

Exploitation of host mechanisms for parental care by avian brood parasites

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ABSTRACT. *Exploitation of host mechanism for parental care by avian brood parasites.* - Parasitic birds and their hosts engage in a coevolutionary arms race in which hosts have evolved fine egg discrimination that has in turn selected for sophisticated egg mimicry in many parasites. Paradoxically, however, very few have evolved chick mimicry. This has been traditionally interpreted as evidence that hosts fail to discriminate between chicks because of the existence of an evolutionary lag or equilibrium (costs) in the host-parasite arms race. Here, I show that none of these hypotheses can satisfactorily explain the nearly total lack of chick mimicry. Alternatively, parasitic chicks may be highly constrained to evolve mimicry of host young when both belong to phylogenetically-distant taxa with very different developmental pathways. Data on genomic divergence from DNA hybridization studies support this possibility. I suggest that nonmimetic parasites prevent rejection by exploiting a set of "imperfect" behavioural mechanisms in hosts. First, perceptual and developmental constraints, among other factors, limit the efficiency of chick-recognition mechanisms, particularly prior to fledging. The scarce evidence available on chick discrimination across different bird groups is consistent with this assumption. Second, nonmimetic parasites might evolve manipulative signals that elicit preferential care by hosts to compensate for their odd appearance, in order to decouple the recognition and rejection mechanisms. Some experimental and observational data suggest that hosts may favour parasitic chicks over conspecific young of similar characteristics. Thus, unless we take into consideration the proximate mechanisms involved, it will not be possible to obtain a comprehensive view of this problem from an evolutionary perspective.

KEY WORDS. Brood parasitism, Parental care, Communication, Evolution, Reproduction, Aves

Introduction

About one per cent of the living bird species are obligate brood parasites. They lay eggs in the nest of a different species, called hosts, who incubate them and care for the chicks. Obligate brood parasitism has independently evolved in seven bird groups (fig. 1). Parasitic birds comprise about 95

species in 19 genera (there are no breeding records for some honeyguides and cuckoos). All but one (99%) species (the duck *Heteronetta atricapilla*, not considered here) are altricial: Their nestlings are nidicolous and depend entirely on the host for food and warm. In no other vertebrate group has brood parasitism evolved to such an extent as in altricial birds (Payne, 1977a).

Brood parasitism has attracted much attention

during recent years as a model for the study of coevolution. First, brood parasites and their hosts exert strong selection pressures against each other. Most cuckoos and honeyguides directly kill the host's eggs or chicks soon after hatching by evicting or injuring them, while other parasites often outcompete the host chicks to starvation. Parasites are often cared for during long periods, delaying or thwarting another nesting attempt of their hosts (Payne, 1977a). As a consequence, the breeding success of the host becomes severely depressed. In many host populations, a parasitism rate of 10% may cause a decrease in host fitness as high as that caused by nest predation (Rothstein, 1990). Second, many host-parasite systems involve only one species of each party, allowing a great potential for specific adaptations and counteradaptations to evolve. Most American hosts of either cowbirds or cuckoos interact with a single species of parasite, and in those tropical areas where the diversity of parasitic cuckoos is high, most host species are parasitized by a single species of cuckoo (fig. 2). In contrast, some species of cowbirds and honeyguides are highly generalist and parasitize many different hosts, while the remaining ones (including most cuckoos) are more specialist, usually favouring a few major hosts in a particular area (fig. 3). Thus, brood parasites and their hosts are engaged in a coevolutionary arms race in which very sophisticated adaptations have evolved in the form of defences and counterdefences (Davies & Brooke, 1988, 1989a,b; Rothstein, 1990).

The common host defence against parasitism is rejection of parasitic eggs, usually by ejecting the egg or abandoning the whole clutch. Egg-recognition by hosts is accomplished through learning: During their first breeding attempt, they imprint on their own clutch and later will reject any egg of a different type (Victoria, 1972; Rothstein, 1974, 1975a, 1978a). Egg-rejection by hosts is a specific defensive adaptation against brood parasitism. For example, some passerine species are unsuitable hosts for the European cuckoo *Cuculus*

canorus, because either nest in small cavities or feed their chicks food other than insects that the cuckoo can not assimilate. Unsuitable cuckoo hosts, which presumably have never co-evolved with the cuckoo, are less likely to reject odd eggs experimentally placed in their nests than suitable hosts, many of which are currently parasitized (Davies & Brooke, 1989a; Moksnes et al., 1990). This same prediction holds for different populations of the same host species, one of which has a long history of sympatry with the parasite, and another allopatric. Experimental evidence of lower rejection rates in allopatry than in sympatry has been found for the meadow pipit *Anthus pratensis* and the white wagtail *Motacilla alba*, two British hosts of the European cuckoo, in Iceland (Davies & Brooke, 1989a). Southern populations of a common host of the brown-headed cowbird *Molothrus æer* in Canada, the American robin *Turdus migratorius*, rejected cowbird eggs from all experimentally parasitized nests, while in allopatric northern populations robins accepted cowbird eggs in 30% of nests. Robins never rejected conspecific eggs, suggesting a specific response to cowbird parasitism (Briskie et al., 1992). Magpies *Pica pica* in two areas of Spain where they are heavily parasitized by the great spotted cuckoo *Clamator glandarius*, readily rejected model eggs placed in their nests, particularly when the eggs did not resemble those of cuckoos. However, in allopatry (Sweden) magpies accepted both types of eggs (Soler & Møller, 1990).

Egg rejection has in turn selected for counteradaptations by parasites. Egg discrimination by hosts has two potential associated costs: (i) mistakenly rejecting own eggs due to recognition errors (recognition cost), or (ii) damaging own eggs while attempting to reject the parasitic egg (rejection cost) (Davies & Brooke, 1988). Unless hosts can witness the parasite "red-handed" laying the egg, they may be uncertain about whether the nest has been parasitized or not. Hosts are more willing to reject a mimetic model egg when simultaneously presented with a stuffed cuckoo,

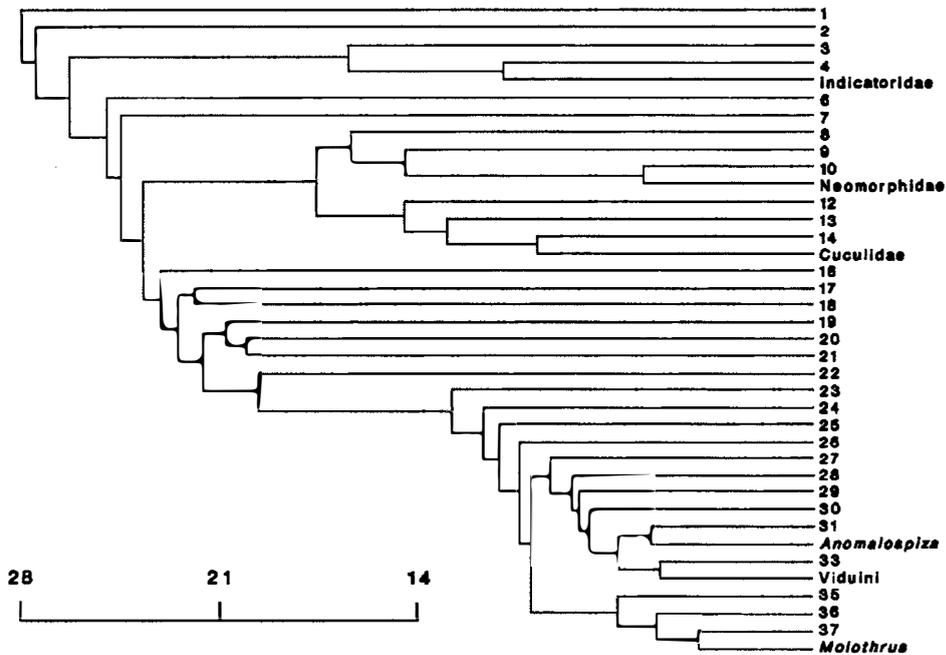


FIGURE 1. Divisions of class Aves determined by DNA-DNA hybridization distances (delta T_{50H} values) showing parasitic and their sister taxa (from Sibley & Ahlquist, 1990; cowbird taxonomy following Lanyon, 1992). The scale shows delta T_{50H} values for the older half of the tree. Relevant branches and nodes with representative examples (in brackets) are as follows (figures for parasitic groups are species/genera). Endings of categorical names indicate taxonomic rank: Parvclass (-AE), Superorder (-MORPHAE), Order (-IFORMES), Infraorder (-IDES), Parvorder (-IDA), Superfamily (-OIDEA), Family (-idae), Subfamily (-inae), and Tribe (-ini).

Branches: 3. RAMPHASTIDES (toucans, barbets); 4. Picidae (woodpeckers); 5. Indicatoridae (honeyguides, 17/4); 8. OPISTHOCOMIDA (hoatzin); 9. CROTOPHAGIDA (anis, guiras); 10. Non-parasitic Neomorphidae (roadrunners *Geococcyx*); 11. Parasitic Neomorphidae (*Tapera* and *Dromococcyx*, 3/2); 12. COCCYZIDA (American cuckoos *Coccyzus*); 13. CENTROPODOIDEA (coucals); 14. Non-parasitic Cuculidae (*Coua*, *Phaenicophaeus*); 15. Parasitic Cuculidae (*Cuculus*, *Clamator*, etc. 54/13); 31. Non-parasitic weaver birds (*Ploceus*, *Quelea*, etc.); 32. *Anomaloepiza imberbis* (may not be Ploceinae); 33. Estrildini (*Lagonosticta*, *Taeniopygia*, etc.); 34. Viduini 15/1; 37. Non-parasitic Icterini (*Psarocolius*, *Molothrus badius*); 38. Parasitic cowbirds *Molothrus*, 5/1.

Nodes: 3-5. PICAIE-PICIFORMES; 8-38. PASSERAE; 8-15. CUCULIMORPHAE-CUCULIFORMES; 8-11. CROTOPHAGIDES; 10-11. NEOMORPHIDA-Neomorphidae; 12-15. CUCULIDES; 13-15. CUCULIDA; 14-15. CUCULOIDEA-Cuculidae; 22-38. PASSERIFORMES; 26-38. PASSEROIDEA; 28-38. Passeridae; 31-32. Ploceinae; 33-34. Estrildinae; 35-38. Fringillidae; 36-38. Emberizinae; 37-38. Icterini.

[Árbol filogenético de la Clase Aves donde se muestran los grupos de aves parásitas y sus taxones hermanos. La longitud de las ramas y la escala representan valores de divergencia genética (delta T_{50H}).]

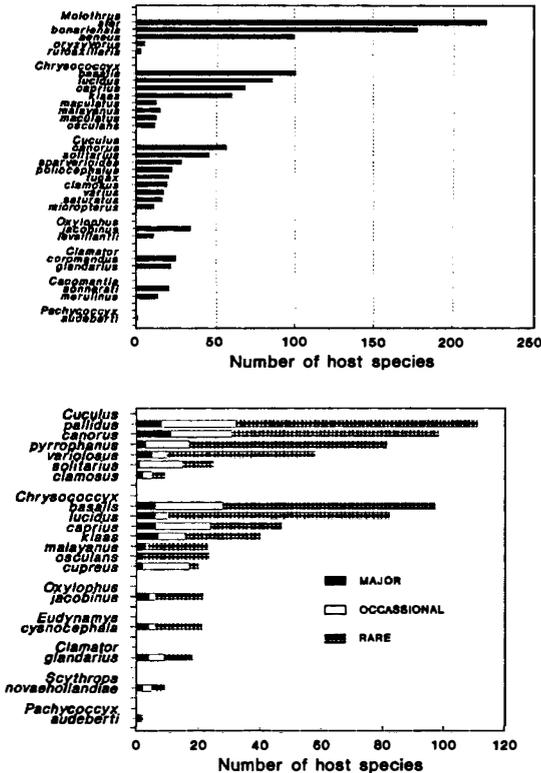


FIGURE 2. Host niche breadth of different brood parasites. Above: maximum number of host species with reliable records of parasitism (ROP). (Sources: Haverschmidt, 1967; Wyllie, 1981; Friedmann & Kiff, 1985; Lanyon, 1992). Below: Number of host species for parasitic cuckoos based on ROP. Most cuckoos specialize on a few favourite hosts in a given area, making the above values not very informative. Biological (B) hosts are those known to have raised a cuckoo chick. For African and Australian species, Major (M) and Occasional (O) hosts are B hosts, M being those with a frequent and consistent number of ROP (Rowan, 1983; Brooker & Brooker, 1989a). For African species, the number of Rare hosts has been completed according to Fry et al., 1988. For the European cuckoo, M are frequent B hosts (Wyllie, 1981).

[Número de especies hospedadoras en diferentes parásitos de cría. Arriba: número máximo de hospedadores con registros fiables de parasitismo. Debajo: número de hospedadores de cucos parásitos.]

probably because the decoy reduces such uncertainty (Davies & Brooke, 1988; Moksnes & Røskoft, 1989). In response, parasites have evolved secretive laying behaviours which minimize the time of laying (Steyn, 1973; Gaston, 1976; Macdonald, 1979; Brooker et al., 1988; Davies & Brooke, 1988). But the main counterdefence by parasites is sophisticated egg mimicry (Baker, 1942). Many species of cuckoos lay polymorphic eggs, each type (*gens*) closely resembling a major host. Mimicry in cuckoo eggs is a unique coevolved response to host discrimination. Alvarez et al. (1976) showed that magpies rejected nonmimetic model eggs of different shapes, sizes and colouration patterns, while real or model great spotted cuckoo eggs, which closely mimic those of magpies, were as readily accepted as conspecific eggs. In the European cuckoo, Brooke & Davies (1988) estimated the rejection rates of several hosts against model cuckoo eggs of different *gentes*. All major cuckoo hosts in Britain have a *gens* which lays a mimetic egg, with the exception of the dunnock *Prunella modularis*. As expected, all but the dunnock discriminated between mimetic and nonmimetic model eggs.

Most other parasites also lay eggs resembling those of their major hosts (Payne, 1967), and some have developed mimicry like that of cuckoos (e.g., cuckoo weaver *Anomalospiza imberbis* [Vernon, 1964]; giant cowbird *Molothrus oryzivorus* [Haverschmidt, 1967; Smith, 1968]), suggesting that egg discrimination may be widespread. This conclusion, however, raises a problem. With a few exceptions, brood parasites have never evolved mimetic chicks and hosts fail to discriminate against them. Most hosts care for parasitic chicks strikingly different from their own, and cuckoo hosts capable of egg discrimination accept many different chicks experimentally placed in their nests (Alvarez et al., 1976; Davies & Brooke, 1989b).

Apparently, parasites have mimetic eggs, but not mimetic young, because, for some reason, hosts can reject eggs but not chicks (Davies & Brooke, 1988). While several hypotheses account for the lack of

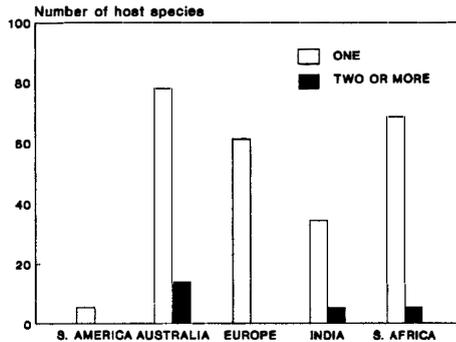


FIGURE 3. Number of species of passerine hosts according to the number of cuckoo species parasitizing them in different geographical areas (Major sources: Ali & Ripley, 1981 corrected according to Becking, 1981; Rowan, 1983; Brooker & Brooker, 1989a).

[Número de especies de paseriformes parasitadas por una o más especies de cuco en diferentes continentes.]

chick discrimination, no satisfactory explanation has been found for this remarkable difference in host behaviour (Rothstein, 1982a, 1990; Harvey & Partridge, 1988). Alternatively, absence of chick mimicry may arise for reasons other than lack of chick discrimination. In this paper, I will suggest that hosts can evolve chick discrimination, and parasites prevent rejection by mechanisms other than mimicry, in particular by exploiting a pre-existing set of host behaviours which are adaptive in the absence of parasitism.

A theoretical framework for the study of chick discrimination

"Discrimination", i.e., differential host responses

towards two items (say, parasitic vs. host chicks), implies "recognition" (the cognitive or perceptual ability to distinguish between them) but not necessarily "rejection" (an appropriate behavioural response in terms of host defences). Lack of chick discrimination implies lack of chick rejection but it tells nothing about whether hosts fail to reject chicks because they can not recognize them or do not respond appropriately.

Rejection requires three mechanisms to be functional: (i) the perceptual and cognitive mechanisms for recognizing a chick; (ii) a rejection response (e.g., ejecting, deserting, or refusing to feed the chick); and (iii) a linking motivational mechanism that triggers rejection once the parasite has been recognized. Recognition also requires a chick trait (the signature) that provides parents with cues about chick identity (Beecher, 1989). A parasite could prevent rejection by (i) avoiding recognition (e.g., mimicking host chicks); (ii) direct interference with host's rejection behaviour, which is unlikely considering the huge power asymmetries between parents and chicks in altricial species; and (iii) manipulating the motivational mechanisms underlying host parental behaviour, so as to decouple the recognition and rejection mechanisms.

Compared to egg-discrimination (Victoria, 1972; Rothstein, 1974, 1975a,b, 1978a, 1982a,b, 1986, 1990; Kemal & Rothstein, 1988), little attention has been paid to mechanisms of chick discrimination. The most comprehensive accounts are those of Beecher (1982, 1988, 1989) on avian kin recognition, a problem similar to recognition of brood parasites (Blaustein et al., 1987). When chicks benefit from providing signature cues, we can identify three possible cases of signature expression and two types of recognition mechanisms (Beecher, 1982):

Case I. The parent directly learns the chick's signature when there is reliable circumstantial evidence as to identity (e.g., nest location), and then uses it when such evidence is absent (e.g., after fledging).

Case II. The parent learns a model common signature from a different relative (e.g., itself, its mother or nestmates) and then matches the chick's signature to such model. Recognition occurs in the absence of any prior contact with chicks, and without any reliable circumstantial evidence of kinship.

Case III. The signature is the direct outcome of a genetic mechanism within the individual that directly reflects its genotype, i.e., some portion of the genome is perceptible to parents. The degree of similarity of the signatures of two individuals will be correlated with their degree of relatedness. Recognition occurs via the similarity of different, inherited signatures, without any circumstantial evidence or prior contact with chicks.

Type 1. The parent recognizes chicks as kin when their signature matches a model signature learned earlier: (i) the signature of that very chick (Case I), or (ii) the signature of the parent or another common relative, which is identical to that of the chick (case II).

Type 2. The parent recognizes chicks as kin when their signature is sufficiently similar to an existing model signature, where the two signatures are distinctly different but their degree of similarity is predictive of genetic similarity. The model can be either learned from an individual other than the chick (case II) or otherwise recognition relies on a genetic mechanism which estimates the proportion of genes shared by parents and chicks (Case III).

Case I recognition is maladaptive for hosts, because parasites reared in the nest will be recognized as kin. However, individual signatures are not needed here, as interspecific parasites provide hosts with many species-specific distinctive features which can be useful as recognition cues. Case II and Case III recognition allow individual recognition as well as species-specific recognition (Beecher, 1982) and could be potentially useful for discriminating against brood parasites. Two groups of hypotheses have attempted to explain why, in spite of it, hosts fail to discriminate against non-mimetic parasites.

Evolutionary lag hypotheses

Hosts may lack the ability to recognize or reject the parasite because of a lag in the host-parasite coevolutionary arms race, i.e., lack of either enough genetic variation or evolutionary time for a rejecter mutant to spread (Rothstein, 1982a).

Lack of appropriate mutations may explain why some hosts (e.g., British dunnocks or Swedish magpies) fail to reject both parasitic eggs and chicks (Davies & Brooke, 1989b; Soler & Møller, 1990). However, it is less clear whether it could account for the lack of chick discrimination in species otherwise capable of egg-rejection. Such species already have mechanisms for recognition, decision-making, and rejection of alien propagules at the nest. Virtually all species of altricial birds may have the capacity to discriminate among different nestlings on the basis of nestling size and behaviour, as suggested by studies on food distribution within broods (see below), and to eventually promote the nutritional independence of chicks by withholding food at the end of the nesting period (Davies, 1976). In fact, ejecting a small nestling may be a simpler mechanical task than ejecting an egg (Rothstein, 1990; Harvey & Partridge, 1988). Apparently, birds capable of egg-rejection are not intrinsically limited to also show chick-rejection and there are no obvious reasons to explain why hosts should not employ an already existing set of mechanisms to reject both parasitic eggs and chicks (Rothstein, 1990).

When parasites (e.g., evicting cuckoos) kill all the host young soon after hatching, it pays more to reject an egg (and hence save the whole brood) than a chick (which may have already destroyed some of the host young, if not all). Even if hosts reject by abandoning the whole clutch, they will benefit more by doing so early (at the egg stage) than later in the season (i.e., after incubation), when prospects for, and benefits of laying a replacement clutch may be lower. This may be particularly important for birds

breeding at high latitudes with short breeding seasons (Moksnes et al., 1993). Consequently, selection is stronger for rejecting eggs than chicks, and a chick-rejecter mutant will take longer to evolve (Davies & Brooke, 1988).

This argument is erroneous when applied to a single newly-hatched chick. Eviction behaviour in the European cuckoo does not normally occur until 8-12 hours after hatching (Wyllie, 1981). It takes only a few minutes to eject a real nonmimetic egg (Rothstein, 1977, 1982a; Moksnes et al., 1993). Even if recognizing and making the decision to reject a hatchling cuckoo took several hours, hosts could save their brood in many cases. This possibility is even more feasible for late- (e.g., *Chrysococcyx* cuckoos; Gill, 1983) and non-evicting parasites. In terms of reproductive value, a clutch about to hatch is actually more valuable than during the laying period: The nest-site has proved to be safe, the eggs have survived the phase when predation is highest (Redondo & Carranza, 1989), the risk of brood parasitism has fallen to zero, the embryos no longer need to be incubated, parental condition may have deteriorated as a consequence of pre-hatching investment, and poorer environmental conditions late in the season would make an equally successful replacement clutch less valuable.

