

Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not?

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Mimicry is one of the most conspicuous and puzzling phenomena in nature. The best-known examples come from insects and brood parasitic birds. Unfortunately, the term 'mimicry' is used indiscriminately and inconsistently in the brood parasitic literature despite the obvious fact that similarities of eggs, nestlings and adults of brood parasites to their hosts could result from many different processes (phylogenetic constraint, predation, intraspecific arms-races, vocal imitation, exploitation of pre-existing preferences, etc.). In this note I wish to plead for a more careful use of the term. I review various processes leading to a similarity between propagules (both eggs and nestlings) of brood parasites and their hosts and stress that: (1) mimetic and non-mimetic similarities should be differentiated, (2) a mere similarity of host and parasite propagules provides no evidence for mimicry, (3) mimicry is more usefully understood as a (coevolutionary) process rather than an appearance, and (4) mimicry terminology should reflect the process which led to mimetic similarity. Accepting the mimicry hypothesis requires both the experimental approach and rejection of alternative hypotheses explaining similarities of host and parasite propagules. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, **84**, 69–78.

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INTRODUCTION

Motto: 'The possibility of mimicry in eggs must be treated with caution, as pure coincidence in their colouration is so general a phenomenon. . . . this state of affairs warns us to be very wary about attributing a given resemblance to mimicry.' Swynerton (1916, p. 553).

From mind-boggling similarity among various phylogenetically unrelated butterflies to very generalized 'prey' presented by angler fish, mimicry has attracted human interest for a long time (Wickler, 1968; Komárek, 1998, 2003). Such resemblances result from coevolution (Janzen, 1980) or sequential evolution (Futuyma, 1998) and have been extensively studied among insects (for a review see, e.g. Wickler, 1968) and also brood parasites and their hosts (Fig. 1) (for reviews of brood parasitic systems see Rothstein & Robinson, 1998; Davies, 2000). Insect mimicry gener-

ally provides protection against predation or attracts pollinators (Wickler, 1968; Vane-Wright, 1976), whereas coevolutionary mimicry in brood parasites is a counter-adaptation against host antiparasitic response (Rothstein, 1990).

With respect to avian parasite–host coevolution attention has been focused mainly on mimicry in parasitic eggs and their rejection by hosts (e.g. Davies & Brooke, 1989; Moksnes *et al.*, 1990). Apparent evidence for nestling mimicry in brood parasites received much less attention (for the most comprehensive review see Redondo, 1993).

Is every similarity between parasitic and host propagules an example of mimicry? Various authors realized long ago that this is not the case: for example, eggs of parasite and host can be similar simply because they share the same environment, where they suffer predation from visually orientated predators. If so, then, similarity is cryptic (non-mimetic) and results from convergent evolution (Harrison, 1968; Mason & Rothstein, 1987). In this review I will show

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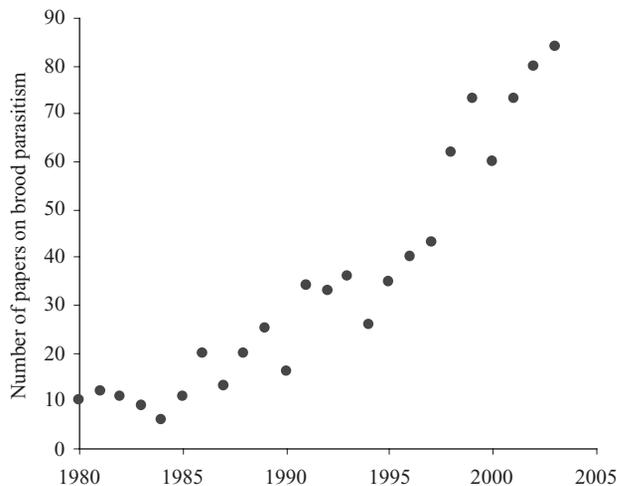


Figure 1. Number of papers on brood parasitism from 1980 to 2003. Second-order polynomial regression of year against the number of papers on intra- and interspecific brood parasitism in birds: $R^2 = 0.92$, $F_{2,21} = 113.1$, $P < 0.0001$; second-order regression coefficient is significant: $t = 2.46$, $P = 0.02$. Data from the Web of Science.

that the issue is even more complex than was previously thought.

When discussing various traits in the context of coevolutionary theories it should be clear if these traits are: (1) specific adaptations and counteradaptations (i.e. result of coevolution between parasites and hosts), (2) adaptations resulting from other (non-coevolutionary) selection pressures, or just (3) by-products of some other – perhaps adaptive – traits (for discussions see Janzen, 1980; Vane-Wright, 1980; Ryan, 1990; Grim, 2002). The following analysis is based on these crucial differences and it is argued that mimicry terminology should reflect the process that led to the given mimetic similarity.

