

Semiotic modeling of mimicry with reference to brood parasitism

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Abstract. Biological mimicry can be considered as having a double-layered structure: there is a layer of ecological relations between species and there is a layer of semiotic relations of the sign. The present article demonstrates the limitations of triadic models and typologies of mimicry, as well as their lack of correspondence to mimicry as it actually occurs in nature. It is argued that more dynamical semiotic tools are needed to describe mimicry in a theoretically coherent way that would at the same time allow comparative approach to various mimicry cases. For this a five-stage model of analysis is proposed, which incorporates classical mimicry theory, Jakob von Uexküll's Umwelt-theory, as well as semiotic and communication analysis. This research model can be expressed in the form of five questions: 1) What is the formal structure of mimicry system? 2) What are the perceptual and effectual correspondences between the participants of mimicry? 3) What are the characteristics of resemblances? 4) How is the mimicry system regulated in ontogenetic and evolutionary processes? 5) How is the mimicry system related to human cultural processes? As a practical example of this semiotic methodology, brood parasitism between the common cuckoo *Cuculus canorus* and his frequent host species is examined.

Over the years, a vast number of writings on mimicry has been published in biological literature, most of these being case studies of specific mimicry resemblances. For instance the bibliography of mimetic phenomena compiled by a historian of biology and mimicry specialist Stanislav Komárek exceeds 5000 items (Komárek 2003: 7). However, there are much fewer systematic accounts of mimicry that aim at providing comparative and comprehensive overview of different mimicry instances. The few existing mimicry typologies appear to be too static for matching the complexity of actual research. It is more common that the case studies form specific traditions of study by including also many ecological aspects of the observed species. Vivid examples are offered by studies on brood parasitism, mimicry rings in *Heliconius* butterflies or wasp–hoverfly mimicry complex. The aim of the present article is to propose a methodology based on biosemiotic research methods that would allow dynamical and comparative description of various mimicry cases. This methodology is exemplified by focusing on one specific mimicry type — brood parasitism.

My article is grounded on the established terminology, in which the phenomenon of mimicry is considered to be a tripartite relationship between: 1) an imitating organism (the *mimic*); 2) an object of imitation (the *model*); and 3) a deceived or confused organism (the *receiver*) (Wickler 1968: 8–10; Vane-Wright 1976: 28, 30; Pasteur 1982: 171–173). All three parties together form a mimicry system that is a relatively consistent structure in virtue of being regulated by relations amongst the participants. For instance in the case of protective mimicry, where a broad-bordered bee hawk-moth *Hemaris fuciformis* resembles a bumblebee for a European pied flycatcher *Ficedula hypoleuca*, the hawk-moth can be considered the mimic, the bumblebee the model and the flycatcher the receiver. The mimic in the mimicry system is generally considered to gain an evolutionary or behavioural benefit and the receiver mostly to suffer because of the interaction. The position of the model varies depending on the specific

mimicry type: in classical Batesian mimicry the model suffers because of the mimic's presence, while in aggressive mimicry the model often benefits. This tripartite mimicry model has its roots in the works of a German biologist Wolfgang Wickler (1965, 1968) and it has greatly improved the comprehension of mimicry by leading to the formalized description of mimicry, establishing of new mimicry types and creating typological schemas of the mimicry systems (for example, Pasteur 1982; Wiens 1978; Vane-Wright 1976). For semiotics the main advantage of this kind of a threefold model appears to be in highlighting the possibility to analyze mimicry from different perspectives: as a communicative relationship between the model and the receiver, as a resemblance-based relation between the model and the mimic, and as a deceptive relation between the mimic and the receiver (see Maran 2008: 99–104)¹. At the same time it seems that the triadic description of mimicry as consisting of the mimic, the model and the receiver also has its serious drawbacks.

Critical discussion of the triadic mimicry model

The tripartite model presumes the presence of the relations of resemblance between three participants mostly concretized as species.² This actually does not appear to be a very common situation in nature. It is more frequent that one of the three positions of the triad is filled by several species: for instance the resemblance between the broad-bordered bee hawk-moth and bumblebees can be confusing also to

¹ This paper is conceptually and terminologically grounded on my previous studies on semiotics of mimicry (Maran 2007, 2008, 2011).

² This does not necessarily mean that there are three species involved in the mimicry system. Quite often two species fill the three roles: for instance the model and the receiver can belong to the same species, as it is usual in aggressive mimicry. Also common mimicry typologies acknowledge such possibility and include the category of bipartite mimicry systems.

shrikes *Lanius sp.* and to several other insectivorous bird groups beside flycatchers. In a similar way, also the position of mimics and models can be filled with more than one species. Furthermore, the number of species and their individuals that can participate in a mimicry system is in many cases not limited; besides the dominant participating species there may also be occasional participants, for instance omnivorous birds, for whom the moths form a small part of the diet and for whom confusing a hawk-moth with a bumblebee is a rare event. In some other cases the involved species cannot be clearly divided between mimics and models and the participating species rather form a fuzzy set of resemblances, called the Müllerian–Batesian mimicry complex. In such case the difference in edibility or dangerousness of the involved species is not clearly established, or it may vary between individuals or develop during their life.