Even if a host loses all its young after the cuckoo hatches, it would do better by rejecting it at any moment later in the nesting cycle than by raising the parasite to independence (Rothstein, 1990). Rejecting the parasite would allow hosts to save much parental effort, particularly after fledging, when energetic demands of chick care are highest (Biedenweg, 1983; Ricklefs & Williams, 1984), as well as to renest again if hosts breed at tropical and temperate climates with extended breeding seasons (Rothstein, 1990). Actually, raising a parasite often takes longer than raising a host brood (table I). Hosts could even accrue indirect benefits if both parasites and hosts show natal philopatry (e.g., cowbirds and viduines, Payne, 1977a): By eliminating the lineage of its local parasites, a host

could lower the probability of it and its kin being parasitized in the future. On calculating the selective advantage of a chick-rejecter mutant, we should do it in relation to its acceptor allele, rather than to an egg-rejecter genotype, unless both strategies are mutually exclusive. If, as suggested above, many behavioural mechanisms for chick rejection are already present in egg-rejecting species, competition between both options may be mild enough to pay evolving a fully functional discrimination mechanism: No matter how good hosts are at rejecting parasitic eggs, it is no use at all after hatching if chicks are not recognized. Among the few parasites with partially mimetic young, some have mimetic eggs as well (Crandall, 1914; Smith, 1968; Ali & Ripley, 1981). Accordingly, it is not obvious that chick rejection always requires a much longer period or higher selection pressure to evolve than egg rejection. Actually, egg-discrimination is lacking (Morel, 1973) or not very accurate (Fraga, 1986) among hosts capable of rejecting non-mimetic chicks.

In a coevolutionary arms race between a brood parasite and its host, the parasite will be one step ahead, i.e., to evolve more efficient adaptations than the host (Dawkins & Krebs, 1979). First, the parasite is under stronger selection for deceiving the host (otherwise being rejected, losing all its reproductive potential) than the host is for spotting the deception (otherwise losing only a fraction of its reproductive effort). Second, the parasite is a "rare enemy"; all its ancestors were, by definition, successful at tricking hosts into rearing them, while the host lineage descends from ancestors which only seldom interacted with the parasite in the past, since the probability of being parasitized is well below 0.5 in most host populations, and often much smaller (Payne, 1977; Rothstein, 1990). Third, selection on traits which are expressed early in the life cycle (e.g., in young parasites) is stronger than on traits expressed later but within the reproductive period (e.g., host parental behaviour), other things being equal (Charlesworth, 1980). Consequently,

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TABLE I. Duration of postnatal parental care for some brood parasites and their hosts.
[Duración del período de cuidado parental en varios parásitos de cría y sus hospedadores.]

Parasite-host	Duration of care (% of hosts) ¹			Source
	N	F ²	T ³	
Indicatoridae:				
<i>Indicator minor-Lybius torquatus</i>	109			Fry et al., 1988; Ginn et al., 1991
<i>Prodotiscus zambesiae-Zosterops senegalensis</i>	164			Ginn et al., 1991
<i>Prodotiscus regulus-Cisticola lais</i>	137			Tarboton, 1975; Ginn et al., 1991
Cuculidae:				
<i>Oxylophus jacobinus-Pycnonotus capensis</i>	137			Liversidge, 1970; Ginn et al., 1991
<i>O. jacobinus-P. barbatus</i>	142			"
<i>Clamator glandarius-Coryvus albus</i> ⁵	68			Mundy & Cook, 1977
<i>C. glandarius-Pica pica</i> ⁵	81	133	114	own data
<i>Pachycoccyx audeberti-Prionops retzii</i>	150			Fry et al., 1988, Ginn et al., 1991
<i>Cuculus solitarius-Cossypha caffra</i>	131			Jensen & Jensen, 1969, Ginn et al., 1991
<i>Cuculus clamosus-Laniarius atrococcineus</i>	110	269	183	Jensen & Clinning, 1974
<i>C. clamosus-L. ferrugineus</i>	131			Jensen & Clinning, 1974, Ginn et al., 1991
<i>Cuculus micropterus-Lanius cristatus</i>	155			Neufeldt, 1966, Dement'ev & Gladkov, 1968
<i>Cuculus canorus-Phoenicurus phoenicurus</i>	133			Khayutin et al., 1982
<i>C. canorus-Acrocephalus scirpaceus</i>	164	180	171	Wyllie, 1981, Brooker & Davies, 1989
<i>Cuculus gularis-Dicrurus adsimilis</i>	135			Tarboton, 1975, Ginn et al., 1991
<i>Cacomantis variolosus-Rhipidura fuliginosa</i>	150			Brooker & Brooker, 1989a, Payne et al., 1986
<i>C. variolosus-Myiagra rubecula</i>	150			"
<i>Chrysococcyx lucidus-Gerygone igata</i>	119			Gill, 1982a
<i>C. lucidus-Acanthiza inornata</i>	146			Brooker & Brooker, 1989b
<i>Chrysococcyx basalis-Malurus cyaneus</i>	150			Kikkawa & Dwyer, 1962, Tidemann, 1986
<i>C. basalis-M. leucopterus</i>	150			"
<i>C. basalis-M. splendens</i>	167			Brooker & Brooker, 1989b
<i>C. basalis-Acanthiza inornata</i>	129			"
<i>Chrysococcyx klaas-Nectarinia amethystina</i>	125			Siegfried, 1981, Jensen & Clinning, 1974
<i>C. klaas-N. fusca</i>	154	207 ⁴	181 ⁴	"
<i>C. klaas-Batis pririt</i>	118	165 ⁴	141 ⁴	"
<i>C. klaas-Sylvietta rufescens</i>	143	200 ⁴	171 ⁴	"
<i>C. klaas-Eremomela icteropygialis</i>	143	187 ⁴	165 ⁴	"
<i>Chrysococcyx caprius-Ploceus velatus</i>	147			Skead, 1952, Ginn et al., 1991
<i>C. caprius-P. ocularis</i>	129			"
<i>C. caprius-Passer melanurus</i>	125			Rowan, 1983, Ginn et al., 1991
<i>C. caprius-Euplectes orix</i>	150			"
<i>Eudynamis cyanocephala-Sphecotheres viridis</i>	165			Crouther & Crouther, 1984, Crouther, 1985
<i>Eudynamis taitensis-Mohoua albicilla</i>	121			McLean, 1988
<i>Scythrops novaehollandiae-Corvus orru</i> ⁵	65			Goddard & Marchant, 1983
Neomorphidae:				
<i>Tapera naevia-Thryothorus sp.</i>	131			Skutch, 1945, Morton & Farabaugh, 1979
<i>T. naevia-Synallaxis sp.</i>	140			"
Passeridae:				
<i>Anomalospiza imberbis-Cisticola aridula</i>	133			Vernon, 1964
Fringillidae:				
<i>Molothrus bonariensis-Zonotrichia capensis</i>	140			Fraga, 1985
<i>Molothrus ater-Sayornis phoebe</i>			140	Woodward, 1983
<i>M. ater-Thryothorus ludovicianus</i>			133	"
<i>M. ater-Sialia sialis</i>			161	"
<i>M. ater-Polioptila caerulea</i>			154	"
<i>M. ater-Cardinalis cardinalis</i>			121	"
<i>M. ater-Melospiza melodia</i>			150	"
Mean±SE ²	134±3.75	191±1.59	153±6.1	

¹ Figures are duration in days for parasitic chicks expressed as a percentage of host chicks during the nestling (N) and fledgling (F) periods and total (T).
² Duration of post-fledging care is likely to be biased towards low estimates for most species. Even so, caring for fledglings lasts for longer than caring for nestlings (Wilcoxon test, Z=1.83, p=0.06, N=4 parasites or Z=2.37, p=0.018, N=7 hosts). Figures given are the

longest of all available values in literature.
³ When nestling and fledgling duration is blank, only total duration was available.
⁴ Minimum estimates. Real duration is likely to be much longer.
⁵ Host chicks larger than parasite's.

anti-parasite defences in the host are expected to be readily counteracted by even more efficient adaptations in the parasite. Dawkins & Krebs (1979) suggested that parasites may employ different mechanisms for eggs and chicks to avoid rejection by hosts: Fine egg mimicry and manipulation of host parental behaviour by young, respectively. The large size, bright gape and intense begging behaviour of a cuckoo chick may act as a supernormal stimulus to which hosts succumb, unable to resist it any more "than the junkie can resist his fix" (Dawkins & Krebs, 1979). A similar idea had been suggested by Heinroth (1959), who reported that European cuckoo fledglings were so efficient at releasing parental responses from other birds, that they even could induce juvenile passerines to feed them.

The possibility that animals may evolve signals which exploit pre-existing sensory preferences in receivers has recently gained acceptance as a model of sexual selection for explaining the evolution of elaborated ornaments in males by female choice (Enquist & Arak, 1993). However, females probably benefit, either directly or indirectly, from mating with a showy male, but it is definitely maladaptive for a host to rear a cuckoo chick. Thus, any mutation which suppresses the host preference for supernormal chicks would rapidly spread to fixation (Rothstein, 1975c). According to Dawkins & Krebs (1979), parasites could retaliate by evolving even more exaggerated signals but this escalation must eventually end up unless such signals can be exaggerated at no cost to the chick. Growing larger, begging louder and developing faster would make the parasite to incur progressively higher costs, limiting the extent to which signals can be exaggerated. If suppresser (i.e., rejector) mutations in the host do not have comparable associated costs, they will spread to fixation. In other words, this hypothesis requires that rejection has an associated cost. This leads us to the following hypotheses.

Evolutionary equilibrium hypotheses

Alternatively, hosts may fail to reject parasitic young because either recognition, rejection, or both are too costly, thereby maintaining the coevolutionary arms race in a stable equilibrium (Rohwer & Spaw, 1988; Lotem et al., 1994).

Rejection costs can limit or completely curtail the expression of host discrimination against parasitic eggs (Rohwer & Spaw, 1988; Rohwer et al., 1989; Røskaft et al., 1990; Petit, 1991). In addition, some findings suggest that egg-discrimination may also entail recognition costs. Reed *Acrocephalus scirpaceus* and yellow-browed leaf warblers *Phylloscopus inornatus* sometimes rejected own eggs when a stuffed adult cuckoo was placed near their unparasitized nest (Davies & Brooke, 1988; Marchetti, 1992). Own-egg ejections in a parasitism-free population of leaf warblers may occur at such high a rate as 5-10% of nests (Marchetti, 1992). Recognition costs could explain why, after not being parasitized for some time, host populations no longer retain their ability to reject parasitic eggs (Cruz & Wiley, 1982) and also why hosts have evolved tolerant mechanisms of egg recognition which apparently minimize the probability of mistakenly rejecting own eggs (Rothstein, 1982b; Lotem et al., 1992). Recognition costs may be particularly relevant as a stabilizing selection pressure against indiscriminate rejection when the host uncertainty about parasitization is high (Kelly, 1987), allowing the equilibrial persistence of intermediate (ca. 50%) rejection rates in hosts of specialized parasites showing secretive laying behaviour, fine egg mimicry, and low parasitization rates, such as cuckoos (Brooker et al., 1990; Takasu et al., 1994; Lotem et al., 1994).

Davies & Brooke (1988) suggested that chick discrimination may entail higher recognition costs

than egg discrimination. Unlike eggs, whose external appearance remains stable during incubation, altricial chicks show dramatic changes during development. Recognizing an egg may thus be a simpler perceptual and cognitive task than recognizing a chick. Chick-recognition would require very complex mechanisms that are difficult or costly to evolve, or otherwise rely on a simpler but less accurate mechanism with a higher probability of error. Recognition mistakes will also be more costly for chicks than for eggs because of the former's higher value to parents. For that reason, most hosts may simply follow a behavioural "rule of thumb" that minimizes the risk of making errors (e.g., "feed any chick in my nest"), but which is however open to exploitation by brood parasites (Davies & Brooke, 1988).

It is easy to imagine several simple, error-free recognition rules which could operate when developmental rates are low and the chick appearance changes little over time. For example, the rule "refuse to feed a pink chick" would allow many hosts of the European cuckoo to reject the parasite just after hatching, at a small risk of rejecting conspecific nestlings of a different colour (Davies & Brooke, 1988). Also, a rule such as "desert a chick much bigger than its parent" would cause rejection well before the parasite attains independence, at virtually no recognition cost. Parasitic young have many other unique features which could be useful as error-free criteria for host discrimination, at least in theory. This hypothesis fails to explain why such rules have apparently never evolved.

The host exploitation hypothesis: towards a synthetic approach

Apparently, neither Evolutionary Lag nor Equilibrium Hypotheses can sufficiently account for the lack of chick discrimination. These hypotheses are not mutually exclusive and each could provide a partial solution to the problem. For example, some

mechanisms involved in chick discrimination may be evolutionarily constrained due to phylogenetic lag, leaving room only for high-cost solutions which can hardly be maintained by natural selection. The Host Exploitation Hypothesis (HEH) holds that lack of chick discrimination is maintained because pre-existing mechanisms underlying parental care and chick recognition in hosts are intrinsically imperfect, allowing brood parasites to exploit them to their own advantage. "Imperfect" here does not mean maladaptive out of the context of brood parasitism, but resistant to evolutionary modification towards a functional improvement as defensive mechanisms for rejecting parasitic young.

1. Exploitation of chick-recognition mechanisms

Hosts might recognize a parasitic chick by two possible ways:

1. To evolve an inherited behavioural program that identifies some signature in the parasite (parasite template), and then rejects it.

2. To recognize a chick which does not match a host signature. A host can acquire information about host species-specific signatures through several mechanisms:

- 2a. A genetic mechanism whose direct outcomes are both the signature (host template) and an inherited behavioural program capable of identifying it in the absence of any previous experience with the signature.

- 2b. Learning the species-specific signature on the basis of previous experience:

- Learning its own species-specific signature (self-matching).

- Learning its chicks' signature, either (i) through an imprinting process during its first breeding attempt, in a way similar to that operating for egg-recognition (Lotem, 1993), or (ii) at each breeding cycle during life (serial learning).

- Learning the signature from a conspecific other than offspring: (i) its parent, (ii) nestmates, or (iii) a mate or neighbour.

2c. Filter-learning the signature from any of the above categories of conspecifics after imposing some stimulus-value constraints, so that only those features which fit into a general template are incorporated.

At first sight, a variety of operative chick-recognition rules could evolve from different combinations of these basic mechanisms in response to appropriate selection. For living birds, however, this is but a Panglossian Utopia. The following points may help illustrating how this selectionist approach reveals itself naive simply by taking into consideration some developmental and proximate causal factors that should not be overlooked if we are to make realistic predictions for given species.

A) Perceptual constraints. The most reliable signatures are probably chemical cues, which allow efficient template-based recognition in the absence of any prior experience. Unlike visual and acoustic cues, olfactory signatures (scent molecules) maintain a simple (often single-locus) and direct correspondence (gene-enzyme or gene-enzymatic product) with the chick's genotype coding for them, as well as with the parent's decoding genetic mechanism (signature-specific receptor molecules). Olfactory signatures allow simple and direct parental labelling and even separate "fingerprinting" of each parent and grandparent labels. Family-specific acoustic and visual labels can occur but multi-locus heritability and complex decoding processes at peripheral CNS make them less reliable. Notably, visual and acoustic features of altricial chicks show enormous changes at a very rapid rate during development, as well as phenotypic flexibility, while chemical cues can remain virtually unchanged or be continuously replaced if unstable, allowing efficient recognition at any age. Kin recognition based upon olfactory cues is widespread among mammals, insects and amphibians (reviews in Fletcher & Michener, 1987). *Birds, on the contrary, are perceptually constrained to rely on visual and acoustic signatures* to recognize their chicks, since

chemoreception is almost inexistent.

B) Confidence of parenthood. Perceptual constraints would make learning-based recognition to prevail over programmed template-based recognition in birds. Rothstein (1974, 1978a, 1982a) pointed out the evolutionary advantages of a learned, as opposed to innate, mechanism of own-egg recognition. However, in the case of chicks, the advantage of such a mechanism may not be so obvious. Parent birds (especially females) have a much higher confidence of parenthood for eggs than for chicks. A female (and a male too if he is at the nest while his mate is laying) can be sure that the egg she has just laid is her own, and so can confidently learn how it looks like. On the contrary, a chick hatching from an egg in the nest may not be its own if a parasite has previously managed to lay it and its presence has gone undetected. *The immediate consequence of parental uncertainty about chick identity is a finite cost of misidentification of chicks in learning-based recognition.*

C) Misidentification costs. If parents learn the signature from its offspring (when parents) or nestmates (when young), they are likely to incur misidentification costs. By serial learning of offspring signatures, parents will learn those of parasites too. An imprinting mechanism like that used for eggs also incurs a misimprinting cost (Lotem, 1993). Since parasites are selected to outcompete host chicks at no inclusive fitness cost in order to secure food, the probability that the nest will contain only parasites during the hosts' sensitive period is very high. If a host imprints on the parasite in its first breeding attempt, it will leave no offspring in its life (Lotem, 1993). Hosts could greatly reduce misidentification costs by evolving template-based mechanisms as well. For example, even if birds recognize eggs by learning, they are still programmed genetically to weigh certain egg parameters more heavily than others (Rothstein, 1978a, 1982b). In those species where innate recognition involving chemical templates is well developed, it has been shown that learning plays a

role (Fletcher & Michener, 1987), suggesting that a recognition system can rely on both learning-based and genetically-programmed mechanisms at a time (Blaustein et al., 1987). Template-matching may restrict the range of stimuli which can be accepted as appropriate, thus decreasing the risk of mistakenly learning the parasite features. Accordingly, *constrained-learning mechanisms of chick recognition may be particularly suitable as host defences* against parasitic chicks.

D) Problems with learning the signature from non-young models. Misidentification costs can be overcome if parents learn the signature (or a model) from an adult conspecific. However, if parasites are recognized shortly before independence, the benefit accrued is negligible. Thus, learning adult signatures is no use. Many visual signatures simply can not be perceived from oneself, and self-perception of own vocal output may involve distortions not present when hearing others. Consequently, self-matching may be particularly ineffective when signatures change over time because this increases their inaccuracy. However, model adult signatures could help reducing misidentification costs by limiting learning of offspring signatures to those chicks showing some resemblance to the model. Recognition could improve with increasing breeding experience, as repeated exposures to adequate signatures may improve the template.

E) Problems with genetically-programmed templates. When visual and acoustic signatures change markedly over time, genetic templates should incorporate enormous amounts of information in order to track developmental changes, or otherwise rely on less-accurate templates making recognition rules to be error-prone.

Specific parasite templates ("it looks like a striped crested cuckoo") will fail to recognize different kinds of parasites but will seldom incur recognition errors. This mechanism selects for parasites changing signatures in any direction to avoid matching hosts' templates, but not necessarily to mimic host chicks. As the latter would require a

higher number of coadapted mutations, non-mimetic polymorphism in chick appearance might be widespread. Similarly, parasite templates may be difficult to evolve from pre-existing traits in hosts; however, recognition of adult parasites could serve as a basis for evolving fledgling templates. Partial chick mimicry may increase recognition errors, decreasing the benefits of rejection: Paradoxically, chick mimicry in parasites and rejection in hosts could associate negatively with each other. There is no evidence that such a mechanism has ever evolved.

Host chick templates ("it does not look like a warbler") will be effective for rejecting any non-mimetic parasite, particularly if it shows conspicuous distinctive features, but it will sometimes cause recognition errors (e.g., if host chicks' signatures go accidentally transformed by environmental factors). Recognition errors can be reduced if signatures consist, only or mainly, of acoustic rather than visual cues because the former: (i) involve fewer and simpler sources of variation and error (i.e., time, frequency and amplitude vs. colouration, plumage, shape, size), and (ii) are generated from within the body and so are less sensitive to external disturbances. Host templates may evolve from pre-existing traits which were functional in social or parent-offspring relationships, or even recognition of individual fledglings by serial learning (see below). Parasites are selected to become mimetic in response to host discrimination. Many features of avian chick recognition and chick mimicry in parasites are consistent with this possibility (see below).

F) Developmental constraints on the timing of recognition. Hosts are selected to recognize the parasite as early as possible in the nesting cycle. Ideally, the parasite should be recognized just after hatching. Although it may pay to reject it later on, there is selection for signatures that allow the earliest possible recognition of parasites. Marked developmental changes of signatures require that reliable signatures must necessarily be age-specific:

Optimal signatures would be those of hatchlings. Altricial birds are born blind, hence unable to learn visual signatures from themselves or nestmates. Auditory channels do not normally open until some days after hatching; until then, the perceived discrepancy between own and external vocal output is highest. A bird can only learn such signatures from its offspring, at a high misidentification cost. Template-based recognition could be useful at this moment, but its effectiveness is limited by the fact that altricial birds across different taxa are most similar just after hatching, and many unique distinctive features (e.g., plumage, behaviour) are not yet expressed. As a chick grows older, these two limitations become reduced but so does the stability of phenotypic traits as a result of rapid development (see next). Consequently, limitations on both adult recognition mechanisms and chick signatures suggest that discrimination of newly-hatched chicks may be particularly inefficient.

In altricial species, most developmental changes occur during the intermediate phase of nidicolous life, from shortly after hatching until shortly before fledging. During this period, rates of morphological and physiological development reach a maximum (Ricklefs, 1983; O'Connor, 1984), coinciding with a period of particularly active behavioural change (Redondo, 1991). Gross developmental changes make this period especially unsuitable for recognizing chicks, as effective rules based upon templates or previously-learned model signatures should incorporate huge amounts of information about developmental changes. Learning signatures from offspring or nestmates may also incur misidentification costs. In contrast, chicks around fledging time show slow rates of development and have attained most of their species-specific distinctive features. As host and parasitic chicks are most dissimilar, template-based recognition mechanisms may be particularly useful at this time. In addition, hosts could use self-matching to constrain learning of its offspring's or nestmates' signature. Therefore, *chick discrimination should be*

best developed around fledging time.

G) Signature reliability. Some chick traits (e.g., body colouration or feather morphology) show subtle and complex developmental changes, while others develop in a more predictable way (e.g., body size, behaviour, and some "signature" anatomical traits like the zygodactyl feet of cuckoos). Recognition rules based upon cues of the first type are more likely to lead to recognition errors.