I suggest that the term ‘nestling mimicry’ and less so ‘egg mimicry’ is usually applied indiscriminately to any similarity between parasitic and host chicks or eggs, respectively (see, e.g. Jourdain, 1925; Lack, 1968; Mundy, 1973; Wyllie, 1981; Davies & Brooke, 1988; Redondo & Arias de Reyna, 1988b; Redondo, 1993; Hughes, 1997; Johnsgard, 1997; Davies, Kilner & Noble, 1998; Gill, 1998; and references in these papers). However, the similarity could result from various proximate processes (as I will show) and only in some of these cases is the similarity mimetic within the generally accepted definition of mimicry: mimicry involves the mimic (e.g. parasitic chick) simulating signal properties of the model (e.g. host chick) which are perceived as signals of interest by a signal-receiver (e.g. fosterer), such that the mimic gains in fitness as a result of the signal-receiver identifying it as an example of the model (Vane-Wright, 1976, 1980; see

also Wickler, 1968). In other words, mimicry is the result of selection imposed by the signal-receiver (Wickler, 1968; also termed the operator by Vane-Wright, 1976; or dupe by Pasteur, 1972). Thus, mimicry is in most cases (but see later) a typical coevolutionary phenomenon, i.e. it arises from a reciprocal interaction between two or more evolutionary lineages (i.e. species or group of individuals within species, e.g. males or females – see intraspecific mimicry), with each party selecting for changes in the other (Dawkins & Krebs, 1979; Janzen, 1980). As similarity may also result from other processes, many cases of similarity between parasitic and host chicks traditionally reported in the literature as ‘mimicry’ are more usefully described as non-mimetic.

The main aims of this note are to: (1) review various processes producing similarities between parasitic and host propagules, and (2) clarify the definition of parasitic coevolutionary mimicry (i.e. similarity resulting from coevolution between parasites and their hosts, but not from other evolutionary or behavioural processes; see also Rothstein, 1971; Rothstein, 1990: 485). I argue that to support the coevolutionary mimicry hypothesis one must show experimentally that a particular host rejects at least some alien eggs/nestlings while it accepts natural parasitic eggs/nestlings more often than it does more dissimilar models or natural alien eggs/nestlings.

On the one hand, during the last three decades dozens of hosts victimized by brood parasites have been tested with non-mimetic, mimetic and conspecific eggs (models or natural eggs) for their egg discrimination abilities (e.g. Rothstein, 1975; Davies & Brooke, 1989; Moksnes *et al.*, 1990; Grim & Honza, 2001b). On the other hand, very few hosts have been tested experimentally for nestling discrimination abilities (e.g. Davies & Brooke, 1988; Langmore, Hunt & Kilner, 2003). Thus it is quite possible that ‘the rarity of chick mimicry in parasitic birds’ (Rothstein & Robinson, 1998) is just a pseudo-problem: an artefact of low research in this area (see also Grim, Kleven & Mikulica, 2003). Hopefully, clarification of the term ‘mimicry’ from the proximate point of view (i.e. ‘what process led to the similarity?’) might foster research interest in this area and could contribute to an improved design for experiments to test nestling-related adaptation in hosts and their parasites.

EGGS: MIMICRY OR SIMILARITY?

Similarity of parasitic and host eggs might result from various processes (Table 1).

(i) *Phylogenetic constraints.* When a host and its parasite are closely related (e.g. parasitic honeyguides, Indicatoridae, and their barbet, Capitonidae and

Table 1. Review of hypotheses that could explain a similarity of host and parasite eggs or nestlings

Hypothesis	Eggs	Nestlings
(i) Phylogenetic constraints	+	+
(ii) Random matching	+	+
(iii) Spatial autocorrelation	+	–
(iv) Nest predation	+	+
(v) Egg replacement by cuckoos	+	–
(vi) Host discrimination	+	+
(vii) Non-random matching	–	+
(viii) Pre-existing preferences	–	+
(ix) Vocal imitation	–	+

Applicability of the particular hypothesis indicated by '+'. Only hypotheses in bold explain mimetic similarity of parasite and host propagules. Other hypotheses explain non-mimetic similarities. All hypotheses are discussed in detail in the text.