The number of participating species in a mimicry system is not the only problem for the triadic description of mimicry. German theoretical biologists Zabka and Tembrock have argued that in many cases the model cannot in principle be reduced to a single species, as it is for instance in the case where decaying meat is mimicked by carrion-flowers to attract flies, which are looking for carcasses to lay their eggs (Zabka, Tembrock 1986: 172). The same type of phenomenon is described by Georges Pasteur as semi-abstract or abstract homotypy (Pasteur 1982: 191) and by Maran (2007: 239–243) as abstract mimicry, the examples of which cover a wide array of phenomena from eyespots to deimatic displays. In the case of abstract mimicry the object of imitation appears to be some abstract meaning in nature and its physical expression, for instance dangerous situations are marked by a sudden change of affairs.

A third source of problems is a possibility that one and the same individual can be simultaneously involved in more than one mimetic resemblance; a combination that can in some cases have structural importance for the mimicry system. For example, in its aggressive mimicry system, the monkfish *Lophius piscatorius* combines cryptic

resemblance of its body surface (mimic) to seafloor rich in algae and other plants (model), and the resemblance of its foremost fin ray (mimic) to a worm (model). The first type of resemblance serves to make the monkfish hard to notice and the second type helps to lure and catch smaller fish (signal-receiver). Both resemblances support each other and are active during the same communicative interaction between the monkfish and its prey species. Such instance of mimicry cannot be easily accommodated by the classical mimicry triad.

When trying to formalize these examples, it appears that systemic approach to mimicry has problems in 1) defining the set of elements (species) that belong to the (mimicry) system as a whole; 2) determining the location of elements with regard to predefined classes of mimics, models, and receivers; 3) presence of classificatory error, that is, the same element can belong to more than one class, or the same element can belong to more than one system. A partial solution to this problem would be to reconsider the mimicry triad to be a logical and conceptual relationship between three entities and not to take this as a necessarily ecological relationship between three species. In some cases the involvement of actual species may correspond to the roles in the mimicry triad, but this is not, by any means, an inevitable condition. Another possibility would be to consider mimicry system as having a double layered structure, consisting of a layer of ecological relations between species and a layer of semiotic relations of sign. Species, or more correctly their particular populations, are indeed the actual biological entities that are involved in different ecological relations such as predation, competition, parasitism and others, and their number and evolutionary characteristics can also change because of a particular relation. The second, semiotic layer would include a specific relation of resemblance, in which case we may ask "What resembles what to whom in what respect?" On this level we are dealing with specific qualities and their similarity in the eyes of a particular

beholder.³ These two layers can combine with each other in many different ways and produce different types of mimicry systems.

In addition to the rigidity of the triadic system of mimicry, also a radical differentiation that is often assumed to exist between mimicry and other adaptations can become an obstacle for studying various resemblances in nature. Quite often we find in scientific literature arguments in favor of regarding one or another resemblance in nature as mimicry: such arguments thus presuppose that a distinct category of mimicry systems does exist. When we think about many occasional similarities between species, about the previous example of facultative mimicry, and about the fact that the recognition/ misrecognition between mimics and models by the signal-receiver is probable, then the clear demarcation line between what is mimicry and what is not disappears. Instead, we should rather talk about a *landscape of mimeticity* in nature or the capability of the natural forms to create confusion. The concept of mimicry would become reserved for well-formed examples of deceptive resemblances but at the same time one should keep in mind the probabilistic nature of the phenomenon.

This discussion is also closely related to the way how the existence of mimicry systems in nature is argued for and proved. The strongest possible proof for mimicry as an evolutionary phenomenon is the demonstration that the change in some evolutionary agent (animate or inanimate) has caused a specific mimicry adaptation to emerge or proliferate. An example of this kind of strong proof are studies on the abundance of dark-winged moths in Great Britain during the rise of coal-based economy in the nineteenth century, where the darkening of the visible environment correlates with the amount of melanismic moths (for example, Berry 1990), although even this case has been an object of disputes. Such strong proofs are however more than rare,

³ A Danish biosemiotician Jesper Hoffmeyer has described such semiotic layer accompanying ecological relations as semethic interactions (Hoffmeyer 2008: 189).

especially in the face of common claims about mimicry as an evolutionary adaptation *par excellence*. More often the existence of mimicry is argued for by indirect proofs, such as the correlation between the specifics of the receiver's sensory perception and the resemblance between the mimic and the model; correspondences of the living areas of mimics and models; indications of predatory pressure such as the relative abundance of the mimic and the model in the diet of a predatory receiver; or the location of injury in the mimic's body regarding mimetic features (such as birds' peak marks on butterfly wings); behavioral responses of the receiver to specific appearances of models and mimics (warning coloration); the receiver's ability to learn from unpleasant experiences with models; experiments with the manipulation of mimetic features, for example, painting mimetic features onto a non-mimetic organism or covering up mimetic features etc. These various arguments are indirect in the sense that although they demonstrate various correlations between mimics and models or illustrate how an organism benefits from mimetic features, they cannot prove that mimetic features have developed because of the specific relations between models, receivers and mimics. At the farthest end of this scale of validity are cases where human senses are used to determine mimetic relations — if a mimic and a model seem similar to us, a mimicry resemblance is judged to exist. A good illustration for such connection between human sensed similarity and supposed mimicry resemblance are the artistic works and academic writings of an American painter and naturalist Abbott H. Thayer (1909).