H) Counteradaptations by parasites. In response to discrimination, parasites are selected to modify those traits used by hosts as recognition cues. Modifications may consist of: (i) convergence with host chicks (i.e., mimicry); (ii) ritualization (e.g., exaggeration) of traits with a communicative function in order to exploit signal preferences in the host (Dawkins & Krebs, 1979) (see below); and (iii) concealing or removing some unique features so that hosts can no longer use them as cues for recognition. The evolutionary rate at which parasites can modify such traits is crucial to determine the outcome of the arms race (Kelly, 1987). Many morphological traits of chicks (e.g., colouration, plumage characteristics or foot shape) are not adaptations to an immature stage of development and hence show little changes, if any, during the transition to independent life. In contrast, other morphological traits (e.g., oral flanges) and most behavioural traits (e.g., vocalizations) of altricial chicks are better explained as adaptations to an immature ontogenetic niche (Redondo, 1991). Such juvenal traits are less constrained to evolve under selection pressures operating during the nestling stages. Moreover, if two traits have similar effects on fitness and at least one trait acts within the reproductive period, selection will act more strongly on the trait which is expressed earlier on life (Charlesworth, 1980). Fast rates of evolutionary change, coupled with strong selection pressures (Dawkins & Krebs, 1979), may allow parasites to quickly evolve effective counterdefences. Some morphological traits with the lower potential for rapid evolutionary change are precisely those less

favoured by selection as reliable recognition cues (e.g., many visual features such as body shape or colouration, or plumage characteristics). On the other hand, many reliable signatures (e.g., behaviour, size or vocalizations) are evolutionarily labile. *Parasites may thus exploit an intrinsic feature of avian mechanisms of chick discrimination, namely the lack of recognition cues being, at the same time, reliable* (i.e., unlikely to lead to recognition failures) *and stable over time* (i.e., resistant to evolutionary modification as counter-defences).

2. Exploitation of host rejection rules

Unlike eggs, which can be either rejected or fully incubated, chicks can be either ejected or disfavoured (e.g., not, or less fed) when not accepted. The pre-existing behaviours from which egg-rejection probably evolved (nest sanitation) favoured ejection as the most likely rejection response, but this may not be the case for chicks. Chick discrimination in the context of normal parental care (e.g., differential feeding of chicks within a brood) provides a more likely evolutionary precursor for chick-rejection behaviour than disposal of dead nestlings, as the latter must be strongly selected against when there are signs that the chick is healthy (Rothstein, 1990). Ejection of living nestlings is virtually unknown among birds, even in circumstances where it could be adaptive, i.e., when target chicks show unambiguous signs of a low value to parents and their presence endangers the remaining valuable offspring (as a non-mimetic parasite would do). For example, some symptomatic diseases of nestlings show a strong contagious distribution across broods, suggesting infective pathogens sometimes confirmed by post-mortem analyses (Redondo, 1989; Castro, 1993). During brood reduction, the intense begging behaviour of irreversibly starving chicks may increase the conspicuousness of the nest to predators over several days (Castro, 1993; Redondo & Castro, 1992b). Apparently, parents only eject nestlings after they are dead. Moreover,

ejection makes recognition errors to be irreversible, while disfavoured chicks may allow a longer period for assessing the identity of chicks, as well as to make reversible decisions if necessary. If, as a consequence of inefficient mechanisms of recognition, hosts are often uncertain about the identity of a putative parasite (particularly prior to fledging), recognition costs can be diminished by disfavoured the chick, instead of ejecting it. Thus, *rejection behaviour should, as a rule, involve hosts disfavoured the chick, rather than ejecting it*. Consequently, many of the signatures employed by hosts to discriminate against parasites will be *juvinal traits, particularly those with a signal function related to offspring need or quality*, to which pre-existing decision-making mechanisms involved in chick rejection are more likely to be tuned to.

3. Exploitation of behavioural rules for parental care

Non-mimetic parasites may prevent rejection by exploiting a different set of host behavioural mechanisms, namely those involved in adaptive parental care in the absence of parasitism (Redondo, in Huntingford, 1993; fig.7). As the host uncertainty about chick identity becomes reduced during development, parasites must compensate for their odd appearance by exaggerating those traits favoured by hosts to care for their own young (e.g., intense begging). In this way, parasites can maintain a high motivation for parental care in the host, in order to functionally decoupling the recognition and rejection mechanisms. Moreover, if hosts can only use chick signals as recognition cues, or can only tune rejection responses to them, manipulation may completely prevent the evolution of chick discrimination (see below).

The HEH should be distinguished from cases where a parasite exploits hosts by cheating them in order to receive preferential care. Here, cheating refers to consistent misinterpretation of parasites' signals by hosts, to the parasite's own advantage.

Cheating is possible because hosts are adapted to a stable signalling system composed by a majority of honest conspecific (offspring) signals (Johnstone & Grafen, 1993). As cheats, parasites can afford to expose themselves by giving conspicuous, exaggerated signals because hosts are constrained to assess (recognize) them (e.g., due to evolutionary lag) (Motro, 1989; Johnstone & Grafen, 1993). Rejection is not the ultimate cause for the existence of dishonest signals in parasites but these may provide a proximate causal mechanism for the absence of chick rejection, or even an ultimate explanation for the absence of chick discrimination in some species (see the last section).

This idea differs from the Supernormal Stimulus Hypothesis (Dawkins & Krebs, 1979) in several ways:

1) The HEH accounts for the hosts' failure to evolve suppression of the preference for exaggerated signals in parasites. These signals are precisely those employed by hosts to allocate their parental expenditure in optimal ways (c.f. Staddon, 1975; Dawkins & Krebs, 1979). Parents are selected to expend more resources in the offspring with greater fitness returns per unit of expenditure (Haig, 1990; Redondo et al., 1993), i.e., in the offspring with a higher need or quality. For example, parents should feed more the chicks who beg more if begging is a reliable signal of nutritional need (Godfray, 1991) or physical vigour (Grafen, 1990). Also, parents should value more the larger nestlings in a brood if they are more likely to survive at the end of the period of parental care (Smith et al., 1989). From a proximate causal (motivational) point of view, parents should be very willing to feed a large nestling who begs intensively, and parasites could exaggerate such traits in order to exploit this preference. A mutant that disfavors large nestlings with intense begging behaviour would reject the parasite but also will make wrong decisions when feeding their own offspring. If the cost of misfeeding own chicks is important, suppresser genotypes may not have a selective advantage over

wild ones, and the mutation will not spread unless the probability of being parasitized is very high.

2) The HEH explicitly assumes the existence of costs associated to exaggerated signals in the parasite (Grafen, 1990; Johnstone & Grafen, 1993). Accordingly, parasites will employ more exaggerated (costly) signals when hosts are more likely to reject them (e.g., late in the nesting cycle, or when host chicks are present for comparison). Signal costs are likely to limit the evolution of counterdefences by parasites. The prevalence of costly signals would in many cases require that hosts, rather than parasites, will pay for the excess costs of signals (e.g., by parasites monopolizing care). In addition, it is not immediately obvious whether hosts given a choice between a conspecific and a parasitic young will show a preference for the latter (c.f. Eastzer et al., 1980; Davies & Brooke, 1988). Parasites are not selected to incur in signal overplay in order to obtain unusually high levels of parental care, but to compensate for their odd appearance so as to secure *adequate* amounts of it (which may, incidentally, exceed those required by young hosts). Other things being equal, however, parasite signals should be more efficient than host signals at eliciting host parental care. This predicts a net preference for parasitic over conspecific chicks by hosts prevented from recognizing the parasite as an "odd chick".

3) The possibility that parasites can successfully manipulate hosts makes sense only under the assumption that chick-recognition mechanisms are inefficient. Otherwise, it is hard to explain why hosts fail to evolve different rules for parasitic and host chicks, or a mixed rule conditional to chick identity (e.g., "suppress the preference for large hungry chicks if they are pink"). The lack of such conditional rules might reflect the low number of traits other than signals which are favoured by selection as signatures.

In the following sections, I will review evidence aimed at testing some of the assumptions and predictions of this hypothesis.

Chick discrimination in birds

Cross-fostering experiments conducted early in the nestling period have shown that, with a few exceptions, parent birds do not discriminate against unrelated chicks at this time (Swynnerton, 1916; Kinsey, 1935; Emlen, 1941; Alvarez et al., 1976; Holcomb, 1979; Davies & Brooke, 1989b; Davies et al., 1992). Most studies seeking evidence of chick discrimination have been conducted with colonial birds which stand a high risk of fostering unrelated conspecific young as a consequence of nest switching. From a functional point of view, nest-switching and adoption in colonial species have many interesting points in common with brood parasitism (Redondo et al., 1994). In both cases, the evolutionary potential for rejection behaviour depends on two variables: (1) the probability of being parasitized (or of fostering an alien chick) and (2) the difference in host nesting success between parasitized and unparasitized nests (Payne, 1977a).

1. Swallows

Parent swallows have evolved mechanisms of individual offspring recognition in species breeding in dense colonies (bank *Riparia riparia* and cliff *Hirundo pyrrhonota* swallows), but not in those breeding solitarily (Beecher, 1982, 1988). Young, on the contrary, are able to recognize their parents in both cases (Burt, 1977; Beecher et al., 1985; Medvin & Beecher, 1986). Acoustic signatures (calls) alone are sufficient to allow recognition (Beecher et al., 1981; Stoddard & Beecher, 1983). In one species, chicks also have distinctive visual patterns but it is unknown whether parents also make use of this information (Stoddard & Beecher, 1983). The sensitive period for learning the chicks' calls does not begin until a few days before fledging (Beecher et al., 1981; Stoddard & Beecher, 1986; Beecher, 1988). Chick calls in colonial species contain more information about individual identity than those of solitary species, suggesting signature

adaptation (Beecher, 1988). Adult colonial cliff swallows were better at discriminating among chick calls of cliff and non-colonial barn swallows *H. rustica* than adult barn swallows and starlings *Sturnus vulgaris*. All birds discriminated more easily among calls of different cliff swallows than barn swallows (Loesche et al., 1991). The first result suggests the possibility that cliff swallow parents are better programmed to respond to conspecific calls, as long as starlings are also capable of comparable acoustic chick recognition (see below).

Non-colonial swallows do not recognize chicks individually on the basis of calls (Medvin & Beecher, 1986). Chicks, however, can recognize their own parents and behave differentially towards alien adults, allowing parents to discriminate against alien conspecific fledglings on the basis of behavioural cues (Burt, 1977). In addition, barn swallow females were able to distinguish between different stages of chick development: In a series of cross-fostering experiments, they preferred young over eggs and showed signs of motivational conflict when young switched were very different in age (Grzybowski, 1979). Non-colonial rough-winged swallows *Stelgidopteryx serripennis* do not respond differentially to unrelated conspecific young or young bank swallows added to their nest. But when the entire rough-winged swallow brood was exchanged with an adjacent bank swallow brood, the rough-winged swallow parents responded to the calls of their own chicks and fed them at the new location. This suggests that non-colonial swallows can respond differentially to their own (or, at least, conspecific) chicks. Instead of different perceptual and memory systems, the difference between colonial and non-colonial swallows appears to operate on different decision rules (Storey et al., 1992).

Although in colonial swallows the probability of fostering may be high, the cost of adoption is low. Chicks can only switch to a foster nest of a similar age when they are able to fly. Consequently,

adoptions occur late in the nestling period, when resident chicks have almost completed growth (Beecher et al., 1981; Pierotti, 1988). However, in some colonial seabirds chicks can move into a foster brood of a similar age very early on life. In these species, adoption is more costly because extra chicks often outcompete or impair the growth of the foster parents' brood (Graves & Whiten, 1980).

2. Gulls

Parent gulls would benefit from recognizing their own chick at two moments in the chick's life: Shortly after hatching, during the early period of mobility when alien chicks can switch to a foster nest, and shortly before fledging. In contrast, chicks would only benefit from being recognized in the latter case and parent-young recognition is well developed at this time (Beecher, 1988). Shortly after hatching, chicks in every species studied can recognize their parents (Evans, 1970; Miller & Emlen, 1975; Beer, 1979; Knudsen & Evans, 1986; Storey et al., 1992). Parents, on the contrary, seldom recognize their own chicks but can discriminate against unrelated chicks on the basis of behavioural (Beer, 1979; Graves & Whiten, 1980; Knudsen & Evans, 1986; Shugart, 1990) or circumstantial cues, such as proximity to nest (Graves & Whiten, 1980). Chick-discrimination develops around the time chicks become mobile and often involves fatal aggression against unrelated chicks attempting to approach the nest. The two exceptions to this rule are cliff-nesting kittiwakes *Rissa tridactyla* and ring-billed gulls *Larus delawarensis*. Due to cliff-nesting, brood unmixing is rare among kittiwakes and high responsiveness both on the part of parents and chicks may lead to accidental downfall. Kittiwake chicks are particularly unresponsive to parents' calls during most of the nestling period and parents may lose least if they use a conservative strategy (never reject) but sometimes feed a strange (Storey et al., 1992). Ring-billed gulls, on the contrary, nest in densely-packed colonies (unlike other gulls, which nest as

far apart as conditions allow; Pierotti & Murphy, 1987) and have evolved fine chick-recognition. Parents initially accept any chick but restrict parental responses to its own brood after 7 days. Learning the chicks' signature requires at least 24 h. The onset of the sensitive period is tuned with the development of chick mobility. Behavioural cues are used in discrimination but auditory, size, and age-related morphological cues are also used. Although visual cues are important, experimental transformations triggered ambivalent behaviour and eventual acceptance of transformed chicks after a few hours (Miller & Emlen, 1975).

3. Other colonial seabirds

Truly colonial seabirds which nest in extremely dense colonies and whose chicks have well-developed mobility early on life have evolved fine mechanisms of chick discrimination. As in swallows and gulls, young also recognize their parents' voices in virtually all cases studied (Tschanz, 1959; Ingold, 1973; Busse & Busse, 1977; Burger et al., 1988; Shugart, 1990). The onset of the sensitive period for parents to recognize chicks is tuned with the development of mobility. Guillemot *Uria aalge* parents can recognize their chick just after hatching (Tschanz, 1959). Terns which nest in densely-packed colonies (e.g., *Sterna fuscata*), can recognize their chicks ca. 5 days after hatching, while royal terns *Sterna maxima*, which nest in extremely congested colonies, can do so on the 2nd day (Miller & Emlen, 1975). As in gulls, parent terns vigorously attack (often fatally) unrelated chicks after recognizing their own young (Burger et al., 1988). In contrast, cliff-nesting species in which nest-location cues are lacking after the chick "jumps" to the sea at fledging, do not develop chick recognition until shortly before jumping (e.g., 10 days in razorbills *Alca torda*, Ingold, 1973; 14-20 days in the brown noddy *Anous stolidus*, Miller & Emlen, 1975). In species forming crèches (e.g., penguins, flamingos or pelicans), parents develop the ability to recognize

their young when they join the crèche, i.e., when circumstantial cues are no longer available (e.g., nest-location in flamingos and pelicans or parent guarding in penguins) (Miller & Emlen, 1975).

In all species studied, acoustic cues play an important role as signature cues (Tschanz, 1959; Buckley & Buckley, 1972; Ingold, 1973; Busse & Busse, 1977; Burger et al., 1988; Shugart, 1990). Visual cues are also used in recognition. Razorbill parents, for example, can more effectively recognize their chicks by auditory and visual signals together than by auditory signals alone (Ingold, 1973). In many terns, chicks show extreme variation in down colour, allowing parents to recognize them individually (Buckley & Buckley, 1972; Shugart, 1990). However, as in ring-billed gulls, parents do not rely on visual cues alone to recognize their chicks (Shugart, 1990). In two different tern species, most parents could recognize their chick when they could hear them but only some could do so when they could only see their silent chicks (Buckley & Buckley, 1972).

4. Ciconiids

Frequent nest-switching has been reported in cattle egrets *Bubulcus ibis* (Blaker, 1969), grey herons *Ardea cinerea* (Milstein et al., 1970), and white storks *Ciconia ciconia* (Redondo et al., 1994). Grey heron and white stork chicks can only abandon their natal nest very late in the nestling period, when fully fledged. However, cattle egret chicks can scramble through the nest-tree branches very early on life and thus may be adopted by a young foster brood, at a high cost to foster parents. Like most seabirds, cattle egret parents often attack alien chicks to death but white stork and grey heron parents are, like swallows, only mildly aggressive. Discrimination against unrelated chicks in these species develops by the age chicks begin to leave the nest, i.e., 12-14 days in cattle egrets and shortly before fledging in herons and storks. At least cattle egret and white stork chicks can recognize their parents as well. In white storks, resident chicks were

much more aggressive than parents against unrelated fledglings attempting to settle at their nest. Recognition in these species is rather crude and appears to be based mainly on behavioural cues. White storks, for example, accept as "kin" any foreign chick who manages to resist the initial attacks by residents and remains at their nest for one or two days (Redondo et al., 1994). Cattle egret parents seem to recognize chicks on the basis of chick's behaviour only, and are virtually unresponsive to drastic alterations of the visual appearance of chicks (Blaker, 1969).

5. Territorial species

All the above cases refer to colonial species in which the risk of fostering unrelated young due to nest-switching is high. In other colonial species, parents have also developed recognition of individual chicks' calls shortly before fledging (e.g., piñon jay *Gymnorhinus cyanocephalus* McArthur, 1982; starlings *Sturnus vulgaris* Elsacker et al., 1986; bee eaters *Merops apiaster* Lessells et al., 1991). This form of individual recognition is not restricted, however, to colonial birds. In many territorial species, parents only feed their own fledglings and refuse to feed unrelated young, suggesting the possibility of recognition (e.g., blackbirds *Turdus merula* Snow, 1958). Direct evidence for individual recognition in territorial species has been found in carrion crows *Corvus corone* (Yom-Tov, 1977), robins *Erithacus rubecula* (Harper, 1985), song sparrows *Melospiza melodia*, coots *Fulica atra*, and red-winged blackbirds *Agelaius phoeniceus* (Peek et al., 1972).

Carrion crow parents accept many different types of chicks placed in their nest during most of the nestling period but attack them when placed on the ground. However, they develop the ability to recognize their young by the time they are ready to fledge (Yom-Tov, 1977). Red-winged blackbird parents recognize their young individually on the basis of acoustic cues a few days before fledging. Learning signature calls is also likely to be involved

in parental recognition of chicks in song sparrows and coots (Peek et al., 1972, and refs. therein). These examples suggest that parental recognition of individual signature calls of chicks shortly before fledging may be widespread in altricial birds.

6. Kin recognition and optimal outbreeding

Female quail *Coturnix coturnix* raised with siblings approached novel first cousins in a testing apparatus more frequently than novel third cousins, siblings, or unrelated individuals. Also, quails reared in mixed groups containing both kin and non kin preferentially associated with siblings later on (Bateson, 1982, 1983; Waldman & Bateson in Beecher, 1988). Such an ability to discriminate between conspecifics on the basis of genetic relatedness despite no prior differential experience (kin and non kin were equally unfamiliar or equally familiar) provides the only well-documented example of phenotype-matching kin discrimination in birds. The signature cues, although not yet investigated, are visual and probably acoustic (Beecher, 1988). In addition, McGregor & Krebs (1982) suggested that great tit *Parus major* females choose mates according to their genetic relatedness, using song resemblance to their father as an indicator. Selection may have favoured mating strategies which result in an optimal degree of outbreeding, i.e., to mate with an individual which is neither too closely nor too distantly related (Bateson, 1982, 1983). Although these studies do not directly bear on the problem of chick discrimination, they are relevant to my discussion because they demonstrate that recognition in the absence of prior experience (by phenotype-matching or recognition alleles), can evolve in birds.

7. Estrildid finches

Estrildids can be found in Africa, South-East Asia and Australasia but only in Africa are commonly parasitized by the closely-related Viduine finches. All estrildid nestlings have a highly specialized begging behaviour and show species-

specific intricate mouth patterns in the gape and tongue (Goodwin, 1982). Parasitic *Vidua* nestlings closely mimic the chicks of their estrildine hosts (Nicolai, 1964). Estrildid finches show selectivity in feeding behaviour towards conspecific young or towards nestlings resembling these. Cross-fostering experiments demonstrate that young of species which differ in gape markings, begging movements, down pattern and other traits are normally fed less or not fed at all (Nicolai, 1964). In a series of experiments, Nicolai (1969) showed that captive estrildids of various species neglected nonmimetic nestlings of other species, and that selectivity sometimes resulted in starvation. On the contrary, Goodwin (1982) showed that cordon bleus *Uraeginthus* showed no discrimination between conspecific and other young if these were of a closely-related species with a similar pattern of mouth markings. The best evidence now available comes from two species: The zebra finch *Taeniopygia guttata* (Z) from Australia and the Bengalese finch *Lonchura striata* (B) from India and South-east Asia.

Zebra and Bengalese finch nestlings develop in a very similar way but they show marked differences in their appearance (e.g., only Z young have natal down), begging behaviour and gape markings (Eisner, 1961; Muller & Smith, 1978; ten Cate, 1982, 1985). At least Z parents pay close attention to the nestling's begging stimuli. When begging, Z nestlings expose the gape and show conspicuous tongue movements. Visual begging stimuli are replaced by acoustic stimuli as nestlings grow older and parental responsiveness to either visual or acoustic signals changes accordingly (Muller & Smith, 1978). Immelmann et al. (1977) showed that wild-coloured Z parents preferred to feed wild-coloured young over white ones, which lack mouth markings. Wild young in mixed broods were fed first and had priority to the first feedings in the morning and, as a result, showed a more rapid mass gain and a higher survival rate. When given a choice, Z and B parents feed conspecific young

preferentially. Heterospecific young were less likely to be fed and, when fed, obtained less food, independently of begging. Selectivity is initiated by the parents, not by the chicks. The preference of Z parents for conspecific young was expressed independently of whether parents had previous experience with conspecific young or not. In B, the preference was expressed despite B parents had previously raised only Z young (ten Cate, 1982, 1985). Further observations of mixed (Z+B) pairs rearing one Z and one B young revealed that the preference did not appear until young were a week old (fledging occurs at 20-25 days). Parents already showed preference for conspecific young during their first breeding attempt (without any prior experience) but there is some evidence that first time breeders are less selective than experienced breeders and also that the type of offspring they rear will affect their willingness to look after similar young in the next brood (ten Cate, personal communication). In addition, estrildid parents (e.g., Z) can recognize all their fledged young individually and fledglings also recognize their parents (Goodwin, 1982). This evidence indicates that mechanisms of chick-discrimination in estrildids may involve a complex imprinting-like mechanism constrained by some species-specific template. The existence of genetically-programmed templates is most evident in certain species which do not easily imprint sexually on a different species if fostered by it, but show sexual preferences for conspecifics independently of rearing experience (Goodwin, 1982). It is not known why precisely estrildids have evolved chick discrimination but it seems unlikely that any selection pressure favouring it (e.g., facultative interspecific nest parasitism or usurpation by other estrildids, risk of hybridization, etc., Goodwin, 1982) were much stronger than obligate interspecific parasitism, or were exclusive of estrildids among all bird groups. Perhaps only ancestral estrildid forms were equipped with a mouth pattern that made them to be pre-adapted for evolving this unique signature system.