woodpecker, Picidae, hosts, or parasitic viduines, Viduinae, and host estrildids, Estrildidae), the similarity of egg appearance is probably the result of common descent (Payne, 1967; Lack, 1968; Sorenson & Payne, 2001). A similar case can be made for facultative parasites: both black-billed cuckoos *Coccyzus erythrophthalmus* and yellow-billed cuckoos *Co. americanus*, that occasionally parasitize each other, various passerines or conspecifics, have bluish-green eggs (Hughes, 1997; Lorenzana & Sealy, 2002). Obviously, no selection for similarity (genuine mimicry) in the context of intraspecific parasitism is needed. This also holds for the initial stages of intrageneric parasitism. However, although the initial similarity would be due to phylogenetic constraint, it may be maintained later by stabilizing selection. For example, in the case of Müllerian mimicry the mimetic process can act to prevent divergence of the aposematic pattern that might otherwise occur (Mallet & Joron 1999; Beatty, Beirincx & Sherratt, 2004). Nevertheless, the case of *Co. erythrophthalmus* and *Co. americanus*, discussed here, the stabilizing selection for similar egg coloration must be extremely weak as the frequency of intrageneric parasitism is very low. Furthermore, stabilizing selection is an unlikely cause of similarity of eggs of parasites and their hosts which breed in holes (barbets, woodpeckers) or dark-domed nests where physical constraint (low illumination) prevents visual discrimination (tactile discrimination has been documented only once: Mason & Rothstein, 1986).

(ii) *Random matching.* Eggs of the brown-headed cowbird *Molothrus ater* sometimes resemble eggs of acceptor hosts (Rothstein & Robinson, 1998). This similarity cannot be caused by host response to parasit-

ism (acceptors cannot select for mimicry and female cowbirds are not host specialists, thus even host rejection cannot lead to the evolution of egg mimicry). *M. ater* parasitize large numbers of passerines (> 200; Rothstein, 1990), which of course show limited interspecific variation in the appearance of their eggs. Consequently, an occasional similarity between parasitic eggs ('a general passerine type'; Lack, 1968) and host eggs might be an inevitable result of parasitism on a large pool of host species (Rothstein, 1990). Chance or accidental similarity clearly has nothing to do with 'mimicry' (Vane-Wright, 1976, 1981).

(iii) *Spatial autocorrelation in the diet of hosts and parasites.* Cherry & Bennett (2001) hypothesized that similar diet or other environmental similarities could influence the coloration of both host and parasite eggs in the same way (the same explanation was first suggested by Baldamus, 1853, cited in Jourdain, 1925). Thus the similarity would not be the result of selection for colour matching. The results of Cherry & Bennett (2001) are in line with the hypothesis but this requires further testing.

(iv) *Nest predation.* Conspicuous parasitic eggs might increase the risk of predation of hosts nests (Harrison, 1968; see also Mason & Rothstein, 1987). Thus, predation could select for an inconspicuous appearance in both host and parasite eggs; both types of eggs would consequently converge on the same coloration. Therefore, the similarity would result from convergent evolution (not coevolution), would be an example of crypsis (not mimicry) and could not be accepted as an adaptation (but as a by-product of selection for crypsis in the same environment; see also Vane-Wright, 1980). However, egg colour does not influence nest predation rates in open-nesting passerines (Weidinger, 2001) and there is also no support for this hypothesis in the most common host of the common cuckoo *Cuculus canorus* – the reed warbler *Acrocephalus scirpaceus* (Davies & Brooke, 1988).

(v) *Egg replacement by competing female cuckoos.* Some already parasitized host nests are visited by a second cuckoo, which can remove the first parasitic egg. Such selective egg removal is advantageous as only one cuckoo chick can be raised per host nest due to parasitic nestling eviction behaviour and as a rule the first egg laid hatches first. In this case the model is the host's egg, the mimic is the egg of the first cuckoo and the operator is the second-arriving cuckoo. The resulting mimicry can be considered as an example of class D mimicry (see Vane-Wright, 1976: 46). This is interesting as Vane-Wright (1976) considered this category, where operator and mimic belong to the same species while the model belongs to a different species, as 'logically empty with respect to purely bio-

logical systems'. Egg predation by female parasites laying in already parasitized nests was hypothesized to explain similarity between parasitic and host eggs in Horsfield's bronze-cuckoo *Chrysococcyx basalis* (Brooker & Brooker, 1989, 1990), but is unlikely to be an important force behind the evolution of egg mimicry in *Cu. canorus* (Davies & Brooke, 1988).

