COMMENTARY

Perspectives and Debates: Mimicry, Signalling and Co-Evolution (Commentary on Wolfgang Wickler – *Understanding Mimicry* – With special reference to vocal mimicry)

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Abstract

In his stimulating discussion, Wolfgang Wickler criticizes fuzzy usage of term mimicry by drawing attention to its original definition by H. Bates. Mimicry refers to functional 'model–mimic–selecting agent' trinity (with varying number of species involved) when the selecting agent (i.e. signal receiver) responds similarly to mimic and model to the advantage of the mimic. Concurring with Wickler I argue that convergence is neither necessary nor sufficient to support similarity as evidence for mimicry and that it is artificial and unproductive to classify mimicry with respect to ontogeny (innate vs. learned similarity) or model species identity (learning from conspecifics vs. heterospecifics). Using butterfly 'eye'-spots, I argue that just identifying each of the supposed model, the mimic and the selective agent, and even demonstrating that mimic-model similarity affects the agent's behaviour, provides no conclusive evidence for mimicry. Even a demonstration that the mimic benefits from receiver response may not provide conclusive evidence for mimicry. Using avian brood parasite–host egg and nestling mimicry, I emphasize that without experimental manipulation of the hypothesized mimetic traits, it is impossible to test the mimicry hypothesis robustly. Due to fundamental constraints on human perception, some cases of mimicry may in fact be just a by-product of human inability to perceive relevant differences between animal phenotypes (what is similar for human eye, nose or ear may not be viewed, smelled or heard as similar for relevant animal observers), whereas many cases of real mimicry may escape our attention from the same reason ('hidden' mimicry). Surprisingly, the same mimetic phenotype may show completely different effects on selective agents under different ecological circumstances. Finally, relatively dissimilar species may be more mimetic than highly similar model–mimic pairs because mimicry may be more fruitfully understood as a co-evolutionary process rather than a similarity.

Terms like 'mimicry', 'mimesis', 'mimetism', 'masquerade', 'crypsis' and 'camouflage' are often used with different or even contradictory meanings in the literature (no specific references needed – this issue becomes obvious after reading a dozen of randomly chosen articles or books that use those terms). This confuses students and researchers alike. Therefore, discussions about definition of terms, like the stimulating contribution by Wickler (2013), are essential – without shared opinions on what we mean by

particular terms, the science is doomed to fail (imagine that my understanding of what constitutes an 'adaptation' would not match your opinion; then citing my work as an evidence for adaptation in your work would be meaningless; see Williams 1966).

At the same time, such debates also cannot, in principle, be concluded to everyone's satisfaction because criteria underlying particular definitions are inevitably (partly) subjective. Just like a scientific ('Latin') genus name may refer to two completely

different organisms (*Arenaria* both flies in the air and photosynthesizes on land – depending on whether you are a zoologist or a botanist) also a term may refer to two completely different meanings; for example, 'adaptation' in evolutionary and behavioural biology is a very different thing from 'adaptation' in physiology and neuroscience (or, for that matter, in the literature and film-making). Obviously, a similar phenomenon may work not only between different fields of sciences but also within a particular branch of science; a behavioural ecologist would favour a functionally based definition ('mimicry is primarily deception, everything else is not important for definition of mimicry'), whereas a taxonomist may privilege a phylogenetically based definition ('mimicry is convergence, everything else is not important for definition of mimicry'). Just as the results may be determined by methods of investigation (Grim 2005a) or analyses (e.g. Trnka et al. 2012), criteria determine definitions. In the end, it is our own *decision* how we classify and define natural phenomena; the devil lies, among other things, in the fact that natural phenomena are mostly continuous, whereas definitions and terminological labels are necessarily categorical (Grim 2005b).

Keeping the above-mentioned qualifications in mind, it is still important to discuss what we mean by particular terms (e.g. Vane-Wright 1976, 1980). Sometimes it helps to return to original definitions, before the terms in question got misused and muddled in the literature. This is why W. Wickler went back to H. Bates who mixed the functional concept of mimicry with convergent evolutionary process, thus setting the stage for future confusions. Here, I am going to provide both specific comments on W. Wickler's opinions and additional ruminations on mimicry imbroglios.