Thus, the problem with the perception of mimicry in mainstream biology has two sides. First, mimicry is often seen as a distinct phenomenon that has definite borders and secondly, it is also supposed to be provable as such. Many classical examples of mimicry in nature and also arguments used to explain these do not, however, correspond to this wide-spread idea. To alleviate this problem and to bridge the gap between mimicry systems theory and actual case studies, it would be beneficial to have more dynamical descriptions of resemblances in

nature that would not take the existence of mimicry as a clear-cut tripartite system as a prerequisite. For providing such tools of description, biosemiotic approach can turn out to be helpful, first because of structural methodologies that are available in semiotics, and also because biosemiotics does not rely on evolutionary functionality as a primary criterion for delimiting research objects, which makes it more responsive to such features of organisms whose advantage to their carriers is not obvious at first sight.

Toolbox for modeling mimicry

A wider and semiotics-based methodology, proposed in this paper, is not strictly grounded on a single theoretical foundation but consists rather of a group of various methods that could be used like a toolbox to approach different types of mimetic resemblances. In building this approach, I have integrated aspects of the classical mimicry theory, Jakob von Uexküll's Umwelt-theory, and semiotic and communication analysis into a model of five-level analysis. Questions related to the meaning and significance of a deceptive resemblance are not part of these tools, but are rather considered as a part of the initial research hypothesis that is either supported or rejected as an outcome of the analysis.

The first level of analysis departs from the classical tripartite Wicklerian model consisting of a mimic, a model and a receiver. Rather than trying to match this to every mimicry system, I would extend it to a general principle, and ask what kind of configurations mimicry could take. For instance mimetic resemblances in monkfish could be expressed as a compound model that includes one mimic and one receiver, but two models: the background of the environment and the movement of a worm-like prey of the fish (see Fig. 1a). In a similar way, also mimics and receivers could be manifold. The mimetic resemblance of cuckoo bumblebees (subgenus *Psithyrus*) could in

most cases be described as a compound model that includes one mimic and one model (a particular bumblebee species) but two receivers: bumblebee host species (being simultaneously the model and the receiver) and insectivorous birds (see Fig. 1b). On this level of analysis it is also possible to distinguish in general terms between mimicry and other types of resemblances. If it is possible to point out all three parties — a mimic, a model and a receiver, given that the receiver is not a human observer — then the resemblance can be regarded a mimicry system. If this condition is not met, then some other type of resemblance, such as similarity because of an evolutionary affinity or convergence or some resemblance induced by human cultural description should be suspected.

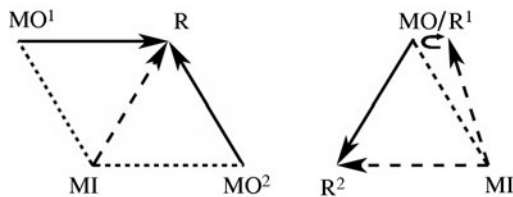


Figure 1. Schematic representation of complex mimicry systems. The unbroken arrow line represents the communicative relation between the model (MO) and the receiver (R) that is exploited by the mimicry system. The dashed arrow line represents the deceptive relation between the mimic (MI) and the model. The dotted line represents the relation of resemblance between the mimic and the model. *Left:* monkfish with two distinct models $MO^{1,2}$ (a worm and the sea bottom). *Right:* cuckoo bumblebee with two distinct receivers $R^{1,2}$ (a bumblebee host and an insectivorous bird, a host R^1 being at the same time also a model MO).

The second level of analysis proceeds from the Umwelt theory of Jakob von Uexküll, and focuses on the corresponding body structures of the mimic, the model and the receiver or the properties of the original and the imitated signal, as well as used communication

channels and behavioral regulation (*Merkwelt* and *Wirkwelt* in Uexküllian terms). On this level of analysis a more specific description of the resemblance can be achieved. For example, from a general biological perspective, one can say that in a broad sense, the fly orchid *Ophrys insectifera* as a plant is a mimic, but proceeding from Uexküll's theory of Umwelt, the similarity between the plant and the female of a particular wasp species is much more specific by being bound only to the outer surface of blossoms (see Maran 2007: 237). The second level of analysis enters the field of qualitative phenomena, by describing the specific percepts and activities that are employed in mimicry. Umwelt analysis *sensu* Uexküll (1982: 52–57) can bring out the correspondence or the non-correspondence between the perceptual capabilities of the animal receiver and the body structures of the mimic and the model. This enables to reason if the mimic and model are deceptively similar for the receiver, or, are they even perceptible at all. Paying attention to the *Wirkwelt* and the behavior of the receiver regarding the mimic and the model allows us to make conclusions about the relevance of the resemblance for the receiver. This is a significant question, as in many cases the deceptive resemblance between two objects does exist for the receiver, but it is irrelevant like it is irrelevant for an average human to distinguish between bumblebees and bee hawk-moths that mimic these. By such argumentation, mimicry becomes grounded in the ethological functionality and not in the evolutionary functionality that would be much more difficult to prove.