(vi) *Host discrimination*. Dissimilar parasitic eggs can be rejected by a host, which selects for egg mimicry in parasites (Davies & Brooke, 1988, 1989; Moksnes *et al.*, 1990). The match between parasitic and host eggs is genuine mimicry and increases with increasing rejection rate (Brooke & Davies, 1988).

Clearly, Cases (i) (ii) and (iii) have nothing to do with coevolution at all, Case (iv) is crypsis, and only Cases (v) and (vi) are examples of mimicry. Thus, the mere similarity of host and parasite eggs provides no evidence for mimicry. Furthermore, it is fundamental to differentiate Cases (v) and (vi), as only the latter process can be described within the framework of coevolution between brood parasites and their hosts as an interspecific asymmetric arms-race (Dawkins & Krebs, 1979). A nice example of Case (v) comes from splendid fairy-wrens (*Malurus splendens*) that accept even strongly non-mimetic eggs (Brooker & Brooker, 1989). However, parasitic eggs laid in their nests by *Ch. basalis* are highly 'mimetic' (see plate 3c in Davies, 2000) probably as a result of egg replacement by competing female cuckoos (Brooker & Brooker, 1990). This similarity is an example of mimicry, but it is fundamentally different from mimicry which evolved by host rejection of dissimilar eggs – mimicry in Case (vi) results from an interspecific arms-race while mimicry in Case (v) results from a conspecific arms-race (see Dawkins & Krebs, 1979). However, this hypothesis needs stronger evidence than that provided so far by Brooker & Brooker (1989, 1990).

NESTLINGS: MIMETIC OR JUST SIMILAR?

In the literature on brood parasites, mimicry is the most frequently cited example of an adaptation evolved by parasites as a response to host discrimination (e.g. Rothstein & Robinson, 1998; Davies, 2000). Applying the same criteria (mimetic similarity is a coevolutionary counter-adaptation against host anti-parasitic behaviour) for eggs and nestlings shows that the match between parasitic and host chicks can also be a consequence of various processes (Table 1), and many similarities are non-mimetic.

(i) *Phylogenetic constraints*. Closely related species show similar traits not because they were selected to be so but just because they are closely related. I am aware of no published case of this phenomenon in

obligate parasitic birds. In facultative parasites, palatal structures are indistinguishable in closely related *Co. americanus* and *Co. erythroptalmus* (Nolan, 1975) that sometimes parasitize conspecifics and each other (Hughes, 1997; Lorenzana & Sealy, 2002). In an extreme case, phylogenetic inertia works in all conspecific parasites – parasitic and host nestlings are identical from the start. Chicks are similar but clearly non-mimetic.

(ii) *Random matching*. Many cases of similarity between parasitic and host nestlings (Redondo, 1993) are unlikely to withstand close scrutiny. For example, nestling *Cu. canorus* begging vocalizations closely resemble ('mimic') those of a *A. scirpaceus* brood (Davies *et al.*, 1998). This similarity seems like perfect mimicry (see sonograms in Davies *et al.*, 1998 and Fraga, 1998). However, evidence for mimicry cannot be obtained by a comparative description: experiments are needed as parasitic coevolutionary mimicry by definition results from host (operator) discrimination (Rothstein, 1990: 485; see also Rothstein, 1971). The vocal similarity between *Cu. canorus* and *A. scirpaceus* nestlings is not mimicry as: (1) *A. scirpaceus* readily feeds nestlings of several other species introduced into their nests (Davies & Brooke, 1988, 1989; Davies *et al.*, 1998), (2) *Cu. canorus* begging 'mimics' the host chicks' begging only during a part of the nestling period when the dietary requirements of the parasite match those of the host brood and 'mimicry' disappears later when begging increases in old *Cu. canorus*, and (3) the begging call structure in *Cu. canorus* nestlings does not vary according to *Cu. canorus* host races (Butchart *et al.*, 2003). Furthermore, various species of passerines sometimes feed a single parasitic chick despite the fact that various 'fosterers' have different nestling begging calls (Sealy & Lorenzana, 1997), indicating that very rough (and clearly non-mimetic) similarities of begging calls can lead to the feeding of alien chicks. The similarities of begging call rates between cuckoo and fosterers' chicks of different host species (Butchart *et al.*, 2003) can be explained by the fact that begging behaviour of altricial nestlings reflects offspring past experience (Kedar *et al.*, 2000; Rodríguez-Gironés, Zuniga & Redondo, 2002). In other words, a *Cu. canorus* chick that is fed less often than it needs (because the host feeding rules require a higher rate of begging to provide the required level of provisioning) would increase its begging to match the call rate shown by a host's own brood with similar food needs. A learning response by chicks, i.e. a change in the rate but not structure of begging calls, to parental provisioning provides evidence against the cuckoo chick mimicry hypothesis. Increase in begging call rates in response to social context is probably universal among altricial

nestlings, as shown by Rodríguez-Gironés *et al.* (2002), and thus cannot be considered as a specific adaptation against host antiparasitic defence.