Being a behavioural ecologist, I agree that it is useful to keep to the functional definition of mimicry. The key point, following from the fact that it is the signal receiver who brings mimicry into existence, is that 'The natural selecting agent is deceived not because key markings converge but because a stimulus and its meaning to the signal perceiver diverge.' (Wickler 2013). This automatically means that 'the question of analogous versus homologous, and of interspecific versus intraspecific, resemblance between model and mimic is irrelevant for deceptive mimicry to function' (Wickler 2013). Clearly, signal receiver simply responds to particular stimuli irrespective of their origin (innate/learned, homologous/convergent, etc.; see below). Definition and classification of mimicry should respect this biological reality.

The additional argument is that taxonomy is a meaningless factor in assessing mimicry, and this follows from two simple patterns: (1) any two biological species show some kind of similarity at least in some trait. This directly follows from Darwin's notion of a single origin of life followed by 'descent with modification'. Therefore; (2) similarity is not discrete; similarity is a phenomenon of continuity.

Proximate vs. Ultimate Perspective

Wickler views mimicry from the selective agent's perspective. According to him, the origin of similarity does not matter – it can be but need not be a convergence. For him, mimicry is primarily a *perceptual* phenomenon.

In contrast, in my own area of research (avian brood parasitism), mimicry is viewed strictly as *the* most decisive evidence for co-evolution between brood parasite and its host, although there is also the possibility of unilateral 'advergence' of the mimic to the model (Mallet 1999; Hauber & Kilner 2007), that is, 'sequential evolution mimicry' (Grim 2005b). The origin of similarity is critical for judging it as mimetic similarity; mimicry refers solely to cases when similarity evolved *specifically* due to discrimination by host of parasite eggs (Stoddard & Stevens 2012), chicks (Langmore et al. 2011) and adults (Welbergen & Davies 2011). Here, mimicry is primarily an *evolutionary* phenomenon.

Thus, some researchers may approach mimicry from a primarily proximate (mechanistic, perceptual) side, whereas others approach the same phenomenon from a primarily ultimate (natural selection, evolution) side. Before entering a heated discussion about which of these views is more useful, it is important to remember that this opinion discrepancy might simply follow from well-known general research traditions – throughout the 20th century, continental 'German' science was more descriptive and proximate, while insular 'English' and 'New World' science was more experimental and ultimate (see, e.g., works of Konrad Lorenz vs. Nikolaas Tinbergen).

This leads in some cases (but not all cases, of course) to opposing interpretations of similarities we observe in nature. Whydahs and indigobirds (*Vidua* spp.) parasitize African estrildid finches. If an estrild host tries to reject parasitism at the egg stage, it has little chance to do so – both its and parasite eggs are purely white and similarly sized; thus, there are few reliable signatures that could underlie host discrimination decisions. From the Wicklerian point of view, this is mimicry: the selective agent (host) is *perceptually* confused by the resemblance between its own eggs (model) and

parasite eggs (mimic). This forces hosts to accept the egg and benefits the parasite mimic (the latter being a necessary condition for mimicry to occur). From the brood parasitism researcher's point of view, this is not mimicry: *Vidua* (plus the cuckoo–finch *Anomalospiza imberbis*) are a sister taxon of estrildids, and therefore, the principle of parsimony dictates that both taxa inherited the plain white egg phenotype from their shared ancestors. No selection on the part of selecting (sic) agent happened or was necessary for parasite–host egg similarity to occur.

According to the proximate point of view, the origin of similarity is not relevant. In my view, the mimicry theory should be in line with the larger general principles of modern biology: the fundamental criterion behind any biological definition should be whether the phenomenon is an adaptation or a by-product of some other phenomena (Williams 1966). Thus, this fundamental criterion behind the definition of mimicry should be whether the similarity is an evolved adaptation or a mere by-product of some other phenomena (e.g. by-product of phylogenetic descent in the *Vidua*–estrildid example; see Grim 2005b).