8. *Chick-discrimination in birds*

Unlike amphibians, insects and mammals, which can "fingerprint" their offspring by means of efficient phenotype-matching mechanisms of kin recognition based upon olfactory cues, birds must largely learn the visual and acoustic features of the chicks present in their nest (Davies et al., 1992; Beecher, 1988). To date, no evidence for kin recognition by self-matching has been found in any bird (Beecher, 1988). The evolution of more efficient mechanisms of chick recognition is probably limited by the existence of recognition costs, particularly when development is more rapid (Beecher et al., 1981; Knudsen & Evans, 1986). Many properties of avian mechanisms of chick recognition make sense as insurance devices for preventing errors: The absence of recognition or rejection responses in species where selection is weak; the major role played by acoustic and behavioural cues, as opposed to less reliable visual cues; the use of circumstantial cues to help in recognition; the general lack of recognition around hatching time, even in species with sophisticated recognition mechanisms (e.g., estrildids); and the existence of a refractory period which delays recognition until it is strictly necessary. As a rule, parents' recognition of chicks is less precise than chick's recognition of parents. It seems unlikely that parents would be poorer than chicks in regard to this perceptual ability, particularly if they are otherwise capable of recognizing mates or neighbours individually. This strongly suggests that absence of chick discrimination is, by and large, the result of an evolutionary equilibrium maintained by the existence of recognition costs. Consistent with the HEH, selection acts more intensively upon decision-making mechanisms, rather than upon perceptual adaptations.

Most studies have focused on chick-recognition in colonial species. These studies have provided good evidence of serial-learning of offspring individual signatures during the nestling period (Beecher's (1982) case I/type 1 recognition). The

widespread need to recognize individual chicks in this way, not only in colonial species, may be a weakness common to many hosts, since it is open to exploitation by a non-mimetic parasite growing in the nest at the right time. However, recognition of parasites does not require individual signatures, and there is experimental evidence for other types of recognition, as in quail (case II or III/type 2) and estrildid finches. Non-colonial swallows, for example, can discriminate among species-specific begging calls. Estrildid finches also show that one species may be able to use different mechanisms for different purposes, some of which are potentially useful as host defences against parasites. Many species other than birds can utilize more than one recognition mechanism, either alone or in conjunction with one another (Fletcher & Michener, 1987). Therefore, misimprinting costs do not necessarily prevent the evolution of chick recognition (c.f. Lotem, 1993).

Perceptual constraints, recognition costs, and conflicting selection pressures (e.g., serial learning of familiar chick signatures) all make it difficult for hosts to discriminate against parasites during the pre-fledging period. Note, for example, that the only known case where parents can recognize nidicolous chicks (estrildid finches) involves a highly-patterned signature (mouth markings) which remains fairly stable during development (Kunkel & Kunkel, 1975). Parasites may thus exploit the host rule "feed any chick who is in my nest" during most of the pre-fledging period (Davies & Brooke, 1988), and particularly just after hatching. This may explain the puzzling lack of host responsiveness towards a cuckoo chick working hard to evict the host eggs or chicks just beneath the body of its brooding foster parent. Consistent with this idea, most reported instances of interspecific adoption in birds out of the context of brood parasitism, although uncommon anyway, involve parents caring for nestlings; adopting a fledgling is a much rarer event (Shy, 1982), as expected if recognition were best developed after fledging.

Evidence of host discrimination against parasitic chicks

Many hosts can recognize the adult parasite as an enemy and they could use the existing similarity between fledgling and adult parasites as a model signature for developing parasite templates. Experimental evidence of specific recognition of the adult parasite by its hosts has been found in several studies (Alvarez & Arias de Reyna, 1974; Robertson & Norman, 1976; Duckworth, 1991). Dull plumages prevail among adult parasites and parasitic cuckoos show an unusual degree of variation in plumage, including polymorphism, which are likely adaptations to reduce the probability of search-image recognition by hosts (Payne, 1967).

Some observations suggest that parent birds behave differentially towards parasitic and conspecific young. None of these cases involve young nestlings, as predicted if constraints on recognition were age-specific. There are two independent observations reporting that babbler hosts abandoned their cuckoo *Oxylophus jacobinus* chick soon after it acquired its characteristic pied plumage (Sanjeeva Raj, 1964; Gaston, 1976). More interestingly, in three cuckoo species, fledglings are consistently attacked or mobbed by their foster parents when they fly, but parents resume feeding the cuckoo as soon as it stops and begs for food (*Oxylophus levaillantii* and *Pachycoccyx audeberti*, Fry et al., 1988; *Cuculus varius*, Ali & Ripley, 1981). A fledgling *Chrysococcyx basalis* was also observed to be fed and attacked simultaneously by a *Microeca* flyrobin (Kikkawa & Dwyer, 1962). Aggression against fledgling cowbirds *M. ater* by three different host species has also been reported by Woodward (1983). These observations are particularly interesting because they suggest the possibility of a motivational conflict in hosts caring for fledgling parasites, consistent with the HEH. Most cuckoo fledglings show a characteristic inertia behaviour, sitting around the nest site, keeping very

still for long periods and moving only short distances when changing perches, although capable of larger flights if necessary. Tarboton (in Rowan, 1983) suggested that cuckoos behave that way in order to prevent mobbing by small birds (including foster parents) elicited by their raptorial appearance, but this idea seems inconsistent. First, *Chrysococcyx* cuckoos do not resemble raptors. Second, Duckworth (1991) has shown experimentally that reed warblers respond differentially towards an adult European cuckoo and a sparrowhawk (the raptor presumably mimicked by the cuckoo): Cuckoos and raptors are recognized as different enemies. Interestingly, fledglings of the non-mimetic cowbirds *M. ater* and *M. bonariensis* also show inertia behaviour, but not those of *M. rufocollaris*, which mimics host fledglings (Fraga, 1986). I suggest that fledglings of non-mimetic parasites have evolved inertia behaviour because this reduces the risk of being rejected by hosts.

Soler et al. (ms) have shown that magpie parents given a choice between a great spotted cuckoo and a magpie chick late in the nestling period will favour (i.e., feed more likely) the chick-type they were caring for before the experiment. Discrimination was improved when the two chicks were presented outside the nest (a widely-used circumstantial cue about chick identity). This study suggests (i) that some hosts can recognize (or distinguish) chicks; and either (ii) that learning of individual offspring's signatures aided by circumstantial cues may interfere with discrimination, at least before fledging; or (iii) that familiarity with the parasite during the nestling stages may be involved in recognition (or the lack of it). Most honeyguides, for example, parasitize cavity-nesting birds of smaller size and foster parents may have difficulties for becoming familiar with the appearance of parasitic chicks during the nestling period. Barbet hosts of the lesser honeyguide *Indicator minor* are very aggressive towards adult parasites and recognize their foster chick as an enemy, attacking and driving it away, just after leaving the nest. It seems unlikely that

this interaction reflects the inability of honeyguides to cope with chick rejection by hosts. Unlike most other birds, honeyguide fledglings do not follow or pester parents (although they beg loudly from them), receiving little, if any, care out of the nest (Short & Horne, 1985). After fledging, the woodpecker hosts of *I. variegatus* engage in much effort attempting to get the young honeyguide back into the nest to roost for the night (as woodpecker young would normally do), without success. Fledged young of the variegated honeyguide, like those of the greater honeyguide *I. indicator*, are not attacked by hosts but also become independent shortly after leaving the nest. For some unclear reason, honeyguide fledglings seek independence just after fledging. In another experimental study, McLean & Griffin (1991) demonstrated that parent grey warblers *Gerygone igata* were able to discriminate between the begging calls of their own chicks and those of their host-specific parasite, the evicting shining-bronze cuckoo *Chrysococcyx lucidus*, and that this discrimination was made independently of whether warblers were raising a cuckoo or a warbler brood. In some pilot experiments with magpies, we have succeeded in inducing experimental rejection of chicks by giving them a "bizarre" appearance when just about to fledge (fig. 4). Apparently, transformed great spotted cuckoo chicks were less likely to be rejected and more likely to be fed than transformed magpie chicks of similar characteristics (table II). These findings contrast with a former study by Alvarez et al. (1976) in which magpies accepted a variety of chicks of different species, as well as magpie chicks painted with colours, experimentally placed in their nests early in the nestling period.

Finally, cowbird *M. ater* and *M. bonariensis* nestlings show racial variations in rictal flange colour. Such variation is unusual in both cowbird eggs or adults, as well as in nestlings of other passerines. Rothstein (1978b) suggested that differential parental responses by hosts (i.e., a preference for feeding chicks of a given morph) are



FIGURE 4. A great spotted cuckoo chick 18 days old, with its visual appearance transformed artificially (painted black and luminous pink all over with non-toxic dye), was rejected (attacked to death) by a pair of magpies (who also consumed part of the chick's pectoral muscle) within the following two hours after we placed it together with a resident, non-transformed magpie chick 20 days old. A transformed magpie chick cross-fostered to a resident, non-transformed cuckoo chick undersimilar conditions, was also killed (but not cannibalized) by the cuckoo's foster parents.

[Este pollo de cría de 18 días (cuyo aspecto externo fue alterado pintándolo de color negro y rosa fluorescente con pintura no tóxica) fue rechazado (matado y consumido en parte) por los padres de urraca de otro nido, menos de 2 h después de introducirlo junto con un pollo de urraca residente sin transformar de 20 días, como resultado de un experimento para determinar si éstos eran capaces de rechazar pollos al final del período de crecimiento.]

TABLE II. Choice discrimination tests by magpie parents between chicks of different visual appearance. Shown are responses to the experimental introduction of an artificially-transformed chick of a different species together with one of their own non-transformed young¹.

[Elección por parte de padres de urraca entre dos pollos de distinta especie y aspecto externo: uno de sus pollos sin transformar y un pollo de otra especie con su aspecto externo transformado artificialmente.]

Procedure/Chick type	Response		
	Attacked	Not fed	Fed
Alien, Transformed			
Magpie	1	2	1
Cuckoo	1	0	2
Resident, Familiar			
Magpie	-	1	1
Cuckoo	-	1	3

¹ We removed all brood contents from magpie broods caring for chicks of a single species 20-22 days old and replaced them with a resident, non-transformed chick, and a chick of a different species coming from another nest with its external appearance transformed as in fig. 4. Responses were assessed after 2 h by inspecting chicks for any signs of aggression and recording their mass change. Zero or negative mass increments were recorded as not fed.

the selective pressure responsible for this variation (Rothstein, 1978b). Further evidence in support of the evolution of chick discrimination is provided by parasites showing chick mimicry, which I will review next.

Chick mimicry in parasitic birds

Parasitic chicks could mimic the visual appearance, the acoustic properties of the calls or the behaviour of host chicks. Fine mimicry of all these

features, comparable to that of cuckoo eggs, has evolved in only two cases. The first one are viduine finches, which parasitize estrildid finches. Each *Vidua* species is highly specific of a estrildid host and parasitic chicks show a striking resemblance of the mouth parts, external appearance, begging calls and behaviour of the host chicks. There is experimental evidence showing that estrildid hosts discriminate against nonmimetic chicks (see above). The second case is the screaming cowbird *Molothrus rufoaxillaris*, a specific parasite of the closely-related bay-winged cowbird *Molothrus badius*. Screaming cowbird chicks also mimic the morphology and begging calls of their host and, again, there is evidence that bay-winged cowbirds refuse to feed a cowbird chick of a different, nonmimetic species. A third possible case is the giant cowbird *M. oryzivorus*, which parasitizes four species of oropendolas (Icteridae) in Central America (Fleischer & Smith, 1992). In oropendola nests, old chicks are often fed from the outside, so that only the chicks' face is visible. Giant cowbird chicks have a beak and face-iris colouration (yellow and whitish, respectively) similar to that of oropendola chicks. The similarity disappears after chicks have attained nutritional independence ca. two months after fledging, the parasite's beak and face darkening to pure black and the iris becoming dark brown like in the adult (Crandall, 1914; Hilty & Brown, 1986). It is not known whether begging calls are mimetic. This could be considered a genuine case of chick mimicry because it involves juvenile traits perhaps directly related to parental feeding and which develop late in the nestling period, when parents are more likely to discriminate. No study, to my knowledge, has tested whether oropendolas reject non-mimetic chicks but they discriminate against giant cowbird adults and eggs (Smith, 1968). Skutch (1954) observed that fledgling cowbirds and their foster mothers interacted less frequently with the remaining colony members than normal oropendola families; apparently, cowbirds, their foster mothers, or both, suffered from some kind of social

"apartheid".

Consistent with the above suggestion that host discrimination is most constrained early in the nestling period, none of these parasites mimic host chicks just after hatching. Both giant and screaming cowbird and some *Vidua* (e.g., *V. macroura*) chicks are covered with down just after hatching while bay-winged cowbird, oropendola and estrildid (e.g., *Estrilda astrild*) hosts are naked (Nicolai, 1964; Smith, 1968; Fraga, 1986; Ginn et al., 1991). At this age, bay-wings have yellowish skin while screaming cowbirds are pink (Fraga, 1986). Newly-hatched oropendola (*Gymnostinops montezuma*) chicks are blackish, very different from giant cowbird chicks which have a whitish skin (Crandall, 1914). *V. macroura* nestlings have mauve skin while *E. astrild* hosts are pinkish (Ginn et al., 1991).

It has been suggested that two non-evicting cuckoos are also mimetic (Lorenz, 1935; Lack, 1968). The first one is the great spotted cuckoo and its crow hosts. This is erroneous, however, as chicks of this cuckoo bear no visual resemblance with any of its hosts. The second one is the Indian koel *Eudynamis scolopacea*. In India, koels only parasitize crows (*Corvus macrorhynchos* and *C. splendens*) and they do not evict chicks while in Australia they parasitize at least six major hosts of smaller size (magpie-lark *Grallina cyanoleuca*, figbird *Sphecotheres viridis*, four species of friarbirds *Philemon*, and perhaps the red wattlebird *Antochaera carunculata*) and show eviction behaviour (Becking, 1981; Brooker & Brooker, 1989a). Koels are sexually dichromatic (males are black and females brownish, with racial variations) and show geographical variation in fledgling plumage colouration: Indian chicks are typically dull black while Australian chicks are brownish. After independence, fledglings of each sex begin to moult into their characteristic plumage. Moreover, the beak of Indian fledglings is black, while that of Australian birds is pinkish grey (adults in both cases have it greenish) (Ali & Ripley, 1981; Crouther,

1985). These variations strongly suggest mimicry (black koel chicks resemble crow chicks) (Lack, 1968), particularly because female Indian fledglings, unlike Australian koels and most sexually-dichromatic birds, resemble adult males (Ali & Ripley, 1981). However, Indian koels do not show mimicry in traits more directly related to parental care, like gape colouration and begging behaviour (Lamba, 1963), so the similarity could be alternatively interpreted as protective anti-predator, rather than aggressive, mimicry (Rothstein, 1990). This idea, however, fails to explain why no other cuckoo has become cryptic, including other non-evicting species which parasitize crows in other parts of the world (Rowan, 1983; Crouther, 1985). Some species of *Chrysococcyx* cuckoos mimic host young during the earliest part of the nestling period (see below) but become strikingly different later on.

Appart from the existence of chick mimicry, these parasites have other features in common. First, they are host-specific. Rothstein (1990) suggested that host-specificity may result in especially high rates of parasitism, and hence high selection pressures on the hosts, thereby facilitating the appearance of an adaptation (chick discrimination) that is especially hard to evolve. While it is true that mimetic parasites often show high parasitization rates (87% of all host nests in the screaming cowbird [Fraga, 1986]; 35% in *Vidua chalybeata* and 30-70% in *V. paradisaea* [Nicolai, 1969; Morel, 1973; Skead, 1975]; 28-73% in the giant cowbird [Smith, 1968]), and that they may reduce to some extent the nesting success of their hosts (table III), selection pressures are undoubtedly much higher for hosts of other non-evicting parasites lacking chick mimicry whose reproductive success is severely depressed by parasites and which may also suffer from high parasitization rates (e.g., 40-70% in jacobin cuckoos *Oxylophus jacobinus* [Liversidge, 1970; Gaston, 1976]; 30-75% in great spotted cuckoos [Soler, 1990; Zuñiga & Redondo, 1992a]; 25-70% in brown-headed cowbirds, and 60-75% in shiny cowbirds [refs. in Payne, 1977a]).

Alternatively, if for some reason mimetic parasites were less harmful to host chicks, high parasitization rates could arise as an effect, rather than a cause, of chick mimicry via host tolerance. For example, in the giant cowbird, those host colonies where the parasite depressed more the host nesting success showed lower parasitization rates (Smith, 1968). Multiple parasitism of the same host nest is frequent among mimetic parasites. In viduines, a large fraction of parasitic eggs in the same nest are laid by the same *Vidua* female (Morel, 1973; Payne, 1977b). In the giant cowbird, 40% of nests with multiple parasitism contain eggs of the same female (Fleischer & Smith, 1992) and 80% of the nests parasitized by the screaming cowbird contain more than one parasitic egg (Fraga, 1986). In contrast, less than 8% of nests parasitized by *M. ater* contain more than two eggs (Fleischer & Smith, 1968). Chicks of mimetic parasites may thus be more tolerant towards nestmates due to kin selection (Payne, 1977b).

Second, the chicks of mimetic parasites are often reared along with some host young. This is not always the rule, however. For example, Indian koel and crow chicks are only seldom reared together (Lamba, 1963; Ali & Ripley, 1981). Since the benefits of discrimination are higher with host young in the nest (Davies & Brooke, 1988), and the cost of misimprinting is low (Lotem, 1993), it has been suggested that chick mimicry in these parasites is a unique coevolved response to chick discrimination by their hosts. I have extended Lotem's (1993) misimprinting model to the case of a non-evicting parasite. In this model, hosts are allowed to imprint on the type of chicks present in their nest at a given age t in the nestling period during their first breeding attempt, and then reject any different chick type present in the nest at t days during a later breeding attempt. I have introduced some realistic complications such as the possibility that the nest will be preyed upon before t days (in which case the host remains naive), and the possibility that either parasite, host chicks, or both

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TABLE III. The decrease in host reproductive success caused by some late- or non-evicting parasites with varying degrees of chick mimicry. Shown is the reproductive success in parasitized nests expressed as a percentage of that in unparasitized nests of the same host population.

[Exito reproductor en nidos parasitados (en % respecto de los no parasitados) para hospedadores de algunos parásitos que se crían junto con los pollos del hospedador según el grado de mimetismo de sus pollos.]

Parasite-host	Reduction in host reproductive success		
	%	Estimate ¹	Source
Mimetic:			
<i>Vidua chalybeata-Lagonosticta senegala</i>	81.0	A,t	Morel, 1973
"	72.0	B,t	"
<i>V. wilsonii-L. rufopicta</i>	7.5	A,t	Macdonald, 1980
<i>V. macroura-Estrilda</i> sp.	69.0	A,t	Macdonald, 1980
<i>Molothrus rufoaxillaris-M. badius</i>	62.0	B,t	Fraga, 1986
Average ±SE ³	53.7±15.7		
Partially Mimetic:			
<i>Chrysococcyx lucidus-Gerygone igata</i>	5.4	A,t	Gill, 1983
<i>Eudynamis scolopacea-Corvus splendens</i> ²	56.6	C,t	Lamba, 1963
<i>M. oryzyvorus-Zarhynchus wagleri</i> &	42.0	A,t	Smith, 1968
<i>Cacicus cela</i> ^{2,4}	54.3	B,t	"
Average ±SE ³	52.8±26.3		
Non Mimetic:			
<i>Oxylophus jacobinus-Turdoides striatus</i> ²	53.3	A,t	Gaston, 1976
"	53.1	C,t	"
<i>O. jacobinus-T. caudatus</i> ²	43.8	A,t	Gaston, 1976
"	43.0	C,t	"
<i>Clamator glandarius-Corvus albus</i> ²	42.1	A,t	Mundy & Cook, 1977
<i>C. glandarius-Corvus corone</i>	87.1	A,t	Soler, 1990
<i>C. glandarius-Pica pica</i> ²	21.8	A,t	own data
"	24.0	B,t	"
"	15.4	A,p	"
"	18.0	B,p	"
<i>Molothrus bonariensis-Agelaius xanthomus</i>	50.0	B,t	Payne, 1977a
"	47.4	C,t	"
<i>M. bonariensis-Zonotrichia capensis</i>	63.3	C,t	Payne, 1977a
"	27.3	C,t	King, 1973
<i>M. bonariensis-Mimus saturninus</i>	30.1	A,t	Fraga, 1985
"	32.3	B,t	"
<i>M. bonariensis-Dendroica petechia</i>	34.5	B,t	Post et al., 1990
<i>M. bonariensis-Vireo altilogus</i>	57.2	B,t	Post et al., 1990
<i>Molothrus ater-Empidonax virescens</i>	88.5	C,t	Payne, 1977a
<i>M. ater-Dendroica petechia</i>	71.0	A,t	Burgham & Picman, 1989
"	53.4	A,p	Weatherhead, 1989
<i>M. ater-Dendroica kirtlandii</i>	25.6	A,t	Rothstein, 1975c
"	22.0	C,t	Payne, 1977a
<i>M. ater-Chondestes grammacus</i>	36.4	C,t	Payne, 1977a
<i>M. ater-Sayornis phoebe</i>	7.2	A,t	Rothstein, 1975c
<i>M. ater-Vireo olivaceus</i>	29.0	A,t	Rothstein, 1975c
<i>M. ater-Junco hyemalis</i>	55.5	A,t	Wolf, 1987
<i>M. ater-Agelaius phoeniceus</i>	89.0	C,p	Røskaft et al., 1990
"	65.0	A,p	"
"	62.5	A,p	Weatherhead, 1989
Average ±SE ³	44.20±3.51		

1 Field measures of reproductive success. A: Average number of host fledglings per nest; B: percentage of nests producing at least one host fledgling; C: percentage of host eggs surviving to fledging; t: all nests, including both partial and whole-brood losses; p: excluding nests with whole-brood losses, many of which (e.g., predation) are not due to parasites.