The third level of analysis proceeds explicitly from semiotics as the study of signs and sign systems and focuses on meaningful units that resemble each other in mimicry. This level of analysis addresses the general conditions that make it possible for a confusion to emerge. A starting point for this discussion is an understanding that resemblance in mimicry is not univalent, but that there are different possibilities for resemblance to occur. First, the resemblance can be described as a matter of degree ranging from non-resemblance to absolute similarity. Also concepts used in psychological studies of categorical perception,

such as boundary perception, common characteristics resemblance, prototype resemblance and others can be employed in distinguishing between various possibilities for a resemblance to emerge. In mimicry studies, three different types of resemblance can be discerned on the basis of Peircean semiotics. This simplest type of resemblance can be described as a relation between one and lots and it is common in camouflage, for instance when a moth is lying on a tree bark. Here the perception of the moth emerges from nowhere and that allows us to relate camouflage to Peircean firstness. The second type of resemblance is present when we are dealing with deceptive similarity between representatives of two species of which one is edible and the other poisonous, as is the case of the typical Batesian mimicry. Such type of mimicry requires comparison, a reference to the second, and seems therefore to relate with Peircean secondness. The third type of mimicry is present for instance in the case of eye-marks on the bodies of insects, fish and amphibians, or in the case of colorful patches on the bodies of many lizards and insects. These patches are kept hidden in the normal body position but flashed during escape. It seems that the unifying aspect of such mimicry systems is a common meaning: thus, for instance big eyes, unexpected movement or warning coloration all signify something dangerous for the receiver. Such abstract mimicry requires that the meaning of the message is understood by the receiver and seems therefore to relate to thirdness. Besides this kind of distinction based on Peircean categories, mimicry can also be described as fixed or adjustable, partial or complete, local or general, individual or collective, embodied or detached, etc. (for discussion on many of those possibilities, see Pasteur 1982).

The fourth level of analysis proceeds from a cybernetic communication analysis of the mimicry system (Maran 2008: 19–24) by focusing on the position and nature of feedback cycles. Feedback enables dynamics to enter the act of communication and it also enables the sender to change its behavioral and communicative activity with respect to the receiver's activity. On the metalevel, feedback in

communication allows to adjust messages and to choose between them, which in the long run enables the development of sign systems. In ecological relations that involve communication, it is possible to distinguish between communicative, ontogenetic and evolutionary levels of feedback regulation (see Maran 2008: 21–22). In communicative feedback resemblance is regulated within a single act of communication. This is a prevalent regulation mechanism in behavioral and adjustable mimics such as the chameleon's changing of colours to correspond to a specific environmental background. Through ontogenetic feedback an individual's personal experiences are formed or expressed. In phylogenetic or evolutionary feedback, genotypic adaptations related to this particular communication act develop or manifest. Distinguishing between different types of resemblance regulation allows us to include among mimicry also such resemblances that are induced by epigenetic memory, for example, by animal cultures where the dependence on genetic causation cannot be proved. This level of analysis helps to focus on dynamical, reversible and individual aspects of mimicry resemblance, such as individual song imitations by many birds, for instance European starling *Sturnus vulgaris*.

The fifth level of analysis proceeds from the cultural level and focuses on the observer's perceptual involvement in the mimicry system as well as on the cultural and scientific status of the phenomenon. This level of analysis deals with the human observer in relation to the mimicry system. The starting point for this discussion is understanding that Umwelten of the human observer and of other living beings participating in a mimicry system are likely to be different. Besides deceptive similarities perceptible to the human observer, there may also occur situations when the messages of the model and the mimic are situated with respect to the Umwelt of the human observer in such a manner that from the latter's viewpoint, they do not seem similar (for example, the red helleborine *Cephalanthera rubra* and the bellflower *Campanula* sp. are similar to a bee

but clearly different to the human eye). Likewise, a whole communication system may be left concealed from the human observer. The location of a deceptive similarity in relation to the Umwelt of a human observer may bring about a biased choice of the object to be studied and may lead a nature scholar to under- or over-interpret some mimicry cases.

Besides the relations between an observer's sense organs and a mimicry resemblance also the cultural-historic component of mimicry needs attention. There are mimicry systems that have a long history of being studied because of the peculiarities of the history of science. For example, mimicry in butterflies is a well-established field partly because of the activity of the nineteenth-century naturalists in collecting insects. A collector's main interest is to identify items correctly. This desire of the naturalists helped to advance systematics but at the same time drew attention to the confusions and ambiguities in nature, including mimicry. In addition, descriptions of mimicry resemblances may also include cultural, religious or mythological layers. This is related to a historically much earlier search for and interpretation of signs of nature (so called *signatures*) that have been believed to have their origins in a supernormal or divine source. The cultural layer, which remains clearly out of the biologists' scope, can still interest semiotics that interprets resemblances in nature and in human culture not as distinct fields but as a continuous complex phenomenon.

Applying semiotic modeling to brood parasitism

As a practical example of the semiotic analysis of mimicry, I am going to use the methodological tools introduced above to describe brood parasitism as one specific case of deceptive resemblances in nature. More specifically, I will take under observation the semiotic and ecological relations between the old world cuckoos, especially the common cuckoo *Cuculus canorus*, and its frequent host species in passerine

birds. This example has been thoroughly studied by contemporary evolutionary biology and is therefore suitable for testing the methodology. I will focus mostly on the resemblance of eggs although I will shortly discuss also other resemblances related to brood parasitism. The analysis is based on various sources of biological literature, but my argumentation and point of view will remain semiotic.