According to Wickler, even particular individuals, of otherwise unpalatable species, that do not accrue or sequester poison, become automatically Batesian mimics of their Müllerian conspecifics. From a strictly perceptual view, this is again correct – the selective agent avoids palatable individuals because it confuses them with their poisonous conspecifics. From an evolutionary point of view, this is not correct – failure to accumulate poison by some individuals is just a failure, and the resulting confusion of selecting agent is just a fortuitous by-product of this failure. The difference between mimetic and non-mimetic similarity parallels the difference between adaptation and by-product. Williams (1966) gives numerous similar examples of fortuitous beneficial effects that are clearly no adaptations.

Mimicry from a Signalling Perspective

Mimicry can be defined as the opposite of crypsis. Crypsis is a decrease in signal to noise ratio (as emphasized by Wickler); thus, cryptic animals mimic background that is irrelevant to receivers. In contrast, mimicry is the increase in signal to noise ratio; thus, mimetic animals mimic biologically relevant ('interesting') aspects of the receivers' environment. Crypsis escapes receivers' attention, mimicry draws receivers' attention. Crypsis is concealment, mimicry is conspicuousness. Crypsis is noise, mimicry is signal.

Signal is defined as 'an act or structure that alters the behaviour of another organism, which evolved because of that effect and which is effective because the receiver's response has also evolved' (Davies et al. 2012, p. 395). Therefore, introducing 'signal' as an explanatory term automatically introduces 'co-evolution' (between sender and receiver), and so these two cannot be separated under this definition. It is, however, crucial to distinguish between signals and cues – the cue 'can be used [by receiver] as a guide to future action… but this feature has not evolved for that purpose' (Davies et al. 2012, p. 395). From the sender's point of view, signal is an adaptation, whereas cue is a by-product of something else.

Mimicry arises because the receiver perceives the signal (not a cue) released by the (prospective) mimic, responds to it, and the mimic evolutionarily responds by a change in its phenotype. Due to this (see also below discussion of human perceptual constraints), it might be more useful to view mimicry as a co-evolutionary process rather than phenotypic similarity (cf. Anderson et al. 2009; Stoddard & Stevens 2012).

Ad 'Taxonomists and Predators; Pseudomimicries'

As for arithmetic mimicry (a mirror image of Müllerian mimicry), it might be argued that any benefit from 'overeating' and 'dilution' effects would be soon countered by extra-intensity of predation: due to increased rate of encounters with its prey, the predator would develop a search image for that particular prey. This would increase its predation success (within-generation time scale), consequently increasing the predator's population density (between-generation time scale) and, thus, decreasing prey fitness (other things being equal). Also, joining a swarm may often result of joining individual being at the periphery of the swarm, where predation risk is increased.

In a comment on Vane-Wright (1976), Wickler argues: 'An ethologist … argues that the predator does not erroneously take coleoptera for hymenoptera but just responds in the same way to what it perceives to be one and the same stimulus'. In my view, this conflates a proximate description (predator responds to similar stimuli in the same way) with an ultimate interpretation of what happens (by avoiding palatable prey, the predator decreases its fitness). This is because the word 'erroneously' implicitly refers to negative fitness consequences for the predator.

I do not agree that the selecting agent should not be termed 'dupe' because it 'benefits from its response to [the signature produced by] the model'. What is going on solely between the model and the selecting agent

(i.e. the mimic ignored) is not relevant because, in fact, it is the existence of the mimic (with model-*like* phenotypic traits) that leads us to consider mimicry as a phenomenon at all. Elsewhere, Wickler himself states 'deception as key element of mimicry'. Importantly, signatures of model and mimic are never identical; they are, more or less, similar. Similarity in general depends on the length of co-evolution between mimic and selecting agent; obviously, similarity of model–mimic signatures must be, for purely statistical reasons of improbability of perfect initial similarity, initially crude and only later, in evolutionary time, become more detailed due to actions of the selecting agent (Stoddard & Stevens 2012). Thus, the pattern that the selecting agent responds similarly to signatures of model versus those of the mimic always follows from the imperfection of its recognition system (i.e. too permissive discrimination thresholds, *sensu* Reeve 1989). Because the selecting agent, by definition, will also commit acceptance errors (i.e. confuses the mimic with the model), I feel it is not derogatory to dub selecting agent 'dupe'.