2 Parasites that may prey selectively on unparasitized nests (mostly eggs), rendering % values higher than actual mortality caused by parasitic chicks.

3 One-way ANOVA, F=0.10, df=2,9, p>0.9. N=number of parasite species in each category.

4 Host colonies free from parasitic insects (Smith, 1968)

will be present at the nest at t . My results confirm Lotem's prediction that such a mechanism of chick recognition will result in discrimination of brood parasites only under very restricted conditions, namely for parasites which are harmful to hosts but which cause little mortality to host chicks before the age t (e.g., parasites which depress the quality, rather than the number of host chicks), and especially when parasitization rates are moderately

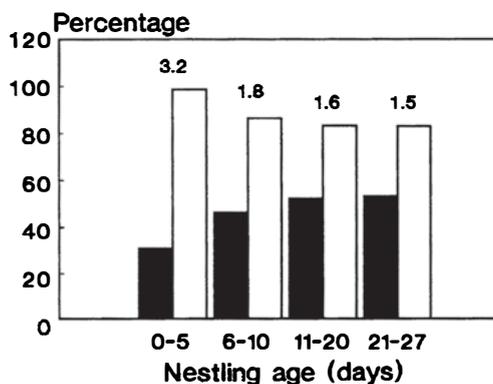


FIGURE 5. The reproductive success of a putative chick-rejecter (R) mutant magpie that eliminates parasitic great spotted cuckoo chicks at different ages t in the nestling period (abscissa), as compared to that of an acceptor (A) parent and of unparasitized broods. Only broods for which mortality causes could be reliably determined, and where chicks that hatched successfully had not been preyed upon at age t are considered. Shown is the average number of young at fledging (21-27 days) left by R (open bars, $N=12-13$) and A (filled bars, $N=78-36$), expressed as a percentage of the average number of fledglings in unparasitized broods of similar characteristics ($N=87-69$) (Santa Fe, Granada, 1990-1992). Figures above bars show the selective coefficient of a t -days R relative to its A allele, calculated as the R/A ratio of fledging success. A refers to parasitized broods where at least one cuckoo hatched and remained in the nest at age t . R are parasitized broods where at least one cuckoo hatched but no longer remained in the nest after age t because it either disappeared from natural causes or was artificially removed. The trend for R to do better than A across all ages is significant (paired $t=4.6$, $df=3$, $p<0.02$). Considering only those A broods with no more than three cuckoo hatchlings does neither alter trends nor significance. Predation rates after hatching were similar for parasitized and unparasitized broods except between 10 and 20 days, when 11% ($N=163$) and 3.4% ($N=89$) of broods, respectively, were preyed (Chi-square, $\chi^2=3.5$, $df=1$, $p<0.03$). Otherwise, the selective advantage of rejection is underestimated because it assumes equal prospects of juvenile survival for chicks in R and A broods, i.e. it ignores that cuckoos decrease the quality of host chicks down to near zero.

[Exito reproductor de un mutante de urraca (R, barras blancas) que rechaza a los pollos de críalo a diferentes edades t durante el desarrollo, comparado con el de su alelo aceptador (A, barras oscuras). Se muestra el número de volantones en nidos parasitados donde al menos un críalo nace y permanece hasta la edad t (A) y en nidos donde nace al menos un críalo pero desaparece (de forma natural o artificial) antes de t días (R), excluyendo en todos los casos nidos predados antes de la edad t . Las cifras sobre las barras muestran el coeficiente de selección de R en relación a A, calculado como el cociente R/A del número de volantones, dependiendo de la edad a la que R se expresa.]

high. However, the assumption that hosts can only recognize chicks by imprinting on offspring signatures is not supported by current evidence on avian chick discrimination, as shown above. No species seems to recognize chicks in this way while evidence for alternative recognition mechanisms less likely to incur misimprinting costs has been found in some hosts (e.g., estrildids).

The argument that chick discrimination has evolved only when foster parents can save most of their own chicks after rejecting the parasite (Davies & Brooke, 1988) makes sense when we compare non-evicting parasites causing little or no chick losses with those that kill host chicks shortly after hatching (e.g., evicting cuckoos and honeyguides). However, it is not clear why hosts have failed to evolve chick discrimination against other non-evicting parasites which take several days before outcompeting host chicks to starvation (i.e., the remaining three species of cowbirds, non-evicting cuckoos of the genera *Oxylophus*, *Clamator*, and *Scythrops*, and the parasitic weaver). Table III shows that, with the exception of viduines, the reduction in host nesting success is not particularly

low in mimetic parasites as compared to other non-evicting ones. Hosts of these parasites could save many of their own young and improve the growth of the surviving ones (Soler & Soler, 1991) if they were able to reject the parasite during the nestling period (as presumably did hosts of mimetic parasites in the past). Rejection could pay even in the case of very harmful non-evicting parasites, such as the great spotted cuckoo when parasitizing magpies (fig. 5), or late-evicting parasites, such as *Chrysococcyx* cuckoos (see below). Hence, it remains problematic why chick mimicry-discrimination has not evolved in most non-evicting parasites. Moreover, although the presence of host young undoubtedly increases the benefits of chick discrimination, this is not to say that rejecting an evicting parasite has no selective advantage at all, as discussed above. Alternatively, discrimination may improve when parents have the opportunity to compare chicks, i.e., when both are present in the nest simultaneously (Davies & Brooke, 1988). This possibility makes sense considering that recognizing chicks may be not a simple perceptual task, particularly during the pre-fledging period. However, this idea also fails to account for the nearly total lack of chick mimicry among non-evicting parasites. Coexistence with host young seems to facilitate, but not determine, the occurrence of chick mimicry.

I therefore prefer a different explanation for the occurrence of chick mimicry in these parasites. If we look at the phylogenetic relationships between each group of parasites and their hosts (fig. 1, table IV), it follows that widowfinches and the two mimetic cowbirds are the only three cases in which the parasite and its hosts belong to closely related taxa, at or below the level of subfamily. Table IV shows that phylogenetic proximity, as estimated by DNA-DNA hybridization studies, is quite low for all the host-parasite systems, except for the three mimetic ones, which are specific of closely-related hosts. What I conclude from this comparison is that the evolution of chick mimicry may be severely

constrained when parasites and hosts belong to distantly related taxa, as a result of differences in their developmental pathways. After all, a cuckoo which is being raised by a small warbler must develop into a cuckoo, not a warbler. Consequently, we should expect only moderate degrees of chick mimicry to have evolved in such cases. Morphological mimicry of a major host will irreversibly commit a parasite to develop into a given phenotype affecting many different body parts, while egg or vocal mimicry only affects a few traits. In this sense, host-specificity seems a necessary requirement for chicks to evolve mimicry, particularly of morphological traits with a low degree of phenotypic flexibility (unlike calls) and that (unlike egg-shells) may interfere with many adult traits.

As viduines are the closest relatives of estrildines (Sibley & Ahlquist, 1990), they could evolve fine chick mimicry, even during the nestling stages, in response to the unique pre-existing mechanism of chick-recognition based upon mouth markings. The degree of relatedness between both groups may be even higher than suggested in table IV, as differences in generation times may overestimate the degree of genomic divergence (Sibley & Ahlquist, 1990). Most estrildids breed when less than a year old while viduines do not breed until the first (females) or the second year (males) (Payne, 1977a). Despite the phylogenetic proximity between *Vidua* and the tribe Estrildini (formerly dismissed by Nicolai, 1964), the system surely involves convergent mimicry. Recent molecular evidence has demonstrated that specific host-*Vidua* associations have evolved after recent colonization with rapid coadaptive mimicry of new hosts, rather than as an ancient coadaptive cospeciation of parasites and hosts (Payne et al., 1993). Different subpopulations of the same *Vidua* species may specialize on and mimic different subspecies (Nicolai, 1964) or even genera of estrildid hosts (up to four non-closely related genera of estrildids, Payne & Payne, 1993). However, the extent of chick similarity between any

TABLE IV. Degree of genomic divergence between taxa of brood parasites and their hosts, estimated by DNA-DNA hybridization.

[Niveles de divergencia filogenética entre taxones de parásitos de cría y sus hospedadores determinados por hibridación de ADN.]

Parasitic taxon ¹	Closest host taxon ¹	Major host taxon ¹	Degree of genomic divergence (delta T ₅₀ H) ²	Number of host taxa ³		
				Gen.	Subf.	Fam.
Piciformes, Indicatoridae:						
<i>Indicator</i>	Picidae	Coraciae, Passerae	11.0-26.3	24	12	12
<i>Prodotiscus</i>	Passeriformes	Passeri	26.3	8	5	5
Cuculiformes:						
Cuculidae	Passeriformes	Passeri	23.7	1-67	1-24	1-14
Neomorphidae	Passeriformes	Passeriformes	23.7	2-5	1	1-2
Passeriformes:						
<i>Anomalospiza imberbis</i>	Cisticolidae	Cisticolidae	11.1	2	1	1
Viduini	Estrildini	Estrildini	5.4	4	1	1
<i>Molothrus rufoaxillaris</i>	<i>M. badius</i>	<i>M. badius</i>	1.2-4.0	1	1	1
<i>M. oryzyvorus</i>	Icterini	Icterini	1.2-4.0	3	1	1
<i>M. aeneus</i>	Icterini	Passeri	(1.2-4.0)-12.8	20	6	6
<i>M. bonariensis</i>	Icterini	Passeriformes	(1.2-4.0)-19.7	42	12	9
<i>M. ater</i>	Icterini	Passeriformes	(1.2-4.0)-19.7	70	17	14

1 See fig. 1.

2 Values in brackets for cowbirds refer to the range of delta T₅₀H values among Icterini (Sibley & Ahlquist, 1990).

3 Sources: Ali & Ripley, 1981 corrected after Becking, 1981; Rowan, 1983; Fry et al., 1988; Brooker & Brooker, 1989a; Sibley & Monroe, 1990.

host-parasite dyad is higher than among host-host or parasite-parasite dyads (Nicolai, 1964, 1969; Payne et al., 1993). Mimicry between screaming and bay-winged cowbird chicks is also high (Fraga, 1986). The closest relative of the screaming cowbird is not, however, its host (which probably deserves a different generic status as *Agelaioides badius*), but the giant cowbird (Fraga, 1986; Lanyon, 1992), again suggesting true mimicry.

Koels are now considered a superspecies including three allospecies: The Asian koel from India to Northern New Guinea (*E. [scolopacea]*

scolopacea), the black-billed koel from Sulawesi (*E. [scolopacea] melanorhyncha*), and the Australian koel from Southern New Guinea to Australia (*E. [scolopacea] cyanocephala*) (Sibley & Monroe, 1990). In the Australian koel, two races (*E. c. cyanocephala* and *E. c. subcyanocephala*) can be distinguished (Beehler et al., 1986; Brooker & Brooker, 1989a). Adult male koels have a uniform black plumage in all groups, while females are more variable. In the Australo-Papuan race *subcyanocephala*, females have black head and upperparts like some fledglings (2 out of 9 [22%] in

Lack's (1968) sample) of the Indian *E. scolopacea* (Beehler et al., 1986). Females of the black morph can also be found in some Indian populations (Andaman and Nicobar Islands) (Ali & Ripley, 1981), and black bills occur in the *melanorhyncha* allospecies. This means that koels could be particularly unconstrained for mimicking a quite simple, but conspicuous, trait of host fledglings (black colouration), simply by expressing it to a greater extent and/or at an earlier point in development. This is supported by the developmental sequence of black plumage in males: Immature Australian males in pre-migratory moult strongly resemble some Indian fledglings and adult *subcyanocephala* females (Ali & Ripley, 1981; Crouther, 1985). On the other hand, some fledglings from Sulawesi, Moluccas and New Guinea are also brownish-black all over like Indian fledglings (3 out of 4 in Lack's sample), despite there are no records of parasitism on crows in Australia or New Guinea (Brooker & Brooker, 1989a). The uniqueness of this trait is obvious and confirms the idea that, as a group, cuckoos may be highly constrained to evolve chick mimicry of their passerine hosts except under extraordinary circumstances: (i) Indian koels fail to mimic other traits of crow chicks; (ii) since all major hosts were black in India, but not in Australasia, koels became mimetic only in India; and (ii) the peculiarity has more to do with koels than with crows, as other non-evicting cuckoos which parasitize crows (*Clamator glandarius* in Africa and *Scythrops novaehollandiae* in Australia, both with an adult plumage very different from that of crows and koels), have failed to evolve any trace of mimicry (Rowan, 1983; Goddard & Marchant, 1983).

Shining cuckoos *Chrysococcyx lucidus* from New Zealand are remarkably similar to their specific grey warbler host chicks shortly after hatching (Gill, 1983). Apart from being the same size, both have the skin grey-pink, white long natal down on the back and crown, pale yellow rictal flanges and grey bills. Australian forms of *C. lucidus* do not mimic

any of their 10 major hosts, and show a pinkish-orange skin, short down on the crown only, and bright yellow rictal flanges (Brooker & Brooker, 1989a). It is not known whether warblers show chick rejection, but they fail to reject the nonmimetic eggs of the shining cuckoo (Gill, 1983; Brooker & Brooker, 1989a). Two other Australasian species of shining cuckoo are also very similar in the colour of skin and natal down to the nestlings of their specific hosts (refs. in Gill, 1983): *C. malayanus minutillus* has a pale pinkish skin and pale yellowish down on its crown and back while *C. malayanus russatus* has a black skin and white down on the crown, resembling their respective main hosts *Gerygone olivacea* and *G. magnirostris* (Brooker & Brooker, 1989a). No other *Chrysococcyx* species have natal down, and skin colour ranges from pink or mauve (*basalis*, *cupreus*) to olive (*klaas*) and black (*osculans*, *caprius*) (Brooker & Brooker, 1989a; Fry et al., 1988). Such variations really suggest the existence of mimicry in some species. During the later stages of the nestling period, *Chrysococcyx* cuckoos no longer resemble host chicks at all, being much larger than their foster parents and contrasting with the visual appearance and behaviour (except for calls) of warbler chicks, in a "typical" evicting-cuckoo fashion. Unlike other evicting cuckoos, shining cuckoos are late evicters, being 1-5 (Jensen & Jensen, 1969) to 3-7 (Gill, 1983) days old at eviction. European cuckoos, for example, show eviction behaviour when less than 2 days old (Wyllie, 1981). Consequently, shining cuckoos often co-exist with host chicks for several days after hatching, allowing warbler parents to compare both types of chicks. Also, the selective advantage of early rejection is particularly high in this case: Should hosts reject the cuckoo before eviction, they would save all their young (unlike non-evicting cuckoos, which gradually outcompete host young one by one, and unlike early-evicting cuckoos, which destroy all the host's brood too early). As an exception that confirms the rule, the case of shining

cuckoos also helps illustrating the above ideas. First, the presence of natal down is an ancestral trait in cuckoos (see below). Apparently, all parasitic forms have lost it, except the three shining cuckoos parasitizing *Gerygone* hosts, whose nestlings have natal down. The high variation in nestling colouration within the genus is unusual among cuckoos or other birds and may have facilitated mimicry of host chicks. Thus, like in koels, mimetic traits were especially easy to develop. Second, the three mimetic species are, like the Indian koel, host-specific (e.g. *C. lucidus* in New Zealand but not in Australia). And third, chick mimicry in this system where host and parasite are distantly-related is restricted to the very first stages of nestling development, when developmental constraints are minimal due to morphological similarities. As shining cuckoo chicks do not mimic hosts late in the nestling period, it is difficult to explain mimicry by invoking low misimprinting costs (c.f. Lotem, 1993), unless grey warblers were especially good at discriminating newly-hatched chicks (which seems unlikely).

The hypothesis that mimicry between parasites and their hosts is mainly constrained by their taxonomic affinities is consistent with the observed patterns of host-parasite associations among parasitic ants. Ants can evolve efficient, phenotype-matching recognition based upon olfactory cues and there is evidence of chemical mimicry of host pheromones or cuticular recognition labels in some parasitic species. All brood-parasitic inquiline ants are close phylogenetic relatives of their host species, a fact known as "Emery's rule" (Hölldobler & Wilson, 1991). Although some parasitic species may have originated intraspecifically through sympatric speciation (Bourke & Franks, 1991), many others have arisen from a distinct free-living species, and there are no cases in which parasite and host are known to be distantly related (Hölldobler & Wilson, 1991).

Parasitic cuckoos lack the stiff bristle-like natal down (trichoptiles) of other groups of cuckoos and

also lack the brightly coloured palatal papillae found inside the nestling's mouth in these groups (Payne, 1977a). These two traits are absent in parasitic species of the families Cuculidae and Neomorphidae, but present in their non-parasitic members, as well as in other entirely non-parasitic families (according to the classification and phylogeny by Sibley & Ahlquist, 1990; Sibley & Monroe, 1990). Young passerine hosts lack the bristle-like down and have unicolored mouths, suggesting that parasitic cuckoos have lost some conspicuous juvenal traits over evolutionary time. Rudiments of trichoptiles can be found in newly-hatched chicks of some parasitic cuckoos (e.g. *Cuculus micropterus*, Neufeldt, 1966). In an experiment in which we glued white bristle-like feathers to the head and back of newly-hatched magpie chicks, parents always removed the feathers within a few hours, sometimes causing injuries to the chicks in the process. In some parasitic cuckoos, the colouration of the nestling's gape is very similar to that of their major host's chicks (e.g. *Chrysococcyx cupreus*, Swynnerton, 1916). Chicks of the evicting striped cuckoo *Tapera naevia* may show polymorphism in palate and gape colouration, mimicking different hosts in different populations. Chicks from Surinam have bright orange mouths like *Synallaxis* hosts, while those from Panama have it yellow like *Thryothorus* hosts. At least in Panamanian birds, the similarity disappears after independence, the palate becoming red and the gape whitish (Haverschmidt, 1961; Morton & Farabaugh, 1979).

In addition, it has been repeatedly reported that cuckoos, and perhaps honeyguides too, have begging calls which resemble those of their hosts (table V). When about half-grown, great spotted cuckoo chicks showed different begging calls depending on the host species, mimicking both the spectral features and the duration of the calls of their two major European hosts (Redondo & Arias de Reyna, 1988a) (fig. 6). It is remarkable that other species of parasitic cuckoos with evicting nestlings, whose young are raised alone, also show begging

TABLE V. A survey of brood parasitic species with vocal mimicry of host young.
[Especies de parásitos con mimetismo vocal de las crías del hospedador.]

Species	Evicting young	Reared with host young	References
<i>Indicator indicator</i>	+	Never	Jubb, 1966; Fry, 1974
<i>Oxylophus jacobinus</i>	-	1	Fry et al., 1988
<i>Oxylophus levaillantii</i> ²	-	Seldom	Mundy, 1973
<i>Clamator glandarius</i> ²	-	1	Redondo & Arias de Reyna, 1988
<i>Cuculus solitarius</i>	+	Never	Reed, 1968
<i>Cuculus micropterus</i>	+	Never	Becking, 1981
<i>Cuculus pallidus</i>	+	Never	Courtney, 1967
<i>Chrysococcyx lucidus</i> ²	+	Never	McLean & Waas, 1987
<i>Chrysococcyx basalis</i> ²	+	Never	Courtney, 1967; Payne & Payne, 1994
<i>Chrysococcyx caprius</i>	+	Never	Reed, 1968
<i>Eudynamys scolopacea</i>	-	Seldom	Mundy, 1973
<i>Eudynamys taitensis</i> ²	+	Never	McLean & Waas, 1987
<i>Scythrops novaehollandiae</i>	-	Seldom	Courtney, 1967
<i>Vidua</i> spp. ²	-	Often	Nicolai, 1964
<i>Molothrus rufoaxillaris</i> ²	-	Often	Fraga, 1986

1 Variable according to host size. Evidence of mimicry for small hosts where parasitic and host young are seldom reared together has been reported at least for *C. glandarius*.

2 Supported by sonographic evidence

calls which closely resemble those of their hosts (Courtney, 1967; McLean & Waas, 1987). Although passerines and other non-parasitic altricial birds may show some convergence in begging call structure (Redondo & Arias de Reyna, 1988b), such similarities are much less striking (e.g. Popp & Ficken, 1991), suggesting that any apparent mimicry found in cuckoo calls is true mimicry (McLean & Griffin, 1991). Two evicting cuckoos (*Eudynamys taitensis* and *Chrysococcyx lucidus*) have a much larger body mass (126 and 23 g, respectively) than their hosts (18 and 6.5 g) but their mimetic begging calls have a frequency equal or higher than the hosts' calls (McLean & Waas, 1987), i.e. much higher than expected according to their size, since call frequency and body mass are negatively correlated (Redondo & Arias de Reyna, 1988b; McLean & Griffin, 1991; Popp & Ficken, 1991). Fledglings of the glossy cuckoo *Chrysococcyx basalis*, an evicting species, have distinctive begging calls which mimic at least three

of their major Australian hosts (Payne & Payne, 1994). Differences between calls of the same cuckoo using different host species suggest the possibility of the existence of begging-call races comparable to the *gentes* of egg colour and pattern in other cuckoo species.