For the interpreting subjects — birds — the primary question with regard to brood parasitism is related to recognizing eggs. The image of the egg as such can be considered to be a ‘biological universal’ that is meaningful to various species. Most animal taxa have some evolutionary experience with eggs that have been around on our planet for about 500 million years if we start counting from chordates, and even more if we include insects. When we look for the meaning of eggs, the most immediate answer would be ‘reproduction’ — eggs stand for the offspring. This goes with the observation that there are no abstract eggs, eggs always belong to somebody, and in many species eggs are considered worth keeping and defending. On the other hand, many predatory and omnivorous mammals, birds and reptiles view eggs as a possible food source and some species such as egg-eating snakes (*Elachistodon*, *Dasypteltis*) are specialized in them. Besides, egg shells can be used as an indexical sign for detecting the presence of a bird nest, and in order to avoid being revealed, some bird species carry shell pieces away from their nests.

For brood parasites, eggs signify an opportunity to reproduce: cuckoos and other brood parasites tend to lay eggs into nests where some clutch is already present as empty nests can be easily abandoned by hosts. Brood parasitism is a very widespread biological phenomenon. It is estimated that approximately 1% of all bird species use some sort of brood parasitism, including nearly half of 130 species of cuckoos, some cowbirds, indigobirds, whydahs, two genera of finches and some ducks (Payne 1977: 1). Most brood parasites are specialized in specific host species. The common cuckoo has more than 100 potential hosts, the most usual of these include reed warblers

Acrocephalus, leaf warblers *Phylloscopus* and warblers *Sylvia*, robin *Erithacus*, redstarts *Phoenicurus*, wagtails *Motacilla* (Honza *et al.* 2001: 344) (Fig. 2). In some populations of host species brood parasitism may affect up to 65% of all nests (Moskát, Honza 2002).

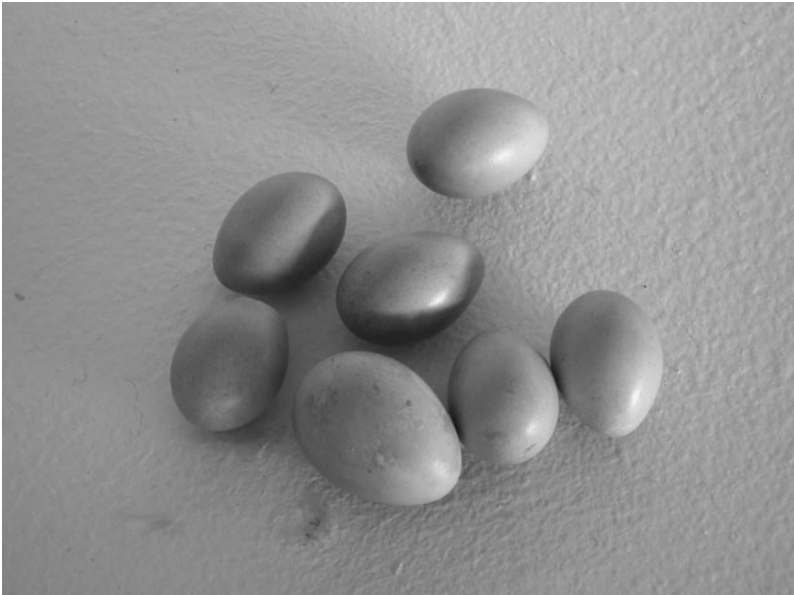


Figure 2. An egg of a common cuckoo in a clutch of a common redstart *Phoenicurus phoenicurus* (collection of the Natural History Museum of the University of Tartu, the author's photo).

If the tripartite model of mimicry is used in the studies of brood parasitism, some difficulties seem to occur. Case-studies in brood parasitism encounter the ecology and biology of parasites and their hosts as a whole set of adaptations that include many types of similarities with different causes. In practical studies a question arises — should all similarities be included under the concept of

mimicry or should they rather be differentiated. A Czech zoologist Tomáš Grim (2005: 70–72) notes that the similarity between the eggs of a cuckoo and its hosts can have several sources: besides mimetic evolution also phylogenetic closeness, or environmental similarities that could influence the coloration of both host and parasite eggs in the same way, or predation pressure by similar visually orientated predators. Even competing female cuckoos can become an evolutionary factor influencing the appearance of eggs when they remove from the host's nest an egg that is least similar to the rest of the clutch — which can be an egg laid by a previous cuckoo (Grim 2005: 71–72). A second argument supporting the claim, that egg mimicry cannot be separated from the overall ecology of the species, is the dependence of the accuracy of recognizing one's own eggs and imitations on the living habits of the host species. For instance, the accuracy is lower in the case of hole-nesting species (for example, redstarts *Phoenicurus phoenicurus*) than in the case of open-nesting species. This can be explained by lower ecological pressure of brood parasites with regard to hole-nesting species: it is difficult for an adult cuckoo to lay eggs into holes, and it is also difficult for a host parent to throw a cuckoo egg out of the nest as well as for a cuckoo chick to throw out host eggs (Avilés *et al.* 2005: 609).

It seems that the complexity of brood parasitism exceeds far beyond the simple triadic structure of the mimicry system and the issue of similarity and recognition between the brood parasite and the host species. In the following I am going to take the egg mimicry in cuckoos as a test case for the abovementioned research methodology, which can be summarized in the form of five questions: 1) What is the formal structure of the mimicry system? 2) What are the perceptual and effectual correspondences between the participants of mimicry? 3) What are the characteristics of resemblances? 4) How is the mimicry system regulated in ontogenetic and evolutionary processes? 5) How is the mimicry system related to human cultural processes?