Egg-Dummies and the Surprising Case of Startling Eyespots

Referring to his classic studies, Wickler (1965, 1968) introduces mouthbrooding cichlid fishes (Haplochrominae, Tilapiinae). Males 'develop egg-dummies which exploit the female's response of snapping up eggs to inhale sperm and fertilize the real eggs already in her mouth'.

The selecting agent may not always benefit from its response to the mimic, at least given the examples of characins and mouthbrooding cichlids. This is because we do not know whether females that would ignore the egg-dummy signatures presented by males and instead focus on other male traits would not have higher fitness than females that do respond to the egg-dummy signatures. In other words, it might be that males 'dupe' females by egg-dummy signatures that might be cheaper to produce than other more honest signals of male quality. A study of individual covariation between egg-dummy phenotype, male quality and causes and consequences of female preferences, would be enlightening.

Cichlid male 'egg-dummies' bring into mind the scenario of circular spots on butterfly wings. Those are historically considered to startle potential predators (Wickler 1968). Spots are paired and notably resemble, *to humans*, predator eyes. However, to use these observations (sic!) to conclude that lepidopteran eyespots undoubtedly (sic) mimic the eyes of avian predators, as habitually performed by all authors in the past, is a

logical error. This is because simple observations of effectiveness of 'eyespots' do not provide any evidence in favour of mimicry hypothesis – this can be tested solely by *experimental manipulation* of supposed mimetic *aspects* of the spots. Stevens et al. (2008) changed the shape, number and symmetry of spots (using artificial prey) and clearly showed that wing spots are effective merely due to a high contrast and conspicuousness and not because they resemble eyes. Both eye-like symmetry and circular shape may simply represent developmental constraints and are not functionally adaptive *per se*, making the startling-eyespot mimicry scenario an 'anthropomorphic conjecture' (Stevens et al. 2008). This example shows that just by identifying the supposed model, mimic and selective agent and even demonstrating that mimic-model similarity affects agent's behaviour, provides no conclusive evidence for mimicry.

Ad 'Mimicry: Gene-Based or Culture-Based'

Before turning to vocal mimicry, Wickler briefly mentions the fascinating phenomenon of cultural mimicry. As a birdwatcher, I feel it is noteworthy to draw attention to this example of mimicry that borders both cultural and vocal mimicry of non-human sounds by humans. I refer to 'pishing' – birders produce squeaking noises to entice birds to a closer approach. This might be one of the older examples of cultural mimicry in natural history – it dates back to as early as the 10th century (Zimmerling 2005). Importantly, the effectiveness of this cultural mimicry is quantifiable – it increases the number of species per study location by 20% (Zimmerling & Ankney 2000; Zimmerling 2005), and it has a known mechanism – structural acoustical similarity to heterospecific alarm calls (Langham et al. 2006).

Ad 'Vocal Mimicry'

Wickler's discussion of widowbirds, bullfinches, ravens, bowerbirds and drongos give a good case for not basing the definitions of vocal imitation and vocal mimicry on their ontogeny (innate or learned, from conspecifics or heterospecifics). This is because various above-mentioned species copy both hetero- and inter-specific sounds in the same ecological context and later may serve as models for their conspecifics.

