to occupy nest sites of higher quality than do young birds (ideal despotic distribution resulting from interference competition), (2) nest-site selection affects the risk of parasitism in various habitats, (3) egg recognition in passerines has a strong learning component (therefore naive breeders tend to accept whereas older birds tend to reject parasitic eggs). Because young naive birds, who tend to accept parasitic eggs, usually breed in low-quality areas where they are frequently parasitised, while old experienced birds, who tend to reject parasitic eggs, breed in high-quality areas where they are rarely parasitised, the distribution of acceptors and rejecters with respect to the risk of parasitism is non-random, i.e. populations of some host species may consist of heavily parasitised acceptors and weakly parasitised rejecters. Therefore, the selection pressure exerted by the host on the parasite should be weaker than if brood parasitism was randomly distributed among naive and experienced breeders and affect adaptations such as egg mimicry. This could explain the existence of imperfect adaptations in some brood parasite-host systems.

Brood parasite-host associations are generally accepted as an excellent example of coevolution because we can be reasonably certain about the reciprocal evolution of adaptations and counter-adaptations (Rothstein 1990). However, despite the fact that brood parasites exert a strong selection pressure on their hosts (Rothstein 1990), defence mechanisms of many hosts against parasites are frequently poor. This is clearly evident from the mere existence of brood parasitism. The existence of imperfect adaptations has been generally explained in terms of genetic, economical and other types of constraints (Dawkins 1982).

Earlier published ideas on constraints affecting host-brood parasite coevolution include several mechanisms (see Table 1). Here I propose a new type of constraint that could play an important role in retarding parasite-host coevolution. The “nest-site constraint” suggests that age-dependent patterns of nest-site selection by hosts can result in higher parasitism rates in acceptors (young birds) than rejecters (older birds); this would

slow down an arms race and lead to the existence of imperfect adaptations in both parasites and their hosts.

The nest-site constraint: parasitised acceptors and non-parasitised rejecters

Coevolution between brood parasites and hosts could be constrained by age-related patterns of nest-site selection in some host species. For example, in the reed warbler *Acrocephalus scirpaceus* individuals that start laying early lay larger eggs, produce larger clutches and generally occupy territories located far away from trees (Øien et al. 1996). In contrast, individuals that initiate laying later, lay smaller eggs and clutches and occupy territories closer to trees (Øien et al. 1996). Because early laying, larger eggs and larger clutches are characteristics of older, more experienced breeders in passerines (e.g. Saether 1990), including the closely related great reed warbler *A. arundinaceus* (Lotem et al. 1992), reed warblers nesting farther away from trees are presumably older, experienced individuals. Furthermore, the available evidence suggests that the increasing distance from trees (potential cuckoo *Cuculus canorus* perches) lowers the incidence of cuckoo parasitism of reed warbler nests (Øien et al. 1996). This suggests that young, inexperienced reed warblers tend to breed near trees, i.e. in areas highly susceptible to cuckoo parasitism (hence low-quality areas), whereas older, experienced individuals tend to breed in areas farther away from trees (hence high-quality areas), where they are less likely to be parasitised by cuckoos. Moreover, experienced breeders can discriminate between their own and cuckoo eggs (this ability is acquired during their ontogeny; see Lotem et al. 1992, 1995) whereas first-time breeders cannot. Thus the age/experience-related learning constraint makes it impossible for naive breeders to respond in an appropriate way to parasitic laying by the cuckoo. Because naive breeders (accep-

tors) are parasitised more often than older breeders (rejecters), the selection pressure driving the evolution of adaptations in the brood parasite, such as egg mimicry, should be weakened. Furthermore, the fact that naive breeders avoid parasitism later in life by avoiding areas with high rates of parasitic laying (i.e. through their territory and nest-site selection rather than through egg discrimination and rejection), suggests that selection for egg discrimination behaviour should be weaker in this situation than in situations when the probability of being parasitised is the same for naive and experienced breeders.

To conclude, I propose that the weak selection pressure exerted on cuckoos by inexperienced host individuals should slow down the evolution of mimicry in parasitic eggs. This should, in turn, weaken selection for discrimination ability in hosts. The fact that both nest-site selection and discrimination behaviour in the host are age-dependent offers an explanation for the existence of poor egg mimicry in some parasites and low recognition capabilities in some of their hosts.

The essence of the nest-site constraint is the age-dependent susceptibility to parasitism mediated through the age-dependent pattern of nest-site selection. This

age-related susceptibility to parasitism in hosts can theoretically reach two extreme states. First, acceptors are parasitised almost exclusively (thus, parasitic egg mimicry is very poor). Second, almost only rejecters are parasitised (thus, mimicry is near perfect). Every parasitised host population must lie somewhere in between these two extremes. If the population is biased in the direction of “only acceptors parasitised”, then selection for mimicry is inevitably lower than if there is an equal probability that a parasitic egg will be laid in the nest of an acceptor or rejecter.