1) *What is the formal structure of the mimicry system?*

Compared to the ecological variety of brood parasitism, its descriptions in mimicry studies remain rather sketchy and superficial. In general overviews and typologies of mimicry, attention is usually focused on resemblance and deception, species combination and cost-benefit relations of the participants. Brood parasitism belongs to bilateral mimicry systems, meaning that two biological species are involved. French zoologist Georges Pasteur (1982: 188) describes the cuckoo's egg mimicry under Kirbyan mimicry (following W. Kirby who noticed this phenomenon in syrphid flies who parasite in the nests of bumblebees). Pasteur writes that this kind of mimicry belongs to the aggressive/ reproductive type in which the model and the receiver belong to one species and the mimic belongs to another species. In his thorough mimicry typology the British entomologist Richard Vane-Wright (1976: 42) describes the common cuckoo as belonging to the anthergic aggressive S1+R-type mimicry. In simpler terms this means that in addition to Pasteur's criteria of two species where the model (the host's eggs) and the receiver (the host adult) belong to the same species, also evolutionary influences and interests are taken into account by Vane-Wright. The mimic's (cuckoo's) influence on the receiver is negative and the interests of the mimic and the model do not coincide.

From the biological perspective in most cases of egg mimicry indeed two participants (with evolutionary memory) are involved in performing three roles in the mimicry system. At the same time the mimicry system can involve an open set of host species as receivers and their eggs as models. There are several host-specific egg patterns in common cuckoo and specific resemblances are genetically determined and transmitted in maternal lineage. At least 11 (Honza *et al.* 2001: 344) or 16 in some estimations (Avilés, Møller 2004: 57) of such lineages or so-called "gents" are known. Eggs with specific patterns are, however, not always laid to the nests of the corresponding hosts, so that the number of occasional host species may be much

larger. This introduces a restrictive condition: if we take the common cuckoo as a species to be the starting point of the description, we should consider egg mimicry as an open system, where the species of neither models nor receivers (nor mimics on the level of genets) are determined. If we preferred the strict tripartite model of mimicry, the level of description should follow the relations of one specific lineage with its host.

When we make a distinction between the biological and the semiotic layers in the egg mimicry of the common cuckoo, several resemblances become observable. The very resemblance between the eggs of the brood parasite and those of the host species seems to be located between the primary and tertiary iconic resemblance. The primary ground of a deceptive resemblance between eggs of cuckoos and hosts is a phylogenetic resemblance of egg shapes of the birds of corresponding size (this also relates to the corresponding behavioral adaptations, such as the readiness of a species who do not have any evolutionary experience with brood parasitism, to treat objects of various shapes in their nests as their eggs, as shown by the studies in classical ethology (Tinbergen 1951: 45)). The tertiary level of iconic resemblances is the relation of camouflage coloration between egg coloration and the surrounding environment to avoid predation. This may influence the coloration of both host and parasite eggs. In addition there exist resemblances at several other developmental stages as correspondences between the behavior of the cuckoo chicks and the chicks of a particular host species (for example Kilner *et al.* 1999) or similarities in the appearance of the adult cuckoo and hawk species (Payne 1977: 8). It becomes clear that on the level of semiotic relations many additional resemblances and connections can be focused at.

2) *What are the perceptual and effectual correspondences between the participants of mimicry?*

Although from the biological viewpoint it may be correct to include the model and the receiver in the same category as in the classification above, from the semiotic and perceptual viewpoints it seems simplifying. Parents of the host species do not need to differentiate between themselves and the other, instead they need to recognize distinct objects — eggs —, and decide which eggs are theirs and which are not. We can consider this type of mimicry to be detached mimicry, where the imitating and imitated objects are distinct from the bodies of the participating animals. Here the second research question, which focuses on specific matching and functional cycles between the species, can provide a more elaborate picture. The main communication channel used to determine the identity of the eggs is mostly the visual channel that may include also patterns which remain outside the human visual sphere in the UV range. Some studies show that also tactile perception of an egg can be relevant, as birds appear to differentiate eggs based on their material and touch sensations (Kemal, Rothstein 1988). Beside perceptual sensations also the indexical place-specificity is an important criteria — many species regard all egg-like things in their nest as their eggs, but if an egg falls out of the nest, the birds will not treat it as an egg anymore. In some cases birds are also believed to estimate the number of their eggs and use this estimation as a basis for distinction (Lyon 2003). The difference in communication channels and criteria used to determine the origin of the eggs, demonstrates that egg mimicry cannot be considered in terms of a simple resemblance or similarity but with respect to complicated processes used by birds for making the distinction (see also point 3).

The reaction of the parents of the host species towards a suspected false egg can provide information about the importance of deceptive resemblance for the birds. The decision concerning the authenticity of eggs often leads to a harsh behavioral reaction: depending on the species, this may involve removing a false egg from the nest, punctuating it or abandoning the nest (Moksnes *et al.* 1991; Soler *et al.* 2002). In relation to this it is also remarkable, that birds abandon their

nests much more easily if they have eggs but do it much more seldom once the chicks have been hatched. A classical evolutionary explanation emphasizes the differences by using an abstract measure of fitness: in the second case, the bird cannot manage to have a second brood and this decreases its fitness significantly. From the viewpoint of the Uexküllian semiotics the difference in number and intensity of possible modalities used to communicate with eggs or chicks can itself provide an answer. With regard to eggs, parents can use the visual and tactile channels for communication. With regard to chicks, the use of the visual and tactile channels becomes much more abundant, auditory channel becomes operational, and there appears dynamic dialogical communication, thus there are more possibilities for the relationship to develop.