That it makes little sense to differentiate between vocal mimicry and imitation is clearly exemplified by Horsfield's bronze-cuckoos *Chalcites basalis* (Langmore et al. 2008). This cuckoo's chick is innately pre-tuned towards begging calls of its primary host species (see also Colombelli-Négrel et al. 2012). However, if the nestling is transferred into a nest of different host

species, the chick gradually adjusts its vocal performance to the begging call structure of that alternate host (Langmore et al. 2008). Thus, vocal mimicry is both innate and learned at the same time. *Chalcites* cuckoos are another strong case against the notion that imitation does not give rise to mimicry.

What Complicates Identification of Mimicry?

Equifinality: Mimicry may be a Mix of Mimetic and Non-Mimetic Similarities

As Wickler argues the convergence among phylogenetically not closely related taxa is neither necessary nor sufficient for mimicry to occur. For example, egg colour of brood parasites and their sympatric hosts may be a convergent result of shared nest predators, diet and environmental conditions (Grim 2005b; Avilés et al. 2007). Here, mimicry is a mix of actual mimicry (i.e. parasite egg vs. host egg similarity selected by host's rejection of foreign eggs) and a by-product of processes that have nothing to do with mimicry (mechanisms that impact egg colour independently of presence or absence of brood parasites). Thus, the same endpoint (shared egg colours) may be reached through different evolutionary avenues (equifinality *sensu* Michel & Moore 1995).

Multifinality: Selective agents may Select for Different Mimicry in a Single Mimic

Different ontogenetic stages of the mimic may also beneficially resemble different models. In Australia, *Chalcites* cuckoo eggs may mimic the colour of the lining of dark domed host nests (Langmore et al. 2009; see also Grim 2011), whereas chicks may mimic host's own young both visually (Langmore et al. 2011) and acoustically (Langmore et al. 2008). In Europe, *Cuculus canorus* cuckoo eggs mimic host eggs (Stoddard & Stevens 2012), whereas the adult parasites mimic raptors (Davies & Welbergen 2008; Trnka et al. 2012).

Selective agent may not Select for Mimicry

Although the receiver may reject some undesirable recipients, this does not automatically select for mimicry, as it may happen when the cue for rejection is not phenotypic. For example, reed warblers (*Acrocephalus scirpaceus*) (selective agent) desert some cuckoo chicks (potential mimics), because the parasite spends too much time in the host nests (Grim 2007). Although visual or vocal mimicry in parasite chicks is empirically possible (Langmore et al. 2011), it cannot

evolve in the warbler–cuckoo system because host existing defences cannot be breached by the parasite (Anderson & Hauber 2007). Despite some chick discrimination, the existing phenotypic similarities between warbler and cuckoo chicks do not represent mimicry.

How our Research Methods Constrain our Understanding of Mimicry?

Methodological approaches and constraints may also have profound effect on what is considered mimicry. Before the application of reflectance spectrophotometry, it was impossible to make a strong test of visual mimicry in non-human taxa, because humans do not perceive the ultraviolet (UV) part of the spectrum visible to many animals. Thus, model–mimic pairs of avian eggs might have gone unnoticed by human researchers simply because the existing similarity was 'hidden' in UV and, consequently, could not draw researcher attention to induce them to start to even study the particular model systems (e.g. Starling et al. 2006). But the opposite holds, too: the limitations of perceivers sensory systems may suggest resemblance or mimicry where there is none. Compared to tetrachromatic avian vision, all mammals – which are di- or trichromatic – are in a sense 'daltonistic' compared with birds that are often tetrachromatic. Thus, objects seen as 'different' by birds may be seen as 'similar' by humans. Moreover, even model–mimic interactions with some evidence for being involved in a mimicry process might have been misunderstood because the observed visual similarities theoretically represented only non-functional correlates of hidden UV-phenotypes with only the latter being the target of evolutionary change driven by selective agents (i.e. the problem of spurious correlation; see also Williams 1966).