Loving the alien: exploitation of host chick-feeding rules

I have suggested that some non-mimetic parasites may prevent rejection, in spite of the host ability to recognize them, by exaggerating those traits favoured by hosts to care for their own chicks in the absence of parasitism (Redondo, in Huntingford, 1993). Caring for a chick and rejecting it are mutually exclusive activities: A parent bird must either feed a chick or refuse to feed it. However, efficient chick care often requires finer

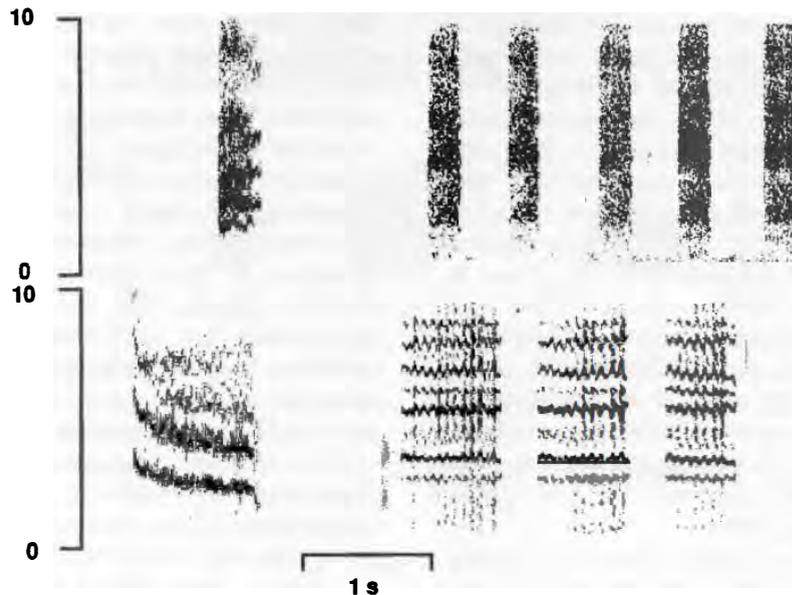


FIGURE 6. Vocal mimicry of hosts by great spotted cuckoo chicks. Sonagrams (150-Hz band-pass filter) of a host chick's begging call during the last third of the nestling period (left) and of fragments of a begging-call series (real time) of a fully-grown cuckoo nestling raised by each host species (right). Above: carrion crow hosts (Guadix, Granada). Below: magpie hosts (Guadix, Granada). There are significant differences in call duration between cuckoos raised by different hosts (repeated-measures one-way ANOVA, $p < 0.05$), but not between cuckoos and their hosts or between same-host cuckoos (repeated-measures two-way ANOVA).

[Mimetismo vocal en pollos de críalo. Izquierda: llamadas de petición de alimento de pollos del hospedador. Derecha: fragmentos de llamadas de petición de alimento de pollos de críalo en nidos de corneja negra (arriba) y urraca (abajo).]

adjustments of parental expenditure than just all-or-none discrete responses. Variations in the intensity of chick begging are accompanied by congruent changes in parental provisioning rate or the amount of food delivered to individual nestlings (Henderson, 1975; Hussell, 1988; Stamps et al., 1989; Smith & Montgomerie, 1991; Redondo & Castro, 1992a). In order to respond to gradual variations in offspring need or quality, decision-making mechanisms involved in parental care must allow parents to show varying degrees of willingness to provide care. In a state-space model of motivation (McFarland & Houston, 1981), *Disfavouring* a chick and

Favouring it can be seen as end-point states within a continuous motivational space, with many possible intermediate states in between. By providing hosts with strong stimuli that trigger intense parental responses, non-mimetic parasites may promote a shift in the host motivational state, driving it away from the *Disfavouring* (Rejection) endpoint towards some intermediate state where parents are willing to care for the chick (fig. 7).

Several studies have shown that food allocation among nestlings in multiple broods of altricial birds is by no means indiscriminate. Parents distribute food differentially on the basis of nestling begging

behaviour and position relative to the parent's body. This allows ample opportunities for nestlings to compete with siblings by begging and jockeying for a favourable position (Smith & Montgomerie, 1991; McRae et al., 1993). In asynchronously-hatched broods, these rules often result in large (old) nestlings being favoured over smaller ones (Ricklefs, 1965; Hussell, 1972; Teather, 1992; but see Stamps et al., 1985), particularly when food is scarce (Rydén & Bengtsson, 1980; Bengtsson & Rydén, 1981, 1983; Gottlander, 1987). In this way, parents may expend their resources optimally by allocating more food to the offspring with greater fitness returns, i.e. the more vigorous nestlings and the nestlings with greater nutritional requirements, if size and begging effort are reliably related to chick need (Harper, 1986; Godfray, 1991) or quality (Grafen, 1990; Haig, 1990).

Magpies, for example, have an existing behavioural rule by which they preferentially feed the hungrier and larger chicks in a brood. During the

first half of the nestling period, magpie chicks are fairly honest when soliciting food from their parents, showing different intensities of their begging display which are reliably related to their nutritional need (Redondo & Castro, 1992a). The reliability of this signalling system is likely to be maintained by excess predation and energetic costs associated to the higher begging levels, as well as by parents exerting considerable control over food allocation at these ages (Redondo & Castro, 1992a,b). During this period, nestlings grow exponentially (i.e. daily mass gain increases with increasing body mass), so that larger chicks need proportionately more food (Castro, 1993). Magpie nestlings hatch asynchronously: Last chicks hatch 1.6 days later, on average, than first-hatched chicks. Asynchronous hatching determines the establishment of size asymmetries among nestlings which cause the death of the lightest chicks due to starvation in about 43% of nests. Chick size at fledging is positively related to juvenile survival

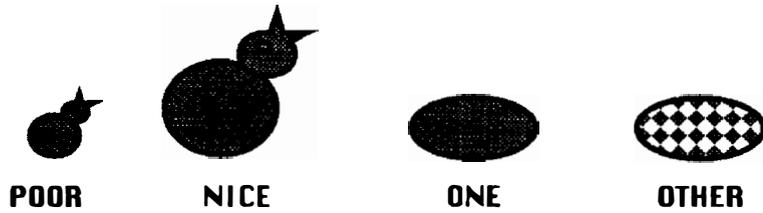
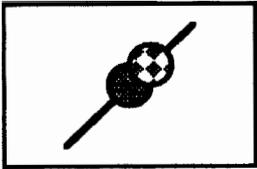
FIGURE 7. A simple graphical illustration of the signal-dependent motivational interference (or "Exploitation of host's chick-feeding rules by a charming parasite") argument. In the absence of parasitism, hosts have an existing motivational discrimination mechanism (Upper) that links parental behaviour to offspring stimuli, making them more willing to favour a chick with a higher perceived level of need or quality, in order to optimally allocate their parental expenditure. In addition, some hosts may be able to distinguish between different chick signatures. If this last recognition mechanism becomes linked to the parental-discrimination mechanism, some mutations may appear that employ different signal-interpretation strategies for different signatures (Middle). Rejecter hosts, capable of discriminating against certain types of chicks which are recognized as alien, evolve rejection rules (neglect a target chick) from pre-existing mechanisms. Rejecters refuse to care for target chicks with a given perceived degree of need and quality while non-alien chicks of similar characteristics are adequately cared for (Middle). Parasitic chicks with more intensive pre-existing signals obtain additional benefits in the form of extra parental resources. In response to discrimination, parasitic chicks that are constrained to evolve adaptations for preventing recognition (e.g. to become mimetic) exaggerate their level of advertisement in order to compensate for their odd signatures, becoming "Charming Aliens". When the degree of signal exaggeration is sufficiently high, the parental-discrimination mechanism may interfere with rejection rules to the point of suppressing them, hence making hosts to care, or even favour, the parasitic chick.

[En ausencia de parasitismo, los hospedadores poseen mecanismos de discriminación que les permiten cuidar más a los pollos con unos mayores requerimientos o un mayor valor reproductivo, y a la vez pueden ser capaces de distinguir diferentes caracteres identificadores (Arriba). Un mutante rechazador, capaz de distinguir entre los caracteres de pollos propios y extraños y de emplear en consecuencia reglas diferentes de discriminación, cuidará menos de un pollo extraño que de uno propio de similares características (Centro). A su vez, los parásitos emiten señales intensas capaces de monopolizar el cuidado parental. Para compensar su desventaja, los parásitos serán seleccionados para exagerar las señales empleadas por el hospedador para discriminar. Cuando el grado de exageración es suficientemente alto, el mecanismo de discriminación parental interferirá con las reglas de rechazo, y el parásito será cuidado o incluso preferido por el hospedador en lugar de sus propias crías.]

DISCRIMINATION

RECOGNITION

Amount of care



Chick need-quality

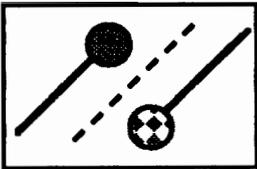
Probability of rejection



REJECTION

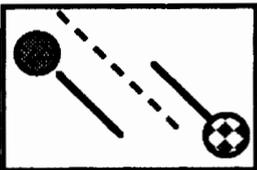
Amount of care

Amount of care



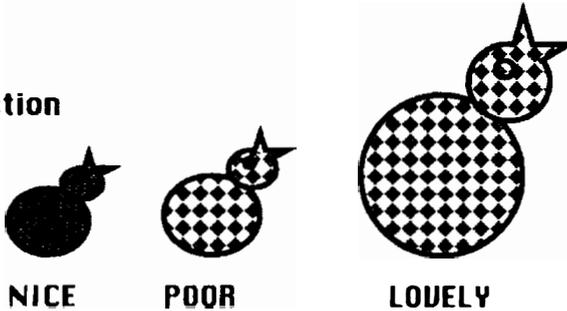
Chick need-quality

Probability of Rejection



MANIPULATION

Chick need-quality



during their first winter (Castro, 1993), which in turn is highly correlated with survival at first breeding (Birkhead, 1991). Consequently, body size in magpies is a powerful indicator of chick quality.

Redondo & Castro (1992a) showed experimentally that magpie parents feed more the chicks with a more intense begging behaviour. In magpies, as well as other birds, smaller nestlings tend to beg more than larger ones. Chick size and begging intensity showed a negative intra-brood correlation in 28 out of 34 nests (Binomial test, $p < 0.01$). In spite of this, chick size and parental feeding were positively correlated in 20 out of 30 natural broods (Binomial test, $p = 0.09$), suggesting that parents also favoured the heavier nestlings in a brood. These two rules showed an interesting interaction: Magpie parents were especially sensitive to the begging behaviour of the heavier chicks in a brood. In another experiment in which we manipulated the food intake of chicks according to their relative size, we obtained that magpie parents clearly favoured the larger chicks when they were the hungrier. However, when the smaller nestlings were the hungrier, all chicks tended to obtain an equal share of the food (fig. 8). Honest begging ensures that larger chicks refrain from begging intensively after being fed (Redondo & Castro, 1992a), allowing access to food to their smaller siblings except when food is scarce.

When a specialized brood parasite like the great spotted cuckoo invades this stable system of parent-offspring relationships, it can selfishly distort it in its own favour. Great spotted cuckoos severely depress the nesting success of magpies. Apart from egg-destruction by female cuckoos (Brooker & Brooker, 1991), the major cause of host mortality in parasitized nests is nestling starvation, typically at an early age (Soler & Soler, 1991) (fig. 9). Field observations at naturally-parasitized nests revealed that very young cuckoos were not aggressive towards host chicks: By and large, the early demise of magpie nestlings was a consequence of cuckoos monopolizing the incoming food, then precipitating

the death of their emaciated nestmates by trampling and crowding them (Alvarez & Arias de Reyna, 1974). The few surviving magpie chicks usually suffered from retarded growth and fledged with a low body mass (Soler & Soler, 1991), thus contributing little, if any, to hosts' reproductive success. We have shown that magpie parents can discriminate between chicks according to size and begging behaviour from an early age. Why do they permit the cuckoo to grow up in their nest, kill their own young, and become familiar to parents prior to fledging, fooling them into accepting and feeding it during another two months after leaving the nest?

Apparently, magpie parents favoured the cuckoo chick because of its larger relative size and more intense begging behaviour (Alvarez & Arias de Reyna, 1974). This could be evidence of parasites having effective signals for eliciting preferential care by hosts. However, many confounding factors suggested alternative explanations for this possibility. Cuckoos hatch earlier than magpie chicks, hence their more intense begging behaviour might be a side-effect of their older age, since nestlings across many species beg more as they get older (Harper, 1986; Redondo & Exposito, 1990). Also, cuckoos may have higher food requirements because of their larger relative size, faster growth rate (Soler & Soler, 1991), or lower-quality diet (Brooke & Davies, 1989). Cuckoo chicks have a distinctive gape colouration, being paler and with more conspicuous spurred palatal papillae than magpie chicks (Valverde, 1971). Within a brood, magpie nestlings usually outnumber cuckoo nestlings, and a distinctive nestling that is in the minority might receive more food if parents alternated the type of nestling fed on each visit to the nest (Rothstein, 1978b). Lastly, a cuckoo that is distinct from the magpie's nestlings and that is in the minority might provide a stronger stimulus than magpie chicks because of habituation (Rothstein, 1978b).

Great spotted cuckoo chicks hatch after 15 days of incubation (Frisch, 1969), ca. 3 days earlier than

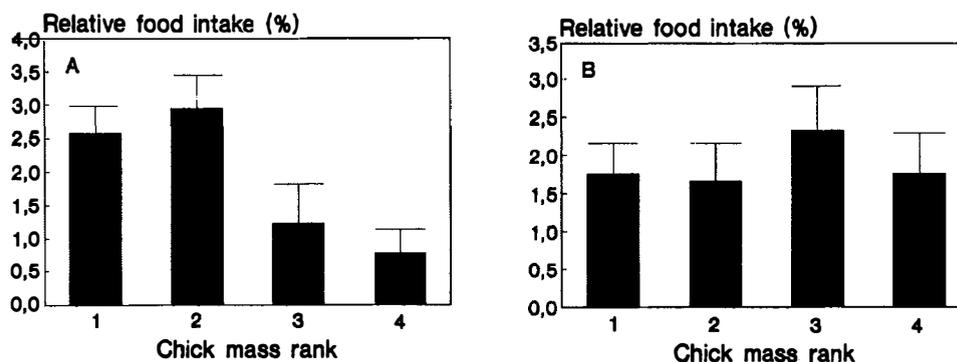


FIGURE 8. Distribution of food by magpie parents according to chick hunger and relative size. In 32 natural, asynchronously-hatched magpie broods containing 4 and 5 chicks, we artificially fed either the two heaviest or lightest chicks 1-3 g of boiled egg to enlarge prior differences in chick begging intensity. We measured chick body mass and returned to the nest 1 h later in order to record the Relative Food Intake RFI of each nestling (mass increments expressed as percentage of initial body mass). Shown are mean (\pm SE) values of RFI by the four nestlings with the more extreme mass ranks (1=heaviest chicks). The largest nestlings were at least 10% larger than their smallest sibs. A: When the two largest chicks were the hungriest; B: when the two smallest chicks were the hungriest. Neither parents nor chicks were tested more than once for either treatment (Doñaña, Huelva, 1989-1990). Tests where parents failed to feed were excluded. Differences between (but not within) heavier and lighter chicks in A are significant (Wilcoxon test, $p < 0.001$) but not in B.

[Distribución desigual del alimento dentro de 32 nidos de urraca con pollos de desigual tamaño. Cuando se incrementó de forma experimental el hambre de los dos pollos mayores (1 y 2), los padres los cebaron más durante la hora siguiente. Cuando, en los mismos nidos, se incrementó el hambre de los pollos pequeños (3 y 4), los padres los cebaron a todos por igual. Los valores de ingesta relativa representados (\pm SE) se expresan como porcentaje del peso inicial del pollo.]

magpie chicks. Early growth of the parasite young is also more rapid than in magpie chicks (Soler & Soler, 1991). Consequently, by the time all nestlings are present in the nest, the cuckoo has become the largest chick in the brood. The initial discrepancy in size between the cuckoo and magpie chicks is much larger than the usual post-hatching size asymmetry caused by asynchronous hatching in non-parasitized nests (heaviest:lightest average mass ratio, 1.6:1). In fact, size differences between cuckoo and magpie chicks approach the maximum values of

asymmetry observed just prior to brood reduction, when mass differences between heaviest and lightest chicks are highest (3:1) (Castro, 1993).

Laboratory experiments conducted with magpie and great spotted cuckoo chicks of a similar developmental stage (i.e. at the point of maximum growth, 8 and 11 days post-hatching for cuckoos and magpies, respectively) kept in isolation (without nestmates) under controlled conditions of food supply demonstrated that cuckoo chicks have an exaggerated, dishonest begging behaviour. For a

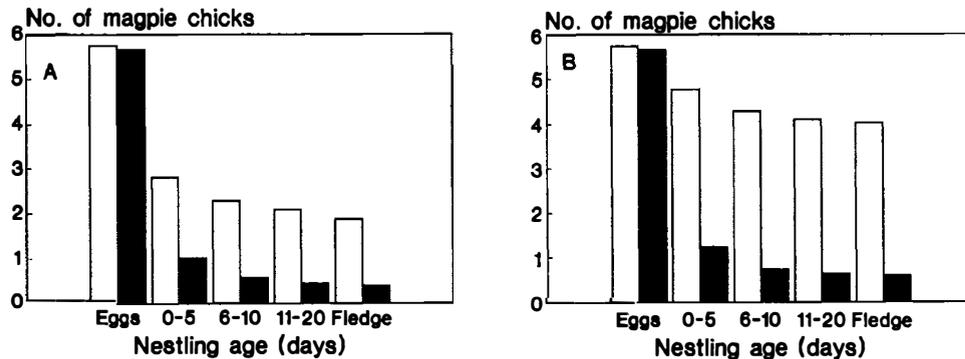


FIGURE 9. Variations in the number of magpie propagules (fully-incubated eggs or chicks) during the nesting cycle in unparasitized magpie nests (open bars) and those parasitized by great spotted cuckoos (filled bars). A: total, considering both within- (mostly starvation) and whole-brood losses (i.e. mostly nest destruction by predators, perhaps including cuckoos, or humans). B: excluding whole-brood losses.

[Número de huevos y pollos de urraca en diferentes momentos del ciclo de cría en nidos no parasitados (barras claras) y en nidos parasitados por el criollo (barras oscuras). A: total, considerando pérdidas totales y parciales de nidos. B: excluyendo pérdidas totales.]

similar degree of need, cuckoos begged for much longer and emitted more calls, both in absolute terms and per unit time, than magpies (table VI). Nutritional need, measured as time since the last feeding, predictably affected the duration of begging bouts, the calling rate and the total number of begging calls emitted by magpie chicks, while cuckoos showed no predictable variation in any of these parameters. Contrary to magpies, no cuckoo chick failed to beg when first stimulated, even if recently fed. When I, as a generous parent, provided food to chicks on demand, magpie chicks usually stopped begging after receiving a few meals. Cuckoos, on the contrary, kept on begging after I fed them many times in succession. Since my protocol involved feeding chicks in response to begging (i.e. gaping and making begging movements and/or calls), cuckoo nestlings were

often fed without completely swallowing the food (magpies seldom begged again before swallowing the previous meal). Some cuckoos, their mouth brimful with food, consistently threw away the food after being fed, just to beg for food again! So I had to use different satiation criteria for the two species: Failing to beg in magpies; and stopping to beg or, more frequently, failing to swallow two consecutive meals, or throwing away the food, in cuckoos.

As a consequence of dishonest begging, cuckoo chicks consumed enormous cumulative amounts of food when fed ad libitum (table VI). Cuckoos, of course, did not assimilate all this food at the same rate they ingested it (otherwise they should have grown at more than twice the maximum rate recorded in field studies); instead, and unlike magpies, cuckoos stored food. Radiological inspection of the chicks' alimentary canal, the

TABLE VI. Begging behaviour in relation to nutritional need and food consumption by cuckoo and magpie nestlings¹. Shown are means and SE (in brackets)

[Comportamiento de sollicitación e ingesta de alimento en pollos de urraca y críalo para diferentes tiempos de ayuno inducidos experimentalmente. Medias y ET en paréntesis.]

	Time since the last feeding (h) ²				P ⁵
	0.5	1.0	2.5		
Magpies:					
Duration of Begging Bouts(s) ³	21.80 (2.37)	19.80 (1.51)	26.80 (1.94)		<0.001
Time Calling (s)	5.50 (0.55)	8.10 (0.83)	9.60 (0.99)		<0.001
Number of Begging Calls per bout	9.50 (1.33)	12.80 (0.36)	16.00 (1.20)		<0.001
Begging Rate (calls/s)	0.43 (0.05)	0.67 (0.04)	0.60 (0.03)		<0.001
Cumulative Absolute Food Intake over 14 h (g)	40.40 (1.68)				
Cumulative Relative Food Intake ⁴ over 14 h as % of body mass	40.80 (1.10)				
Chick Body Mass (g)	106.00 (2.85)				
Cuckoos:					
Duration of Begging Bouts(s) ³	68.00 (9.67)	99.60 (17.08)	79.20 (9.56)		NS
Time Calling (s)	34.90 (6.17)	46.70 (10.28)	35.20 (5.42)		NS
Number of Begging Calls per bout	114.30 (18.70)	169.30 (40.50)	139.30 (22.10)		NS
Begging Rate (calls/s)	1.65 (0.09)	1.64 (0.18)	1.71 (0.11)		NS
Cumulative Absolute Food Intake over 14 h (g)	43.10 (1.12)				
Cumulative Relative Food Intake ⁴ over 14 h as % of body mass	62.00 (2.50)				
Chick Body Mass (g)	66.20 (3.95)				

1 Chicks were collected near dusk the day before and not fed until the next morning. They were kept in individual nest boxes at the laboratory at 27 °C. The feeding schedule involved transporting each chick inside its box into a feeding chamber containing a stuffed adult magpie and a black glove that could be manipulated from behind a screen, and the recording equipment. Chicks were stimulated to beg by moving the stuffed magpie and a hand inside the black glove holding a forceps to deliver the food. Nestlings were allowed to ingest ad lib amounts of food (minced beef heart muscle) once every h during 14 h of daylight. The next morning (ca. 36 h after they were collected), they were returned back to their nest.

2 The degree of food deprivation was manipulated by modifying the above regular schedule with two short (0.5 h) and two long (2.5 h) intervals between feedings at randomly established times of the day.

3 Begging behaviour was recorded during the four feeding sessions following short and long deprivation intervals plus two 1-h interval sessions randomly chosen from the regular feeding schedule. See fig. 12 for methods.

4 The amount of food consumed in each feeding session was measured by weighing food before and after feeding in a precision (0.01 g) balance. Differences in RFI (see fig. 8) between cuckoos and magpies are significant (Mann-Whitney test, P<0.001) for relative but not for absolute food intake.

5 P, minimum tail probabilities in the comparison between levels of food deprivation within species (Wilcoxon test). For all measures, cuckoos differ significantly from magpies at any level of food deprivation (Mann-Whitney test, p<0.05).