I suggest that the structural similarity between *Cu. canorus* and *A. scirpaceus* calls (Davies *et al.*, 1998) (but not other host species studied so far) may be a consequence of: (1) a relatively low variation of nestling begging calls among altricial birds in general, and (2) parasitism of many host species – the greater the host species pool, the higher the diversity of their begging calls and, consequently, the higher the probability of random matching between parasitic and host begging calls (this is analogous to random matching in parasitic eggs; see Case (ii) below and Rothstein, 1990).

Nestlings of the great spotted cuckoo *Clamator glandarius* are sometimes rated as mimetic in their appearance (e.g. Davies & Brooke, 1988). Host magpies *Pica pica* are able to discriminate against (not feed and even actively kill) parasitic nestlings, but only under experimental cross-fostering of a parasite to a previously unparasitized nest (Soler *et al.*, 1995b). Yet *P. pica* discrimination works only at fledgling stage (where no ‘mimicry’ exists), and not at nestling stage (where ‘mimicry’ has been supposed; Davies & Brooke, 1988), probably because *P. pica* learn to recognize their offspring as those that hatched in their nests (Soler *et al.*, 1995b). Thus there is a potential for discrimination but it cannot be used by *P. pica* against parasite chicks, as, under natural conditions, parasitic chicks are present in the nest before *P. pica* fosterers start to learn the appearance of their offspring. Moreover, under natural conditions magpies preferentially feed supernormal parasites (Redondo, 1993; Soler *et al.*, 1995a; see also discussion in Grim & Honza, 2001a). All these data indicate strongly that the similarity between *Cl. glandarius* and *P. pica* nestlings is not mimicry, but is probably attributable to a low variance in altricial nestling appearance (to the human eye almost any altricial nestlings are similar enough to indicate the possibility of mimicry). On the other hand, vocal similarity between *Cl. glandarius* and its host is probably explained by a learning response in parasitic chicks (Redondo & Arias de Reyna, 1988b; see Case (ix) later in this section). Clear evidence for the vocal mimicry hypothesis could only be obtained by demonstrating that hosts discriminate against chicks with dissimilar begging calls.

(iii) *Spatial autocorrelation*. This hypothesis most likely cannot be applied to nestlings (for details see the section on eggs).

(iv) *Nest predation*. In principle, this hypothesis may apply to nestlings (see the logic of the argument in the section on eggs). However, I am aware of no evidence in favour of the hypothesis that predation selects for cryptic nestling plumage in altricial birds.

(v) *Egg replacement by cuckoos*. Female cuckoos can replace only eggs, thus the hypothesis can be tested only at the egg stage.

(vi) *Host discrimination*. Some parasitic nestlings resemble host progeny in appearance (viduines: Payne, Woods & Payne, 2001; screaming cowbird *Molothrus rufoaxillaris*: Fraga, 1998) or vocalizations (*Ch. basalis*: Langmore *et al.*, 2003) and experiments have shown that dissimilar chicks are penalized by hosts. These examples can be accepted as parasitic chick mimicry.

(vii) *Non-random matching – parallel evolutionary modifications in response to common factors*. This hypothesis considers only vocal mimicry; see also Case (ix). Redondo & Arias de Reyna (1988a), Briskie, Martin & Martin (1999) and Haskell (1999) showed that similar environmental factors (e.g. nest-type dependent predation, habitat structure) may lead to convergence in the design of nestling begging calls. Thus, a similar environment could result in the evolution of similar begging calls in parasitic and host nestlings without any discrimination by fosterers (see also McLean & Waas, 1987).

(viii) *Pre-existing host preferences*. When interpreting any trait within an evolutionary framework it is crucial to differentiate between its evolved original function and the current effect of the particular trait (e.g. Ryan, 1990; Futuyma, 1998). Therefore, it should be noted that no special discrimination of parasitic chicks (analogous to a discrimination of parasitic eggs) evolved by hosts in response to parasitism is needed for the evolution of similarity of parasitic and host nestlings. I suggest that if fosterers have innate preferences for certain nestling traits (e.g. red gape, Götmark & Ahlström, 1997), similarity of parasitic and host nestlings may result (e.g. both host and parasite nestlings with redder gapes would be fed more and have better survival than would those with gapes of different and less preferred colour; consequently parasite and host chicks would converge in their appearance).