Another limitation of most studies (at least, within my study area of avian brood parasitism) is to focus on single mimetic traits. Example: cuckoos of the genus *Cuculus* were for a long time noticed for their uncanny similarity to hawks (*Accipiter*) (Payne 1967). Recent research showed that presence of the underpart-barring (shared by cuckoos and hawks) reduces mobbing by potential cuckoo hosts (Davies & Welbergen 2008; Welbergen & Davies 2011). Thus, it seemed that cuckoo 'hawk-mimicry' was represented by the underpart's phenotype. However, Trnka et al. (2012) tested the same hypotheses and, additionally, manipulated not only the underpart-barring (presence/absence) but also another conspicuous trait shared by cuckoos and sparrowhawks – the yellow eye.

Although this latter study validated the findings of Welbergen & Davies (2011) by detecting statistically significant effect of underpart-barring on host responses, it also shed a completely different light on the problem. This is because only 5% of explained variation in host behaviour was attributable specifically to underpart-barring; in a striking contrast, 95% of explained variation was attributable specifically the eye colour (both traits together explained 66% of variation in host behaviour). This finding also makes good behavioural sense: hosts arrive to their nests always from above and, therefore, always see intruding cuckoo's head but rarely see its underpart (as evidenced by photographs showing interactions of cuckoo and its host at the latter's nest, e.g., p. 19 in Yoshino 1999). Also, passerines mobbing cuckoos attack not their underparts, but their head (p. 12 in Yoshino 1999). The implication is that the focus on a single trait in the former study gave misleading impression what constitutes the major component of mimicry in the cuckoo–hawk–host complex.

The just discussed example of hawk-mimicry provides an additional level of complexity to our understanding of mimicry. The surprising twist to the hawk-mimicry story is that in England underpart-barring *decreased* host aggression (Welbergen & Davies 2011), whereas in Slovakia, the same trait *increased* host aggression (Trnka et al. 2012). How to explain this seeming paradox? Ecological context is the cue (analogously to perceptual context in cognitive studies, see p. 46 in Matlin 2006). At the England site, sparrowhawks are common. Thus, barred underparts denote deadly enemy and trigger host escape. At the Slovakian site, sparrowhawks are absent. Thus, barred underparts denote brood parasite and trigger host aggression. It seems that geographically variable costs and benefits associated with responses to model and mimic may revert the nature of interactions (escape/attack) between mimic and its selective agent (for detailed discussion, see Trnka et al. 2012). Although one possible interpretation of cuckoo-hawk similarity is that cuckoos are innocuous (for *adult* hosts) Batesian mimics of deadly hawks, it may be that in some populations/species, the evolution improved host discrimination abilities to the point where mimetic cuckoo–hawk similarity is no longer effective (i.e. hosts are not 'fooled' by a previously evolved mimicry and, instead, use the mimetic traits themselves as cues to specifically recognize the brood parasite). In parallel, Stevens et al. (2008, p. 526) also mention that lepidopteran wing spots may either decrease and increase predation risk, depending on the quality of the surrounding background.

Mimicry is not Similarity

In his Conclusions, Wickler homes in on the fundamental issue of confusing similarity with mimicry. This echoes with common misconception in my own study area, avian brood parasitism (Grim 2005a,b). In fact, jumping from the observation and documentation of mere similarity to an interpretation of that similarity as being mimicry is not substantiated. This is due to three theoretical reasons, all of them supported by ample empirical evidence.

First, similarity is continuous. Mimicry is a label and, thus, a category. Therefore, there is a risk that we fail to detect many cases of mimicry simply because they are below our own, human 'this looks like mimicry' sensory–perceptual–cognitive threshold.

Second, the existence of obvious (to humans) similarity between *supposed* model and mimic may result from many processes, several of them having nothing to do with mimicry. Similarity due to common descent, of course, is simply an inevitable by-product of phylogeny, not mimicry (see plain white eggs of viduine parasites and their estrildid hosts). Despite seemingly large variation in their phenotypes, avian plumage or egg colours occupy only smaller part of potential colour space, that is, the range of colour birds can see (plumage: Stoddard & Prum 2011; eggs: Cassey et al. 2012). The combination of large number of bird species and the limited variation in their colour phenotypes inevitably means that many species are strikingly similar simply due to a statistical chance. Obviously, any such similarities are not necessarily mimetic. Also, convergence due to common environmental factors, like diet composition which affects avian colours, is clearly non-mimetic.