FIGURE 10. Radiography of a magpie (left) and a great spotted cuckoo chick (right) obtained by Computerised Axial Tomography after 24 h of ingesting food ad libitum in the laboratory. Chicks were given a contrasting powder (barium sulphate) 12 h and just before inspection, some traces of the former can be seen as clear areas at the bottom of the cuckoo's body cavity (the latter is visible in the mouth cavity). Note the larger volume occupied by the intestine (the deep black area at the very bottom of the body) in the cuckoo chick, despite its smaller size.

[Radiografía TAC de un pollo de urraca (izquierda) y uno de crfalo (derecha) tomada 24 h después de ser alimentados ad libitum en el laboratorio. 12 h antes, se suministró a los pollos una sustancia de contraste de la que pueden apreciarse trazas en forma de zonas claras al fondo de la cavidad corporal del crfalo. Nótese el mayor volumen, en proporción, del aparato digestivo del crfalo.]

morning after the day when they were allowed to ingest food ad libitum, revealed that cuckoos had a comparatively larger volume of food in their guts (fig. 10). Further direct observations of a few dissected nestlings of a similar age showed that cuckoos differed from magpies in having a relatively larger (about twice, in percentage of lean mass) oesophagus and gizzard. However, the liver and the absorbing intestine were similar in both species, suggesting that cuckoos differed from magpies mainly in their capacity to secure, rather than assimilate, the food. Calorimetric analyses of faeces in 8-d cuckoo and 11-d magpie chicks fed on the same laboratory diet during a 24-h cycle, confirmed that both species had virtually the same assimilation efficiency.

Field experiments demonstrated that magpie parents given a choice between a cuckoo and a magpie chick actually favoured the cuckoo. We removed all nestlings from magpie broods 3 to 8

days old and replaced them with one nestling of each species of about the same age in different size combinations. A control experiment was performed with two magpie nestlings under the same conditions. Results showed that, consistent with previous findings, the heavier magpie chick in controls was preferentially fed when the asymmetry in nestling body mass exceeded a threshold value (fig. 11). Cuckoos, on the contrary, were preferentially fed independently of their relative size. When smallest, they did better than a comparable magpie chick by never being consistently disfavoured. Cuckoo chicks were clearly preferred over magpie chicks when they were the heavier chick, as in naturally-parasitized broods; the larger the mass asymmetry in favour of the cuckoo, the larger its food share (fig. 11). Such host rules exploited by parasites are probably adaptive and thus may be resistant to modification without incurring a cost. For example, favouring large and hungry

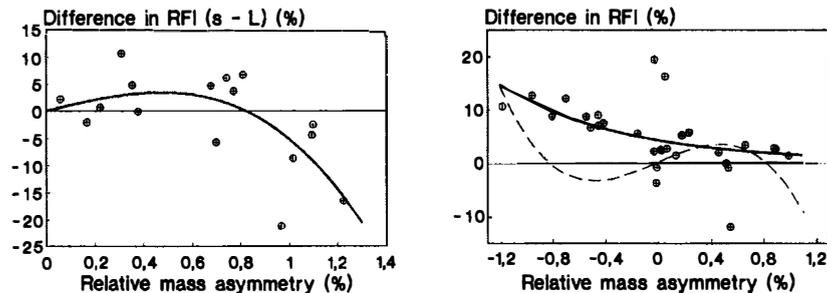


FIGURE 11. Choice experiments by magpie parents between a cuckoo and a magpie chick (right) and between two control magpie chicks of different relative sizes (left) plotted against the difference in body mass between both. Shown are differences between the RFI of the two chicks in experimental broods containing one chick of each type 2-6 days old (right: cuckoo minus magpie; left: small magpie chick minus large magpie chick). Values of relative mass asymmetry in abscissa are the difference in body mass between chicks (right: magpie minus cuckoo; left: larger minus smaller) divided by their average mass. This variable controls for existing biases in RFI caused by variations in absolute body mass. LEFT: In the magpie test, the data points were fitted to a non-linear polynomial regression model (ANOVA, $p < 0.01$) subject to the following realistic restrictions: $y = 0$ when $x = 0$ (equal chicks are fed the same); if so, y must be positive for small values of x (because parents must be allowed to feed both chicks equal absolute amounts of food, hence larger RFI for smaller chicks, but y is continuous, so that this must occur for x near zero). Actually, when chicks were similar in size, parents fed them equally but neglected the smaller chick when size differences exceeded some threshold x value (roughly equal to one, which means that the large chick is 3 times as large as the smaller one). RIGHT: The non-linear regression curve in the magpie test is shown as a dashed curve in the cuckoo test for comparison. In the cuckoo test, the data fitted to a non-restricted negative exponential model (ANOVA, $p < 0.01$) better than to a linear one. When cuckoos are smaller than magpies, they are equivalent to the smaller magpie chick in controls and x are positive like in the magpie test. When cuckoos were larger or equal than magpies, parents always favoured them, but both chicks were fed equally when cuckoos were much smaller than magpies. Overall, cuckoos had higher RFI than magpies in 86% of tests, irrespective of their relative size (Wilcoxon, $p < 0.001$). There are no differences depending on whether magpie parents were caring for magpie, cuckoo chicks, or both prior to test (one-way Analysis of Covariance, $p > 0.2$). Abscissa values outside the range shown in both figures are unrealistic under natural field conditions (so it does not matter if model curves approach infinitum when $|x| \gg 0$). There were no overall differences in the initial mass of cuckoos ($24.2 \text{ g} \pm 2.4 \text{ SE}$) and magpies ($26.8 \text{ g} \pm 3.7 \text{ SE}$) in the cuckoo-magpie test (Wilcoxon test, $p > 0.5$, $N = 29$ broods). The initial mass of cuckoos in those tests where the cuckoo was the larger chick ($35.4 \text{ g} \pm 5.4 \text{ SE}$, $N = 17$) did not differ from that of the larger magpie chick in controls ($29.6 \text{ g} \pm 2.9 \text{ SE}$, $N = 16$) (Mann-Whitney test, $p > 0.6$). The initial mass of cuckoos in those tests where the cuckoo was the smaller chick ($14.6 \text{ g} \pm 1.8 \text{ SE}$, $N = 12$) did not differ from that of the smaller magpie chick in controls ($14.1 \text{ g} \pm 1.2 \text{ SE}$, $N = 16$) ($p > 0.9$). See fig. 8 for definitions and further field protocols. Data from Santa Fe, Granada, 1990-1991.

[Elección por parte de padres de urraca entre un pollo de urraca y uno de críalo (derecha) o dos de urraca (izquierda) de diferente tamaño de 2 a 6 días de edad. Se muestran las diferencias en ingesta relativa (críalo menos urraca y urraca pequeña menos urraca mayor) en relación con la asimetría relativa de tamaño, calculada como la diferencia entre masas (urraca-críalo o mayor-pequeña) dividida entre la masa media. Los datos se ajustan a un modelo de regresión no lineal. El modelo para el experimento control aparece en línea punteada en el gráfico de la derecha. Cuando la diferencia de tamaño sobrepasa un cierto límite, la urraca pequeña no es cebada. El críalo no es discriminado en iguales circunstancias y resulta claramente favorecido cuando es el mayor de los dos.]

chicks may not only help magpie parents to fulfil their nestlings' demands but also may be important in facilitating adaptive brood reduction (i.e. disfavouring small, late-hatched chicks until they starve to death). Husby (1986) obtained experimental evidence that facultative brood reduction is adaptive for magpie parents. Evidence from other species suggests that male parents may be more sensitive to begging behaviour, and to feed large nestlings more than smaller ones, than female parents (Bengtsson & Rydén, 1981; Stamps et al., 1985; Gottlander, 1987). In such cases, cuckoos may exploit fathers' rules more easily than mothers' rules. Interestingly, Neufeldt (1966) found that shrike *Lanius cristatus* mothers did not feed, or fed their nestling Indian cuckoo *Cuculus micropterus* much less than their mates. Like chicks of other species (e.g. Stamps et al., 1985), cuckoos were sensitive to parental differences in begging rewards, begging more from fathers already from an early age.

Our study with great spotted cuckoos and magpies seems to support the HEH: Parasites have evolved adaptations which exaggerate those traits favoured by hosts to care for their own chicks in the absence of parasitism, thus receiving preferential care. Clearly, great spotted cuckoos cheat magpie parents by means of dishonest begging signals, as predicted by recent models of signalling between non relatives (Johnstone & Grafen, 1993). Intense begging in such cases must be beneficial because, apart from the energetic cost it might entail, begging attracts predators to magpie nests (Redondo & Castro, 1992b). Exaggerated begging could benefit cuckoos for reasons other than prevention of chick rejection by magpies. For example, like other traits (e.g. a larger gizzard), dishonest begging may just help cuckoos to outcompete magpie chicks. However, this idea fails to explain why dishonest begging is independent of the presence of magpie chicks in the nest, as in the above laboratory experiment. Actually, cuckoos beg more intensively late in the nestling period, often when magpie

chicks are less numerous or long after they are dead. In addition, no begging model based on intra-brood competition, whether between sibs or brood parasites (Harper, 1986; Motro, 1989), predicts that chicks will waste the food, even when it is plentiful (Godfray, pers. comm.).

Exaggerated begging is widespread among many different taxa of brood parasites, both in species with evicting and non-evicting chicks. Begging by young paradise whydahs *Vidua paradisaea* is so vigorous that if chicks are artificially placed in the brood of Bengalese finches, only the parasites will be fed, despite B parents can recognize their own chicks (ten Cate, 1982, 1985). However, the usual whydah host, the Melba finch *Pytilia melba*, feeds both parasitic and host chicks. According to Nicolai (1969), Melba finches can recognize the parasite on the basis of slight differences in mouth markings and would reject it if whydah young do not manage to compensate by its more vigorous begging. Paradise whydah and melba finch young differ in the relative size of some mouth markings, and in the colour of skin, natal down and fledgling plumages (Skead, 1975). Apart from begging longer and more intensively, paradise whydah chicks hatch earlier and larger, and grow faster than host young (Nicolai, 1969). This example lends direct support to the HEH: Unlike non-parasitic zebra finches, exaggerated begging in whydah chicks is efficient at preventing rejection (disfavouring) by Bengalese finch parents. In the case of cuckoos, exaggerated begging seems to occur in parasitic species only (table VII). In addition, evicting cuckoos like the European cuckoo, which are reared alone and do not have to compete with host chicks, have long, repetitive and stereotyped begging calls like those of great spotted cuckoos (fig. 12, table VII). All over the world, field observers have been impressed by the intensive begging of fledgling cuckoos. An example which I particularly like is Skead's (1952) description of begging by the Diederik cuckoo *Chrysococcyx caprius*: "As soon as it leaves the nest, the hunger calls become insistent, persistent

TABLE VII. A survey of parasitic species and non-parasitic cuckoos according to their chick begging calls. [Llamadas de petición de alimento en especies parásitas y en cucos no parásitos.]

Species	Description of begging calls	References
Non parasitic cuckoos:		
<i>Coccyzus americanus</i>	low buzz	Bent, 1940; Potter, 1980
<i>Coccyzus pumilus</i>	low	Ralph, 1975
<i>Geococcyx californianus</i>	soft buzz	Bent, 1940
Parasitic species:		
<i>Indicator indicator</i>	intensive ¹	Fry et al., 1988
<i>Oxylophus jacobinus</i>	"	Gaston, 1976
<i>Oxylophus leuallantii</i>	"	Steyn & Howells, 1975
<i>Clamator glandarius</i> ²	"	this paper
<i>Pachyococcyx audeberti</i>	"	J. Fanshawe, pers. comm.
<i>Cuculus vagans</i>	"	Cranbrook & Wells, 1981
<i>Cuculus solitarius</i>	"	Reed, 1969
<i>Cuculus clamosus</i>	"	Reed, 1968
<i>Cuculus micropterus</i>	"	Neufeldt, 1966
<i>Cuculus canorus</i> ²	"	this paper
<i>Cuculus pallidus</i>	"	Kikkawa & Dwyer, 1962
<i>Chrysococcyx lucidus</i> ²	"	Gill, 1982a
<i>Chrysococcyx basalis</i>	"	Courtney, 1967
<i>Chrysococcyx klaas</i>	"	Skead, 1952
<i>Chrysococcyx caprius</i>	"	Reed, 1968
<i>Surniculus lugubris</i>	"	Cranbrook & Wells, 1981
<i>Eudynamis scolopacea</i>	"	Lamba, 1963
<i>Eudynamis taitensis</i> ²	"	McLean & Waas, 1987
<i>Tapera naevia</i>	"	Haverschmidt, 1961
<i>Vidua paradisaea</i>	"	Nicolai, 1969
<i>Molothrus aeneus</i>	"	Carter, 1986
<i>Molothrus bonariensis</i> ²	"	Gochfeld, 1979; Fraga, 1985
<i>Molothrus ater</i> ²	"	Broughton et al., 1987

¹ Intensive, conspicuous begging calls. When not explicitly stated, the call's verbal description includes at least one of the following adjectives: endless, exaggerated, insistent, loud, persistent, repetitive or vigorous.

² Supported by sonographic evidence.

and perpetual". *Cuculus* chicks also have a constant high level of food motivation (Khayutin et al., 1982; own observations), suggesting the possibility of dishonest begging. Ian Wyllie (1981) wrote: "Even when just fed the young cuckoo continues to gape and call for more food". The loud and persistent begging calls of European cuckoo nestlings easily

reveal their location to human observers, and attract other birds in the neighbourhood to the nest (Wyllie, 1981), so they probably attract nest predators too (Wyllie, 1981; Brooke & Davies, 1989; see also Gochfeld, 1979). Apparently, the function of exaggerated begging in evicting cuckoos is not to maintain congruently high rates of food

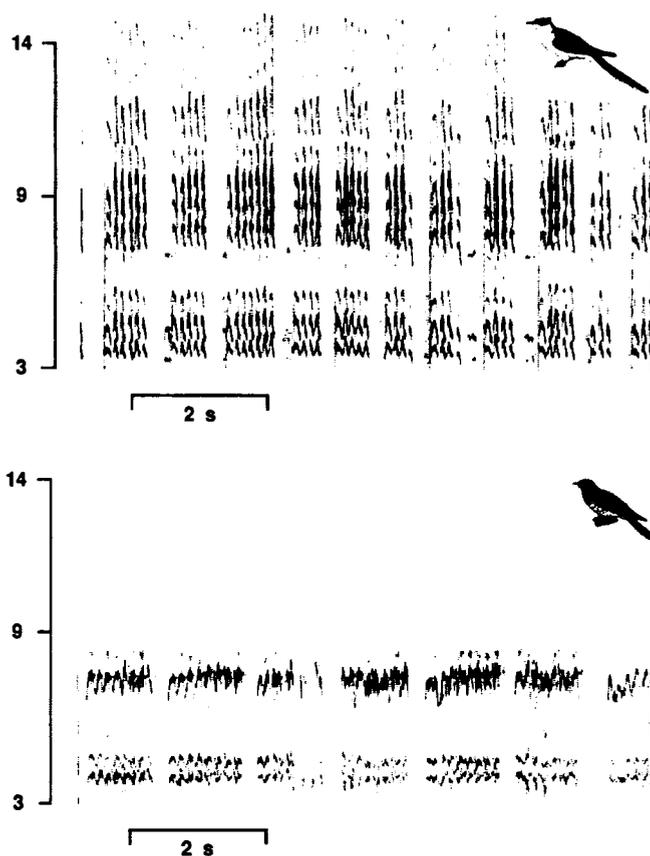


FIGURE 12. Long, repetitive and stereotyped begging calls in parasitic cuckoo chicks. Above: Fragment of a (magpie, Santa Fe, Granada) great spotted cuckoo (8 days old) begging call. Below: Fragment of an (rufous scrub-robin *Cercotrichas galactotes*, Los Palacios, Sevilla) European cuckoo (10 days old). European cuckoo chicks raised by reed warblers (Wicken Fen, Cambridgeshire) gave similar calls. Both chicks were recorded in the laboratory, under similar conditions of food intake (equivalent to 1-h deprivation time in table VI). In both species, older chicks will call at higher rates. Calls were recorded through a condenser microphone AKG 568 EB attached to a Sony WMD6C cassette recorder, and analyzed in a real-time sonagraph KAY 5500 (Kay Elemetrics Corp.) with a transform size of 300 Hz.

[Fragmentos de llamadas de petición de alimento de un pollo de críalo de 8 días criado por urracas (arriba) y de un cuco europeo de 10 días criado por alzacolas (abajo).]

provisioning by foster parents, as shown by studies suggesting equal feeding rates for parasitized and comparable unparasitized broods (see below). According to the HEH, these non-mimetic parasites may require loud begging precisely in order to maintain a standard level of care. Alternatively,

exaggerated begging by evicting parasites like the European cuckoo, which need a much longer period of parental care than a host's brood, may ensure that the hosts do not desert by providing them with a strong stimulus to prolong the period of care (Wyllie, 1981). However, there is little evidence

that the timing of parental care is determined by endogenous factors (e.g. the absolute age of chicks). Parent birds can be experimentally tricked into incubating eggs or feeding chicks for unusually short or long periods simply by replacing nest contents with eggs or chicks in a different stage of development (Emlen, 1941; Holcomb, 1979).

Non-evicting parasites may have, as a rule, more exaggerated begging signals than evicting parasites as a result of more intense selection pressures. While both evicting and non-evicting parasites may benefit from manipulating hosts in order to prevent rejection, (i) only the latter have to compete directly with host young; (ii) hosts may recognize parasites more easily when both types of chicks are present in the nest simultaneously; and (iii) the benefits of early recognition are higher when host young are still present in the nest (Davies & Brooke, 1988). This predicts that non-mimetic and non-evicting parasites will have particularly effective signals at releasing host parental responses. Khayutin et al. (1982) and Brooke & Davies (1989) found that European cuckoo nestlings are not fed at a higher rate than a host brood of equivalent mass, and Gill (1982b) obtained a similar result in grey warblers feeding a shining bronze cuckoo. On the other hand, Woodward (1983) found that eight host species fed fledgling cowbirds *M. ater* more than they fed an equivalent mass of their own young (the opposite never occurred) and concluded that "the loud, persistent calling of fledgling cowbirds [...] is probably their main adaptation for brood parasitism".

The HEH could also provide an explanation for the intriguing phenomenon of fostering. Owen (1912) reported one wren *T. troglodytes*, an occasional host of the European cuckoo, feeding a young cuckoo in a dunnock nest more frequently than it fed its own young in a nearby nest. A parent expending resources in a potential enemy to the detriment of its own young is a remarkable event. However, what makes Owen's observation most unusual is that it involved a still unfledged cuckoo

chick. There are many instances of fledgling parasites (mainly cuckoos) being fed by more than one passerine species, sometimes simultaneously (Ali & Ripley, 1981; Fry et al., 1988; Brooker & Brooker, 1989a), or by hosts other than their actual foster parents (Zuñiga & Redondo, 1992b). Interspecific feeding of fledglings is extremely rare among non-parasitic birds (Shy, 1982) but reports of parasite fledglings being fed by birds other than their foster parents are surprisingly common (table VIII), despite the scarcity of field studies covering the post-fledging period. It is worth mentioning here that a detailed study of the mimetic screaming cowbird *M. rufoaxillaris*, involving many observations of more than 100 individually-marked fledglings, failed to detect any case of fostering (Fraga, pers. comm.). Feeding of the same fledgling by more than one passerine species has been reported for Australian koels (Brooker & Brooker, 1989a) but, to my knowledge, not for Indian birds. Apparently, non-mimetic parasitic chicks are quite charming to parent birds.

It has been sometimes observed in the wild that parent birds preferred to feed a young parasite instead of their own young when they had a choice between both, either because they were caring for a mixed brood after fledging (shiny cowbird *M. bonariensis* and *Icterus dominicensis*, Acosta, 1990; pallid cuckoo *Cuculus pallidus* and hooded robin *Melanodryas cucullata*, Smith, 1989), or because parents caring for their own chicks switched to feeding a young parasite which begged from them nearby (pallid cuckoo and *Petroica goodenovii*, Woodell et al., 1985; European cuckoo and wren, Owen, 1912). Perhaps, like Owen's wren, many cases of fostering where the reproductive status of fosterers was unknown involved favouring fledgling parasites to the detriment (even if momentary) of own young. In fact, most recorded cases of heterospecific adoption of non-parasitic fledglings involved foster parents in breeding condition (Shy, 1982).

Eastzer et al. (1980) tested whether brown-headed

TABLE VIII. Species of brood parasites in which fledglings have been observed to be fed by birds other than their foster parents (excluding adult parasites).

[Especies de parásitos cuyos volantones han sido observados siendo cebados por individuos diferentes de sus padres adoptivos.]

Species	References
<i>Clamator glandarius</i>	Zuñiga & Redondo, 1992b
<i>Cuculus canorus</i>	McBride, 1984
<i>Cuculus pallidus</i>	Brooker & Brooker, 1989a
<i>Cacomantis merulinus</i>	Ali & Ripley, 1981
<i>Cacomantis flabelliformis</i>	Brooker & Brooker, 1989a
<i>Chrysococcyx lucidus</i>	Turbott, 1974
<i>Chrysococcyx basalis</i>	Brooker & Brooker, 1989a
<i>Chrysococcyx caprius</i>	Reed, 1968
<i>Eudynamys cyanocephala</i>	Brooker & Brooker, 1989a
<i>Eudynamys taitensis</i>	McLean, 1988
<i>Molothrus ater</i>	Klein & Rosenberg, 1986

cowbird *M. ater* chicks were preferred over those of several non-parasitic passerines by experimentally parasitizing two common birds: The swallow *Hirundo rustica* and the house sparrow *Passer domesticus* (none of which, incidentally, are common cowbird hosts). They found that no chick species survived to fledging in sparrow nests. When raised by swallows, cowbirds did not survive better than other birds during the nestling stage. However, after leaving the nest, swallows attempted to feed cowbird fledglings much more frequently than other chicks and only cowbirds were actually able to get food from their swallow foster parents. This result is consistent with the HEH: Parasitic chicks have very effective begging signals, particularly at older ages. On the other hand, an experiment with the European cuckoo provided negative results (Davies & Brooke, 1988): Reed warbler parents were given a choice between a cuckoo and one or two warbler nestlings 6-9 days old and they failed to show any clear preference. This experiment, however, involved a small sample (four nests, three of which contained warblers prior to the test) and did not control for

potential confounding factors such as brood size (two tests involved two warblers vs. one cuckoo) or nestling value (warbler chicks fledged at 8-9 days, while cuckoos fledge after 20 days).