The nest-site constraint should apply to any brood parasites that can successfully parasitise naive breeders lacking the egg discrimination ability (parasitising individuals that do not reject the parasite’s eggs is highly adaptive for a parasite; however, this pattern of parasitism is a by-product of the pattern of nest-site selection by the host). By weakening the intensity of selection for specific adaptations, the naive part of the host population could facilitate successful parasitism of the host, thereby also maintaining the brood parasite’s population. Therefore, the age of breeders is an important confounding variable which should be incorporated into models of brood parasitism dynamics and should be controlled for in field experiments.

Table 1. Overview of constraints on brood parasite-host coevolution.

Genetic constraints	(1) gene flow between parasitised and non-parasitised populations (host defence in an isolated population is an example of local adaptation and its necessary prerequisite is philopatry)	Soler et al. 1999
	(2) low mutation rates resulting in the absence of beneficial mutations	Rothstein 1990
Weak-selection constraints	(3) low rates of parasitism (acceptance of parasitic eggs could be adaptive if parasites are rare and risk of recognition errors is high – the evolutionary equilibrium hypothesis)	Rohwer and Spaw 1988, Røskaft et al. 1990
	(4) short exposure of hosts to parasitism (acceptance of parasitic eggs could reflect short evolutionary interaction between parasite and host – the evolutionary lag hypothesis)	Rothstein 1990
	(5) life/dinner principle and rare enemy effect (parasites are always ahead in the arms race because they have more to lose compared to hosts)	Dawkins and Krebs 1979
Ecological constraints	(6) lack of suitable nest sites for re-nesting after nest desertion	Petit 1991
Behavioural constraints	(7) nestling eviction behaviour exhibited by the common cuckoo, which reduces benefits of host’s discrimination	Lotem 1993
	(8) mafia effect – hosts ejecting parasitic eggs are penalised by clutch predation by a parasite	Soler et al. 1995
	(9) cognitive constraints such as poor recognition and discrimination abilities of the host	McLean and Maloney 1998
Morphological constraints	(10) parasite egg mimicry making egg recognition by the host difficult	Rothstein 1990
	(11) within-clutch and between-clutch variation in appearance of host eggs – lower intra-clutch and higher inter-clutch variation of host eggs facilitates recognition of parasitic eggs	Øien et al. 1995, Stokke et al. 1999
	(12) small host size relative to that of the brood parasite – hosts with smaller bills tend to reject by desertion which is more costly than egg ejection; due to lower fitness returns for deserters, the desertion behaviour should spread more slowly than other defences	Rohwer and Spaw 1988, Davies and Brooke 1989, Moksnes et al. 1991

Natural selection should favour individuals with adaptive nest-site choice, and young naive individuals should also be selected for breeding at safe sites. Nevertheless, the nest-site constraint cannot be avoided by naive breeders because the constraint is maintained by intra-specific competition; older, experienced breeders in general monopolise high-quality breeding sites, forcing naive breeders to occupy low-quality territories (ideal despotic distribution, see e.g. Hill 1988, Møller 1991, Petit and Petit 1996). Therefore, it is unlikely that young breeders could avoid the negative effects of the nest-site constraint.

The effect of a nest-site constraint is almost inevitable if three conditions are met: (1) breeders' age affects nest-site selection, (2) nest-site selection affects the risk of parasitism, (3) breeders' age affects probability of rejection of parasitic eggs. Are these assumptions generally plausible? First, the effect of age on nest-site selection of birds is well established for many passerines; in general older breeders tend to monopolise higher-quality nest sites than do young birds (e.g. Petit and Petit 1996). This phenomenon has been established for species breeding in forests (Møller 1991), in more open heterogeneous mixed habitats (Hill 1988), and in open country (Brooke 1979). Second, nest-site selection is known to affect the probability of parasitism in several species breeding not only in reeds (Øien et al. 1996, Moskát and Honza 2000), but also in vineyards (Alvarez 1993), fields (Burhans 1997, Hauber and Russo 2000), prairies (Clotfelter 1998), and forests (Larison et al. 1998). Third, various studies indicate that egg recognition in passerines has a strong learning component (Victoria 1972, Rothstein 1990, Lotem et al. 1992, 1995), providing support for the idea that in general naive breeders are acceptors while older birds are rejecters. As a result, it is plausible that the nest-site constraint could slow down the arms race not only in the reed warbler-common cuckoo association but also in other brood parasite-host systems.

Although the effect of nest-site constraint is almost inevitable if the above-mentioned conditions are met, the hypothesis generates a testable prediction: host species showing the age-dependent pattern of nest-site selection and hence age-dependent susceptibility to parasitism should be parasitised by cuckoos laying less mimetic eggs than species in which the nest-site constraint is absent.

The paradox of parasitised acceptors and non-parasitised rejecters should operate also at a higher general level. Current favourite hosts usually accept parasitic eggs while most hosts that are strong rejecters are not parasitised (Davies and Brooke 1989). Therefore, the evolution of egg mimicry driven by host species with a weak discrimination ability should be slower than that driven by host species with high discrimination ability. Thus, current mimicry in cuckoo eggs should in general be poorer than if cuckoos did also parasitise strong rejecters.

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