Third, the absence of similarity for the human eye does not mean that seemingly dissimilar species are not involved in model–mimic relationship. Mimicry may be restricted to invisible (for humans) parts of the light spectrum (Starling et al. 2006). Also, the selecting agent may be 'interested' (i.e. perceptually tuned) into only a fraction of the model/mimic phenotype (Polačiková & Grim 2010); then measuring the whole model/mimic phenotype (e.g. whole egg, instead of only a part of its surface, namely the blunt egg pole) may mask biologically relevant similarities and differences (Polačiková et al. 2011).

Fourth, the definition of mimicry as a *relationship* among model, mimic and selective agent implicates that there is a co-evolution between the agent's recognition system, the mimic phenotype and the model phenotype. If we understand mimicry not as a

similarity but as this co-evolutionary *process,* we then avoid the risk of mistakenly rejecting dissimilar model/mimic systems as being 'not mimicry' and mistakenly accepting similar model/mimic systems as being 'mimicry'. This leads to a counterintuitive conclusion: imagine eggs of two parasites, parasite 1 lays eggs that are *very* similar to its respective host's eggs, parasite 2 lays eggs that are *poorly* similar to its respective host's eggs. Reading of brood parasitism literature will suggest that great majority of researchers arrive at the conclusion that eggs of parasite 1 are 'highly mimetic', but eggs of parasite 2 are 'poorly mimetic, or even 'non-mimetic' (no need to give references, see virtually any article on cuckoo or cowbird eggs). However, when we empirically measure the rejection rate of parasite 1 and parasite 2 eggs by their hosts, we find that eggs of parasite 1 are often rejected, whereas eggs of parasite 2 are rarely rejected. This leads to exactly opposite conclusion compared with that above: eggs of parasite 1 are 'poorly mimetic', and eggs of parasite 2 are 'highly mimetic'. This directly follows from the definition of mimicry: the function of mimicry is to confuse the selective agent. Therefore, the more eggs of particular parasite successfully confuse the selective agent (to accept them and rear them) the better the mimicry. In other words, mimicry is solely in the eye of the beholder. How model–mimic similarity is judged by humans, subjectively (by naked eye) or objectively (by spectrometry) is irrelevant for measuring the quality of mimicry. Only host *behaviour* (the rate of egg acceptance or rejection) is the ultimate judge of whether mimicry is relatively poor or excellent.

Conclusions

Mimicry researchers should carefully consider the issue of equifinality (Michel & Moore 1995) – similar effects can be produced by multiple causes; this holds also for phenotypic similarity which lures us to invoke mimicry in cases where there is none (Grim 2005a,b; Stevens et al. 2008). At the same time, let us not forget that multifinality (Michel & Moore 1995) can also confuse us, too – egg mimicry may manifest itself in multiple traits and their combinations (Spottiswoode & Stevens 2010), may be limited to only a part of the egg's external phenotype (Polačiková & Grim 2010; Polačiková et al. 2011) and may escape our human attention altogether if we forget to use spectrometers (Starling et al. 2006). Similarity – to human eyes – may, in turn, lead researchers astray: any two natural objects fall somewhere along the continuum of similarities in shape,

colour, pattern, movement, etc. For purely statistical or psychological rules-of-thumb reasons (e.g. despite the *large* number of living bird species, they display a surprisingly *small* set of realized variation in their plumage, Stoddard & Prum 2011), we may tend to see mimicry where there is none. Therefore, similarity for the human eye does not *per se* support the hypothesis of mimicry. In turn, the absence of similarity for the human eye does not reject the hypothesis of mimicry: mimicry may be cryptically 'hidden' in UV-part of the spectrum. Thus, traditional examples of mimicry may just be the tip of the sensory–evolutionary mimicry iceberg.

Acknowledgements

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