3) *What are the characteristics of resemblances?* When we focus on specific characteristics of the resemblance between the eggs, it can be considered as a prototype resemblance or common characteristic resemblance, that is, birds are making the distinction based on some specific characteristics or the generalization of those in model. In the three-fold categorization given above between the firstness-based, secondness-based and thirdness-based resemblance, the egg mimicry will be close to the second option. It is a Batesian-type of mimicry, in which the resemblance requires comparison and actual reference to a second. In the case of brood parasitism, we have a rare case in nature where the objects being compared are actually physically together, lying side by side in the nest. Another peculiarity of the egg-mimicry is the completeness of mimicry (as opposed to partial mimicry) as the resemblance covers most if not all aspects of a complete singular object: shape, size, weight, color pattern, surface structure, etc. In most cases of mimicry the scope of resemblance is much more narrow, being for instance limited to the insects' external cuticulae or the shape of the plant blossoms.

In the case of *Passeriformes*, an ecological relationship with cuckoos and the threat of brood parasitism has influenced their egg recognition mechanisms towards becoming much more accurate. In general, host birds can distinguish their eggs' overall appearance, size (Marchetti 2000), color (Moskát *et al.* 2008) and pattern (Polačiková *et al.* 2010), including markings in ultraviolet (Honza *et al.* 2007). The tertiary iconic relations with the environment can influence the recognition of the brood parasites' eggs, and also individual learning and memory have an important role in recognition. The dependence of egg coloration on environmental conditions in some species (Eurasian reed-warbler *Acrocephalus scirpaceus*) makes the recognition process much more complex as the cuckoo–host egg matching depends on the amount of rainfall in a given spring (Avilés *et al.* 2007). Some species (for example, Hume's leaf-warbler *Phylloscopus humei*) tend to throw out eggs that are bigger than eggs in the clutch on average (Marchetti 2000). Recognition also includes the possibility of a mistake — it has been observed that some birds tend to reject their own eggs if they are “unusual” compared to the rest of the clutch. In addition to the comparison of eggs side by side, egg mimicry seems to include also prototype generation and memorizing of specific types of eggs. In some species like the great reed warbler *Acrocephalus arundinaceus* and chaffinch *Fringilla coelebs* the recognition rate is dependent on the age and experience of the bird (Stokke *et al.* 2004). The host needs to learn from its first nesting how its own eggs look like (Admundsen *et al.* 2002: 367).

4. How is the mimicry system regulated in ontogenetic and evolutionary processes?

Asking about the regulation of egg mimicry in ontogenetic and evolutionary processes enables to describe the mimicry system in terms of dynamics and fixation. In case of brood parasitism, the communicative feedback, understood as a feedback within the single act of communication, has minimal role as eggs are passive and do not

participate in communication with adult birds. The relationship between the eggs and the adult birds follows rather the logic of unidirectional communication or signification (*sensu* Nöth 2001: 72) so that the adult bird is the active subject that recognizes eggs, attributes meaning to them, and acts selectively according to this attributed meaning.

The quickest feedback cycle in brood parasitism takes place on the level of the clutch and depending on the host species there are between a few and ten communication-feedback cycles all together during the life of an individual. The ontogenetic learning and feedback has some role in recognition, as birds may improve their egg-recognition skills on the basis of previous experience. At the same time there is not much individual variety known to exist in the behavior of host or parasites in this ecological relation, nor is the individual experience known to pass from generation to generation by cultural learning. It seems that egg mimicry is by a large degree (compared to many other mimicry systems) genetically induced and controlled. This is also supported by the existence of various genetically induced genets of the cuckoo that differ by their egg appearances and preferred host species. Such relatively fixed mimicry systems allow also bodily fixed adaptations and counter-adaptations to develop, as for instance in some species like blackcaps *Sylvia atricapilla* egg variation in clutch seems to have decreased because of brood parasitism (Honza *et al.* 2004).

5. *How is the mimicry system related to human cultural processes?*

Regarding human cultural involvement and influences egg mimicry turns out to be especially rich and interesting case. The phenomenon itself is known long before the rise of modern science. For instance, Aristotle in his *Historia Animalium* gives a long description and different explanations of cuckoo's nesting behavior:

The cuckoo, as has been said elsewhere, makes no nest, but deposits its eggs in an alien nest, generally in the nest of the ring-dove, or on the ground in the nest of the hypolais or lark, or on a tree in the nest of the green linnet. It lays only one

egg and does not hatch it itself, but the mother-bird in whose nest it has deposited it hatches and rears it; and, as they say, this mother bird, when the young cuckoo has grown big, thrusts her own brood out of the nest and lets them perish; others say that this mother-bird kills her own brood and gives them to the alien to devour, despising her own young owing to the beauty of the cuckoo. (Aristotle 2002, Dd6r)

It even seems that brood parasitism of the cuckoo has turned into a cultural model for describing certain parasitic relations, as there are cuckoo bumblebees *Psithyrus*, cuckoo finches *Anomalospiza* and cuckoo ants *Leptothorax* in the zoological nomenclature. There is also a larger cultural mythological background for interpreting brood parasitism since many European cultures believe in the existence of changelings, the human children swapped by an elf, a troll or some other supernatural creature. The same theme is in different variations much used in contemporary fiction. It appears that the topic of an alien offspring is a strong cultural narrative and often also the primary characteristic that people associate with cuckoos.