The resemblance resulting from pre-existing preferences should be explicitly differentiated from coevolutionary mimicry as ‘adaptations by the parasite should be called counterdefences only if they evolved in response to host defenses’ (Rothstein, 1990) – and coevolutionary mimicry is a counterdefence by definition. Thus, a similarity resulting from pre-existing host preferences (sensory exploitation, Ryan, 1990) should be distinguished from genuine coevolutionary mimicry (see above) because it would not be the result of antiparasitic behaviour (pre-existing host preference is clearly not an antiparasitic defence) and a counteraction on the part of a parasite – the same preferences would be applied to both kinds of nestling.

Under this scenario the similarity between a host and a parasite is not the result of coevolution (Janzen, 1980) but sequential evolution (Futuyma, 1998). Although adaptive (as a discrimination mechanism against a parasite), the preference is not an antiparasitic adaptation but an incidental consequence of the host's pre-existing cognitive machinery (see also Ryan, 1990). Pre-existing preference may perhaps be moulded by selection to establish host ability to reject parasitic nestlings, but such a trait would then be better included under the 'host discrimination' label (pre-existing preference then should be considered as pre-adaptation for discriminative behaviour).

The 'preference hypothesis' can be tested against the 'discrimination hypothesis' mainly by phylogenetic comparative methods. The preference hypothesis predicts that the host parental preference was established before the evolution of nestling traits, i.e. the same preferences will be found in phylogenetically close species that are not parasitized (see also Ryan, 1990).

A teleonomical approach (see Williams, 1966) may also be helpful – under the preference hypothesis it is expected that similarity of host and parasite traits will only be rough (e.g. red mouth colour). Complex mouth patterns seem to be redundant (from the point of view of the signalling theory) outside the context of interspecific recognition. To deliver food successfully, parents do not need to see any complex gape patterns; they only need conspicuous signals. There is no reason why a conspicuous signal should be complex. Thus, species-specific complex traits (e.g. detailed mouth patterns in Estrildidae and their *Vidua* parasites) could hardly be expected to evolve under some non-specific pre-existing preference and indicate specific host adaptation and specific parasite counter-adaptation (genuine coevolutionary mimicry). However, a teleonomical approach is only an auxiliary criterion which cannot replace phylogenetic comparative methods.

It should be noted that pre-existing host preferences could also lead to divergence in appearance of host and parasite eggs – rufous bush chats *Cercotrichas galactotes* accept more model eggs with contrasting spots than they do mimetic eggs. Thus, host preferences could select attractive but non-mimetic colour patterns on parasitic eggs (Alvarez, 1999).

(ix) *Vocal imitation by parasitic nestling.* Courtney (1967) and Mundy (1973) hypothesized that non-evicting brood parasitic nestlings (which are raised with their hosts' young) could imitate nestling calls of their host chicks, and all parasites (both evicting and non-evicting) could imitate calls of fosterers which induce young to beg. I am aware of no clear evidence in favour of this hypothesis (but see Redondo & Arias de Reyna, 1988b); however, it provides a plausible and testable

explanation for similarities in begging calls of parasites and their hosts. Such a mechanism, if found, could be accepted as a case of mimicry only if the particular host rejected non-learning nestlings. If a researcher finds that nestlings of other non-parasitic species phylogenetically related to the particular parasite also imitate calls of their parents, the mimicry hypothesis should be rejected. Imitation would then be parsimoniously explained by phylogenetic constraint as a preadaptation 'for' later parasitism; see Case (i). Only an improvement in an ability to imitate (in comparison with closely related non-parasitic species) would be accepted as mimicry.

To sum up, Cases (i), (ii), (iv) and (vii) are not examples of mimicry; only processes described under Cases (vi), (viii) and (ix) could lead to mimetic similarities between host and parasite chicks. Vocal imitation by parasitic chicks should be accepted as an example of mimicry only if it was obviously selected by host discrimination against non-imitating chicks. Furthermore, coevolutionary mimicry (selected by host discrimination) and sequential evolution mimicry (selected by host pre-existing preferences) should be differentiated.

It should be noted that two explanations – Cases (i) and (iv) – may not be independent. The low diversity of altricial begging displays (frequency and structure of calls, gape coloration) may not result from phylogenetic constraints (i) and can be caused by pre-existing biases of parents that feed only chicks with particular characteristics (iv). This hypothesis ('generality of pre-existing parental biases leads to convergence of begging displays across various avian taxa') can be tested by phylogenetic comparative methods.