Brood-parasitic insects may also have evolved exaggerated signals capable of manipulating the behaviour of their hosts. For example, some dulotic (slave-making) ants have hypertrophied Dufour glands which they use in "propaganda" warfare when raiding a host nest. Such glands release large amounts of pheromones, making hosts to disband, fleeing off the nest, or even to attack each other (Hölldobler & Wilson, 1991). In the parasitic ant *Lassius umbratus*, the founding queen which is about to parasitize a host nest grasps and chews a worker of the host (*L. niger*) and then enters the host nest. There, she is said to become more attractive to the host workers than the original *niger* queen, which finally dies of starvation or is spelled from the nest (Buschinger, 1986). The beetle *Atemeles pubicollis* is a brood parasite of ants. It develops inside the egg chambers of the colony, where the larva begs for food from the workers in a way similar to ant larvae, and also feeds on host eggs and larvae. Hölldobler (in Hölldobler & Wilson, 1991) labelled the food with radioactive isotopes and demonstrated that parasitic larvae were able to obtain proportionately more food from workers than ant larvae, which he attributed to the existence of more effective begging signals in the parasite.

Some misconceptions concealed into egg-shells

In this section I will suggest that deep knowledge of host-parasite adaptations related to eggs, coupled with a fragmentary knowledge of parent-chick relationships, may have obscured our understanding of chick discrimination in avian brood parasitism. Egg and chick discrimination differ from

each other in so many respects that inferences made for chicks under assumptions valid for eggs are suspect of being misleading in many cases.

From the hosts' perceptual point of view, an egg to coevolve with simply consists of a passive, non-living shell showing neither behaviour nor developmental changes. Selection pressures operating at any moment in a bird's life are virtually independent from those operating upon egg-shells. If the colour and pattern of egg-shell pigmentation have any adaptive value within the environment of a host's nest (e.g. protective crypsis), then parasites are selected to mimic them anyway (Harrison, 1968). Moreover, since parasites are free from most parental duties other than egg-production, they are rather unconstrained to vary egg-size in response to host discrimination (Payne, 1973, 1974, 1977b). Unlike egg shells, chicks are not accessory structures but the very bird at an earlier stage of development which has to fit with the many functional requirements of its particular ontogenetic niche (Redondo, 1991). Chick traits are affected by lots of selection pressures operating both at juvenile and adult stages, many of which interact in complex, sometimes conflicting ways. Developmental constraints and adaptive trade-offs make egg-shell traits to be much more evolutionarily labile than chick traits, even behavioural ones; the common, but misleading, belief that behavioural traits evolve at faster rates than morphological characters has not been supported at all (de Queiroz & Wimberger, 1993). Differences in the degree of mimicry between parasitic eggs and chicks could be indicative of congruent differences in host discrimination only under the assumption that chicks can evolve mimicry as readily as egg-shells. I have shown here that such factors have limited the evolution of chick mimicry in parasites, particularly at older ages and when hosts and parasites belong to distantly-related taxa. This, rather than differences in host discrimination, may explain why some parasites have evolved mimetic chicks while others have not.

If hosts were able to discriminate between chicks as efficiently as between eggs, then only those host-parasite systems where chick mimicry is feasible could persist over time. It is because eggs differ from chicks in many other ways that parasites can escape rejection by different mechanisms, mimicry being just one of them. Unlike chicks, egg-shells provide only simple visual signatures which remain stable over time. Visual traits are less likely to be favoured as recognition signatures at the chick than at the egg stage, for reasons given above. Any field study which overlooks acoustic and behavioural similarities between host and parasite chicks will overlook any existing non-visual mimicry too. This has surely underestimated the prevalence of chick mimicry, as host-parasite behavioural interactions at the chick stage are very poorly known.

For many unavoidable reasons (perceptual and developmental constraints, low confidence of parenthood, and conflicting selection pressures [e.g. individual recognition of young]), hosts are much more likely to incur recognition and misidentification costs, and pay a higher prize for it, when recognizing chicks than egg-shells. This may have limited, if not completely prevented, the evolution of chick discrimination before young leave the nest. It is easier to work with immobile eggs than with elusive fledglings. Also, nest sample sizes become inevitably smaller (much to the chagrin of zoologists) as the nesting cycle advances. Consequently, our knowledge of birds at fledgling stages is minute compared with that at egg stages, even for the best studied species (O'Connor, 1984). Let alone brood parasites which are difficult birds to study anyway, even at the egg stage, and most of which live in remote areas. It would not be surprising that, even if discrimination of fledglings were widespread, it had gone largely undetected.

Supporting evidence in favour of such inefficient mechanisms of chick recognition can be found across many different groups of birds. Chick-recognition mechanisms other than indiscriminate imprinting on offspring signatures (i.e. the one

operating for recognizing egg-shells) can theoretically evolve in birds (c.f. Lotem, 1993) and have indeed evolved in at least some of the few groups so far studied (e.g. estrildids). To my knowledge, however, this evidence has been largely ignored in discussions about chick discrimination in brood parasitism (but see Beecher, 1988). Let us assume that birds can only recognize parasitic eggs and chicks by the same mechanism and we shall conclude that chick-recognition will never evolve but in a few rare cases.

Unlike parasitic eggs, chicks can be rejected by disfavouring them, and hosts are indeed expected not to eject chicks out of the nest in the same way as eggs. This assumption is of the greatest importance because the most direct evidence of chick rejection is rejection behaviour itself. Many previous hypotheses dealing with chick discrimination may have suffered by attempting to frame arguments in absolute adaptationist terms rather than as a true evolutionary scenario, with chick rejection evolving (or failing to evolve) from some earlier condition (e.g. distribution of food among chicks vs nest sanitation). If, as for eggs, we expect hosts to reject parasitic chicks mainly by ejection, the conclusion that they never discriminate against chicks seems inevitable.

Finally, parasitic egg-shells can only escape host discrimination by mimicking host eggs. Chicks, on the contrary, can interact in more complex ways with foster parents and, aside from mimicking host chicks, can evolve exaggerated signals which exploit pre-existing preferences in hosts. Mimicry, however, is the cheapest solution if exaggerated signals are costly to produce. Behavioural manipulation is especially feasible in this context because: (i) recognition mechanisms in hosts are very inefficient, and (ii) recognition and rejection rules may interfere with each other at the motivational level: Many of the cues used by hosts to recognize and reject the parasite can evolve into signals which are consistently malinterpreted by hosts as honest indicators of a high chick need or

quality, increasing their willingness to care for the parasite. This idea has sounded intuitively appealing to many observers (Heinroth, 1959; Hamilton & Orians, 1968; Lack, 1968; Dawkins & Krebs, 1979; Wyllie, 1981) but testing it requires a detailed knowledge of the behavioural mechanisms underlying parent-young interactions which is lacking for most host-parasite systems.

Should we expect hosts to discriminate?

I do not intend that the HEH provides a general explanation for the problem of chick mimicry and discrimination in avian brood parasitism. In some (perhaps many) cases, hosts may simply lack recognition or rejection responses due to: (i) lack of appropriate mutations; (ii) lack of enough evolutionary time; (iii) recognition (including misimprinting) costs; or (iv) parasites exploiting the mechanisms for individual recognition ("feed any chick in my nest") because changing such mechanisms would require too many coadapted changes (hence i), too long a time (hence ii) or too costly recognition mechanisms (hence iii). However, none of these possibilities alone can account for the nearly total lack of chick discrimination. Actually, the scarce evidence available demonstrates that hosts *can* sometimes recognize parasites and that parasites *have* indeed evolved chick mimicry to a varying degree. Further work should test whether the former can explain the latter.

In this paper, I have explored the possibility that discrimination could also entail indirect rejection costs (misdirected parental care in the absence of parasitism) when parasites can exploit some intrinsic "imperfections" of parental behaviour. The main difference with other hypotheses is that the HEH predicts the existence of host discrimination in

many (not all, see below) hosts and of coevolved defensive mechanisms (mimicry and/or manipulation) in most parasites. In particular, exaggerated manipulative signals are likely to be widespread because: (i) cheating hosts would always benefit parasites, even if hosts fail to reject them; (ii) after a period of coexistence with hosts, parasites may evolve adaptations that reduce signalling costs; and (iii) parasites could evolve manipulative signals in response to discrimination by a few hosts, then retaining them after starting to parasitize a different, non-discriminating host with similar parental rules. Below, I consider in more detail the two latter possibilities as they bear directly on the HEH.

Good experimental evidence of chick rejection has only been found in hosts of the screaming cowbird and the viduines, both of which will eventually disfavour (but not eject) a non-mimetic parasitic chick placed in their nest early in the nestling period (Fraga, 1986; Nicolai, 1964). No equivalent detailed studies have yet been carried out with hosts of nonmimetic parasites. Similar experiments conducted with hosts of two non-mimetic cuckoos gave negative results (Alvarez et al., 1976; Davies & Brooke, 1989b). However, it may be premature to conclude that these hosts are unable to discriminate, since chick recognition is likely to be poorly developed before fledging. Actually, chick discrimination in bay-winged cowbirds was only evident after fledging (Fraga, 1986) and cuckoo hosts could behave similarly. Swallows, for example, fed a variety of chicks before fledging but neglected all except cowbirds after on (Eastzer et al., 1980), and magpie parents rejected novel chicks painted with colours shortly before fledging, but not earlier on (fig 4, table II).

A simple way of testing this possibility is to perform careful cross-fostering and choice tests similar to those carried out with eggs (e.g. Rothstein, 1982a; Davies & Brooke, 1988, 1989a), at several stages in the nesting cycle. However, I would expect some *a priori* complications in chick-

discrimination studies which should be kept in mind.

Great and lesser expectations from empirical studies of chick discrimination.

A welcome advantage of egg- and chick-discrimination studies in birds is that they permit very accurate field tests of theoretical models from a functional-evolutionary perspective. Many of the mutants (or alternative discrimination strategies) imagined by theoreticians can be easily brought to life (via their effects upon chicks) by experimental manipulations (as Husby (1986) and Magrath (1990), among others, have beautifully shown). Sometimes, it will be possible to obtain reasonably good estimates of Darwinian fitness by taking simple measures from large samples, such as the number of offspring at independence and their quality (e.g. survival probabilities at first breeding as a function of body mass or brood size at fledging), or even quantify the number of grandoffspring actually left by each strategist. Hopefully, such facilities will stimulate a much-needed forthcoming progress in chick-discrimination studies. However, no model will ever provide a realistic picture of the problem if it only approaches it from a functional perspective. All throughout this paper, I have attempted to highlight that, until we know the precise mechanisms underlying recognition, rejection and parent-offspring interactions in hosts, and between hosts and parasitic young, it will hardly be possible to make predictions about the state or possible outcome of the arms race for given species. In particular, any model relying on assumptions framed in absolute adaptationist terms will arrive to meaningless conclusions (e.g. that hosts can either evolve cuasi-perfect discrimination (and parasites becoming fine mimics) or completely fail to do so (so that no further explanations are required)). Other topics in

Behavioural Ecology may have similarly suffered from an arrested development as a result of such a biased approach (Huntingford, 1993). The following considerations will help illustrating this point:

1) It is convenient to know if the host shows learning of individual chicks' signatures. Hosts may discriminate simply on the basis of previous experience: Differential reactions to familiar vs novel chicks may be malinterpreted as evidence of functional (or potentially so) chick recognition in the context of coevolved host defences. Individual chick recognition may be a gradual process, requiring careful control of relevant factors (e.g. chick age or parental experience during previous breeding attempts). Experiments with fully mimetic chicks have overcome this difficulty, so their results are conclusive (Nicolai, 1964; Fraga, 1986; also McLean & Griffin, 1991).

2) Differences between parasitic and host chicks may prompt differential host responses (hence discrimination), but this might occur even in the total absence of chick recognition. What is needed is a set of independent experiments capable of testing: (i) whether hosts can recognize or reject chicks, and (ii) whether parasites' traits help them to be less rejected, particularly if (iii) such traits exaggerate those favoured by hosts when caring for their own chicks. All studies, therefore, have provided only partial support to, or evidence consistent with the HEH, at the most.

3) The above point suggests that, as in studies of parent-offspring recognition, cue isolation experiments will provide more conclusive evidence than cross-fostering experiments (Shugart, 1990). For example, in partially mimetic parasites, experimental transformation of putatively mimetic traits (e.g. the colour of the beak in giant cowbirds, or plumage in Indian koels) would have a greater effect upon host discrimination responses than of non-mimetic traits other than signals (e.g. skin colour). Cross-fostering experiments may overestimate the extent of recognition if hosts respond differentially to other chick traits (e.g.

behaviour) in addition to signatures (Shugart, 1990).

4) Background knowledge of host parental rules may greatly help, or prove necessary for, interpreting results of recognition experiments. Imagine, for example, a species in which females prefer to feed the smaller chicks in a brood and where fathers contribute less than their mates to chick-provisioning (e.g. budgerigars, Stamps et al., 1985). Also imagine a choice or cross-fostering experiment involving a large parasite vs a small host chick showing no differences in average feeding rates between both. Ignoring that such parental rules exist would lead us to conclude that hosts do not discriminate between chicks while, in fact, the opposite is true.

5) One possible (and disturbing) outcome of the host-parasite arms race within the evolutionary scenario proposed by the HEH is that, as a result of manipulation by non-mimetic parasites with exaggerated signals, hosts may virtually lack chick recognition because (i) they have lost it over evolutionary time, or (ii) they were prevented from evolving it after being parasitized (see next section). Most biologists (I too) would feel uncomfortable with this possibility, as it makes the argument almost tautological. In particular, the idea that exaggerated signals in some non-mimetic parasites function as mechanisms for preventing rejection can not be falsified if hosts fail to recognize them (unless we can find a host population in the very process of becoming an ex-rejecter). Such a possibility can only be supported by means of indirect evidence but, fortunately, the hypothesis generates a large set of testable predictions.

Some unfair theoretical outcomes of host-parasite arms races

Parasites are selected to evolve efficient adaptations for exploiting the parental care of the host, deviating limited host parental resources to the detriment of hosts' young. Once parasites become

harmful enough, the host evolves defensive egg and chick discrimination. When parasites and hosts are not closely related, the former are selected to evolve fine egg mimicry and to attain the maximum possible degree of chick mimicry (e.g. by suppressing some conspicuous distinctive features and developing vocal mimicry). However, chick mimicry may be poor enough to allow rejection by hosts, hence parasites are selected to manipulate hosts, mainly by evolving exaggerated dishonest signals (e.g. size, begging behaviour or growth rate) causing severe competitive interference with nestmates. The more exaggerated signals are, the higher interference is and the selection pressure on hosts to reject the parasite, hence the higher is selection on parasites to manipulate hosts. The extent of signal exaggeration by parasites and of chick discrimination by hosts will coevolve in a sort of feed-forward runaway escalation. Excess costs of signal exaggeration in parasites can largely be paid for by hosts: The parasite can reduce the size of the host brood in order to receive the necessary energy for growing larger and begging louder, and to lower the risk of predation caused by exaggerated begging. If hosts are small, parasites must destroy all brood contents at an early age in order to compensate for such costs (e.g. evicting cuckoos and honeyguides). When parasites no longer pay for the extra cost of signals, these may persist even in the absence of rejection.

In this arms race, chick-rejecter mutations at first spread but several different outcomes are possible in theory:

1) If hosts follow parental rules which can not be exploited by parasites, (e.g. to feed the smallest chick), they will win the arms race and the parasite will switch to a different host species or go extinct. Hosts will eventually lose chick discrimination if it entails recognition costs after not being parasitized for some time.

2) When hosts recognize parasites by signatures other than signals, but signals can successfully prevent rejection, rejecter mutants can persist in the

host population because: (i) they do not incur costs when feeding their own chicks, and (ii) although parasites can usually prevent rejection by manipulating hosts, there are some cases where such signals are not sufficient to prevent rejection. For example, if parents identify a small nestling in a brood which begs very intensively as a low-quality chick or as a target for brood reduction, they could reject the parasite whenever, due to late laying, the parasite hatches well after the host's young. If a mutation appears which directly links the recognition mechanism (released by non-signal signatures) with the rejection response, then hosts win the arms race as in 1) above (i.e. parasite's signals no longer prevent, or parental rules no longer interfere with rejection of parasites). Otherwise, parasites may coexist with hosts for a long time, the arms race reaching a stable equilibrium maintained by evolutionary lag (lack of appropriate mutations) and discrimination costs (parental rules can not be modified without incurring in suboptimal offspring care).

3) When parasites' signals can prevent rejection, and all the possible recognition signatures used by hosts have been modified over evolutionary time so that cues other than signals are no longer available (e.g. they have become mimetic, transformed or lost), a new mutation could appear which is able to use a novel non-signal trait as a signature. If so, hosts could maintain rejection behaviour as in 2) above. If not, rejecters are (by definition) those parents who disfavour the chicks with more intense signals, either parasitic or not. The selective advantage of rejecters is inversely related to the degree of signal exaggeration in parasites. If rejecters incur costs when caring for their own young in the absence of parasitism, and the benefits of rejection (e.g. the fraction of the hosts' brood or parental effort saved once the parasite disappears) become negligible because parasites have evolved sufficiently exaggerated signals that only seldom fail to prevent rejection, acceptor mutations will spread to fixation. In the absence of rejection, parasites are

not selected again to produce less exaggerated signals if the extra costs of exaggeration are mainly paid by hosts, to which they are genetically unrelated. At this point, rejecters can not spread again. This is also true if parasites with exaggerated signals begin to parasitize a new host species with similar recognition and chick-feeding rules: The host will be prevented from evolving chick discrimination. Thus, when rejection entails a cost (in this case, misdirected offspring care) and the probability of parasitism is low, rejecter alleles can not spread within a parasitized host population at equilibrium. A formal mathematical demonstration for this possibility is provided by Takasu et al. (1994) (see also Kelly, 1987).

Resumen

Cómo las aves parásitas explotan los mecanismos de comportamiento de cuidado parental de sus hospedadores.

Las aves parásitas de cría ejercen una notable presión de selección sobre sus hospedadores, ya que disminuyen su éxito reproductor. En respuesta, los hospedadores han desarrollado mecanismos de reconocimiento y rechazo de los huevos del parásito. Muchas especies de parásitos han evolucionado huevos que imitan de forma asombrosa los de su hospedador en respuesta al rechazo de huevos no miméticos por parte de éstos. Así, parásitos y hospedadores se encuentran involucrados en una carrera de armamentos coevolutiva que ha favorecido la aparición de sofisticadas adaptaciones y contra-adaptaciones, tal como ponen de manifiesto numerosos estudios experimentales realizados durante los últimos años. Sin embargo, al contrario de lo que ocurre en el caso de los huevos, sólo una minoría de parásitos ha desarrollado pollos miméticos. Este hecho ha sido tradicionalmente interpretado como una prueba de la falta de discriminación hacia pollos no miméticos por parte

de los hospedadores, incluso aquéllas especies que poseen capacidades muy finas de discriminación de huevos.

La ausencia de discriminación hacia pollos ha sido explicada mediante dos hipótesis. De acuerdo con la Hipótesis del Lastre Evolutivo, los hospedadores carecen de la variabilidad genética o tiempo evolutivo necesarios para que un mutante rechazador aparezca o se fije en la población. Según la Hipótesis del Equilibrio Evolutivo, existen costos asociados al reconocimiento y/o rechazo de pollos que compensan los beneficios obtenidos. Ninguna de estas dos hipótesis, sin embargo, proporciona una explicación satisfactoria para la casi total ausencia de mimetismo (y, por consiguiente, de discriminación).

En este artículo, se sugiere una explicación alternativa a este problema. En primer lugar, se demuestra que la existencia de mimetismo de pollos se encuentra restringida a aquéllas especies que parasitan a hospedadores filogenéticamente próximos. Ello sugiere que la evolución de mimetismo de pollos puede verse seriamente limitada por diferencias en los patrones de desarrollo postnatal, ya que (a diferencia de los huevos) el mimetismo de pollos afecta a un elevado número de caracteres sometidos a presiones selectivas conflictivas cuando el ave alcanza su estado adulto. Por tanto, la ausencia de mimetismo no necesariamente refleja una incapacidad para discriminar por parte de los hospedadores.

En segundo lugar, es de esperar que las aves posean mecanismos de reconocimiento de pollos menos eficaces que de huevos, ya que la imposibilidad de utilizar caracteres de identificación basados en señales químicas implica que (i) las aves deben aprender los caracteres distintivos específicos de la especie (con el consiguiente riesgo de aprender los caracteres de un parásito) y (ii) los únicos caracteres útiles (señales acústicas y visuales) experimentan enormes cambios durante el desarrollo postnatal (con el consiguiente riesgo de cometer errores de identificación y rechazar sus propias crías). Los parásitos pueden explotar estas deficiencias en

su propio beneficio, evitando ser rechazados sin necesidad de alcanzar un grado elevado de mimetismo. Diversos estudios sobre el reconocimiento de pollos por sus padres apoyan esta idea.

Incluso si los hospedadores son capaces de desarrollar mecanismos de reconocimiento del parásito, éste podría prevenir el rechazo mediante señales que manipulan el comportamiento del hospedador. Numerosos parásitos parecen haber evolucionado señales comunicativas que exageran aquéllos caracteres empleados por sus hospedadores para cuidar de sus crías de forma adaptativa en ausencia de parasitismo (p. ej., un mayor tamaño o un comportamiento de sollicitación intenso). Tales señales pueden interferir con las reglas de decisión parentales a la hora de rechazar al parásito, induciendo en aquéllos una elevada motivación para cuidar del mismo, con el fin de desacoplar los mecanismos internos de reconocimiento y rechazo. Varios datos observacionales y experimentales sugieren que ciertos hospedadores pueden, de hecho, preferir a pollos parásitos en detrimento de sus propias crías en condiciones similares. Un estudio más profundo de este problema requerirá, por tanto, un conocimiento detallado de los mecanismos que regulan las relaciones paterno-filiales, a fin de integrar el enfoque funcional y causal del comportamiento como única forma de obtener una perspectiva evolutiva realista.

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