This review has shown that: (1) mimicry in both eggs and nestlings is driven by several different processes, and (2) many similarities between host and parasitic young could be non-mimetic. The comparison of parasite and host traits can only indicate a possibility of mimicry, and focus research efforts on particular host-parasite systems. However, there is a problem with this in that very dissimilar chicks may in fact be mimetic (see later). The question, 'is the similarity of host and parasitic chicks mimetic or not?' cannot be solved without experimental exposure of hosts to dissimilar nestlings of other species cross-fostered to their nests. When testing chick mimicry hypotheses, nestlings of some non-parasitic species should be cross-fostered into: (1) the tested host nests, and (2) other nests of their own species (to control for possible confounding effects of cross-fostering). The species chosen for cross-fostering experiments should feed its nestlings a similar diet to that of the host species and its size should be similar to that of the host species (to eliminate the possibility of malnutrition in

cross-fostered chicks caused by limited feeding ability of hosts). It is predicted that if the similarity of parasitic and host nestlings is mimetic then cross-fostered nestlings of a non-parasitic species will show lower survival and/or decreased growth rates in the nests of the host in comparison with their survival in nests of their conspecifics. After establishing host nestling discrimination ability, experimental manipulation of particular nestling traits can be employed to determine cues for chick recognition and discrimination (see, e.g. Soler *et al.*, 1995b; see also Rothstein, 1982).

CONFUSION RESULTING FROM INCONSISTENCIES IN MIMICRY ASSESSMENT

An inclusion in the literature of a particular parasite under the label 'mimetic nestlings' was based predominantly on subjective assessment of similarity of parasite to host nestlings (one does not need to give references here as the reader can see this in almost any randomly chosen paper which includes the words 'nestling' and 'mimicry'; see also Introduction). Not surprisingly, such a subjective approach leads to inconsistencies in attributing mimicry. For example, the cuckoo finch *Anomalospiza imberbis* and Jacobin cuckoo *Clamator jacobinus* are included in a mimetic category of nestlings by Davies & Brooke (1988: table XVI), whereas they are treated as non-mimetic by Davies (2000: 23 and 111).

The confusing nature of this comparative approach is clearly illustrated in the paper by Hughes (1997). The author concluded that eggs of *Coccyzus* cuckoos are mimetic because 'blue-green eggs ... fully or nearly match the eggs of over 70% of their reported host species, a proportion significantly greater than if hosts were being selected at random from the potential host pool' (Hughes, 1997: 1380). Although such a conclusion is appealing, Lorenzana & Sealy (2002) documented an absence of differential response by hosts to non-mimetic (ancestral white-type) and supposedly mimetic (blue) eggs and falsified the mimicry hypothesis. Furthermore, Lorenzana & Sealy (2002) claimed that only 33% of hosts lay eggs that match *Coccyzus* eggs.

These confusions and inconsistencies in approach by various authors point towards two major problems related to the issue of mimicry. These will be dealt with in the next two sections.

A PROBLEM WITH HUMAN STANDARDS

One problem with a description of parasitic eggs or nestlings as mimetic or non-mimetic is that the eggs are assessed not by the eyes of a host but by the eyes of a human researcher (which are irrelevant to the

evolution of similarity between host and parasitic propagules; Dittrich *et al.*, 1993). This problem is especially serious when researchers choose the design (appearance) of mimetic vs. non-mimetic model eggs in egg recognition experiments. There are three different levels of the problem.

- (1) Birds (but not humans) are sensitive to ultraviolet light and some parasitic eggs that appear non-mimetic in visible light are highly similar to host eggs in UV-light (Cherry & Bennett, 2001).
- (2) Considering only visible light cues, one can imagine that human perception and discrimination abilities are either better or worse than those of the relevant host. In the former case, dissimilarity of parasitic and host eggs for the human eye does not imply that parasitic eggs are non-mimetic – they can be mimetic in the sense that they are sufficiently similar to host eggs to fool a host (which is potentially able to reject at least some alien eggs) to accept them.

On the other hand, if human perception is worse than that of a host, a close similarity of parasitic and host propagules to the human eye would clearly not imply mimicry (this possibility is indicated by the fact that some hosts reject up to 100% eggs judged as being mimetic by human observers; Moksnes & Røskoft, 1992).

- (3) Finally, there is an additional problem that does not relate to a quality of the human senses but to the fact that we are predominantly visual organisms. According to human judgement a pinkish-yellow morph of the shining bronze-cuckoo *Ch. lucidus* chick is mimetic of the chicks of its host, the superb fairy-wren *M. cyaneus*, while the black morph is very different from the host's nestlings. However, the pale morph is always rejected while the dark morph is often accepted (Langmore *et al.*, 2003). The reason is that a different sensory modality (vocal cues) is used for discrimination by hosts.

This indicates that human standards are unimportant for evolution (Dittrich *et al.*, 1993). Which of many measurable parameters – egg size, shape, colour, spotting, shine – is more important for our judgement of mimicry? Is a parasitic egg that is the same colour but a different size from a host egg more (or less) mimetic than is a parasitic egg that differs in colour but matches in size?

Thus, I believe that to talk about mimicry one should not compare egg parameters by eye, but be required to show that: (1) a particular host shows at least some rejection of model eggs, and (2) it accepts natural parasitic eggs more frequently than it does more dissimilar models or natural alien eggs. To determine which model is more dissimilar, the dis-

crimination modality or cue (e.g. size, shape, colour) must first be established. The same principle holds for nestlings.

A PROBLEM WITH CONTINUOUS VARIATION AND DISCRETE CATEGORIES

Another problem is our human need and necessity to divide continuous variables into discrete categories. This holds both for parasitic adaptations (e.g. continuous egg appearance in colour, size, spotting, is described as 'mimetic' or 'non-mimetic') and host evolved responses (e.g. continuous variation in the frequency of rejection of parasitic eggs is reduced to label of 'acceptor' or 'rejecter'). Any such categorizing is inherently dependent on the individual tested and the particular circumstances and could lead to confusion when discussing results of various studies. I stress that 'acceptor' or 'rejecter' could only be a label for a particular interaction, not for an individual or species (see also Vane-Wright, 1981). Thus it is crucial to realize that the question, 'Is *A. scirpaceus* an acceptor or a rejecter?' when it ejects or deserts about 40% of *Cu. canorus* eggs (in my study area in the Czech Republic) has no objective answer.

CONCLUSIONS

In an important note Janzen (1980) called for the retention of the usefulness of 'coevolution' by removing it from synonymy of usage with 'interaction', 'symbiosis', 'mutualism' and 'animal-plant interaction'. For example, the dietary needs of a particular mammal could possibly have coevolved with fruit traits. But the dietary needs could also have evolved long ago before the mammal met the plant in its new habitat and started to provision on fruits that fulfilled its already established needs. Thus, the hypothesis of 'coevolution' needs stronger evidence than merely congruence in traits between, for example, mammal-dispersed seed and the mammal (Janzen, 1980). By the same logic, the hypothesis of 'mimicry' needs stronger evidence than a congruence in traits (appearance) between parasite and host eggs or nestlings. Researchers should focus more on the process behind the similarity than on the similar appearance itself.

By definition, mimicry is an adaptation evolved by selection pressure from signal-receivers (Vane-Wright, 1980). Similarities resulting from other forces (e.g. phylogenetic constraint, predation) should not be dubbed 'mimicry'. Thus, it should be stressed that 'to resemble' does not mean 'to mimic' and 'similarity' does not necessarily mean 'mimicry'.

When the appearance of eggs and nestlings changes over evolutionary time as a result of host discrimination, then it is more useful to understand mimicry not

as similarity of appearance but as a process – a coevolutionary process in fact (egg mimicry is either explicitly or implicitly understood as such in the brood parasitic literature, but the same cannot be said for nestling mimicry). To accept mimicry as simply a similarity of appearance (the approach frequently adopted so far) leads to two major problems: the subjectivity of human standards, and the continuous variance of mimetic or similar traits. Poor similarity (to the human eye) may be mimetic, whereas apparently close similarity may have nothing to do with mimicry (see also Vane-Wright, 1981; Dittrich *et al.*, 1993; Cherry & Bennett, 2001). If a host (1) rejects alien nestlings, and (2) accepts parasitic ones, then these parasitic chicks are clearly mimetic even if they do not show any similarity to the human eye.

To support the coevolutionary mimicry hypothesis (for both parasitic eggs and chicks) one should demonstrate that a host rejects dissimilar parasitic propagules as the mimicry is a defence against rejection evolved during coevolution between parasite and host or results from host pre-existing preferences. The use of the word 'mimicry' in other contexts devalues an otherwise very useful term. Differentiation between mimetic and non-mimetic similarities and various sorts of the latter is beneficial as such a process-based terminology would reflect different evolutionary dynamics of particular (non)-mimetic systems. Mimicry is a subtle concept and should not be used indiscriminately.

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