Also scientific studies of egg mimicry of cuckoos can be shaped (although mostly unconsciously) by this strong cultural narrative (see, for example, Schulze-Hagen *et al.* 2009; Smith 1999). Although the egg mimicry of cuckoos is scientifically a rather well-established case, a possible methodological error can arise from substituting the position of the receiver with that of the human observer and proceeding from human perceptual and behavioral possibilities. Concerning studies in brood parasitism, this becomes obvious for instance in the experiments with artificial eggs that are produced according to the human perceptual system and understanding of similarity and difference: “The resemblance was so good that, by visual inspection alone, an observer could not distinguish between the artificial eggs and the genuine cuckoo eggs from the same area” (Moksnes, Røskaft 1989: 27). Artificial eggs could also be described as “similar in size and mass to real cuckoo eggs, made of hard plastic [...] the mimetic egg type painted to resemble eggs laid by the blackcap” (Honza *et al.* 2004: 176).

This question becomes methodologically crucial, as there are differences between human and bird visual systems. The principles of color distinction in birds are different from mammals, and birds are also sensitive to the ultraviolet light. Some parasitic eggs that appear non-mimetic in visible light are highly similar to host eggs in UV-light (Grim 2005: 75; Polaciková *et al.* 2007; Honza *et al.* 2007). In some studies even human test persons are used to test the similarity or difference of eggs in a clutch and the results are used to argue for the resistance of some species to brood parasitism (Honza *et al.* 2004: 177). From the semiotic viewpoint, such studies can be interpreted critically and assumed to provide biased results since the position of the receiver (song bird) is at least partly replaced by that of the human receiver.

The five-stage semiotic analysis of the common cuckoo's brood parasitism demonstrates the complexity of the mimics' and receivers' relations as well as the several layers of resemblance compared to the simple schematization of the tripartite mimicry system. It also shows the specifics of egg mimicry as a detached and complete mimicry resemblance corresponding to Peircean secondness. The validity of the mimicry system could be supported by the strong behavioral reactions of the adult birds (receivers) toward the cuckoo eggs, although at the same time the human cultural narrative and perceptual involvement can also influence the description. The dynamics and development of egg mimicry takes mostly place at the level of genetic information and phylogenetic feedback although there is also some individual learning involved. To fully articulate the specific features of egg mimicry, a comparative analysis should be made also in other mimicry systems, which is a task beyond the scope of the present article.

Conclusions

The present article develops a semiotic methodology for analyzing mimicry systems, while recognizing the limitations of the existing mimicry typologies and attempting to avoid these. Using a selection of dynamical tools for describing mimicry allows to bring forth peculiarities of specific mimicry types and also to compare different cases of mimicry with each other. As an example, the present article gives a literature-based analysis of brood parasitism of the common cuckoo. The semiotic approach developed here has several advantages that find also use in practical analysis. The methodology emphasizes the role of perception in mimicry studies, thereby bridging evolutionary and psychological approaches. In addition the presented methodology does not exclude the cultural aspect in mimicry studies (as it is done in most biological accounts), but allows this to be critically adjoined with the study. The five stages of analysis exemplify different strategies of argumentation and verification of mimicry resemblances, allowing us to construct a range from just-so stories to well-established co-evolutionary adaptations.⁴

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Семиотическое моделирование мимикрии на примере гнездового паразитизма

Биологическую мимикрию можно считать семиотическим феноменом с двухуровневой структурой: уровень экологических отношений между видами и уровень семиотических отношений. В настоящей статье указывается на границы широко распространенных триадических моделей и типологий мимикрии, а заодно отмечается их недостаточная связь с природными явлениями мимикрии. В статье утверждается, что для более когерентного описания мимикрии нужны более динамичные теоретические средства, которые позволили бы провести сравнительный анализ разных случаев мимикрии. Для этого в статье предлагается пятичленная модель, которая соединяет в себе классическую теорию мимикрии, теорию умвельта Якоба фон Юкскюлля и коммуникативный анализ. Суть этой модели можно выразить в пяти вопросах: 1) какова формальная структура системы мимикрии; 2) какие перцептивные и действенные соответствия между участниками мимикрии; 3) какими являются свойства сходства; 4) как система мимикрии регулируется в процессе онто-

гене́за и эволюции; 5) как система мимикрии связана с процессами культуры. В качестве практического примера в рамках данной семиотической методологии анализируется гнездовой паразитизм кукушки *Cuculus canorus* и наиболее частыми видами ее животных-хозяев.

Mimikri semiootiline modelleerimine viitega pesaparasitismile

Bioloogilist mimikrit võib pidada semiootiliseks fenomeniks, millel on kahetasandiline struktuur: liikidevaheliste ökoloogiliste suhete tasand ja semiootiliste suhete tasand. Käesolev artikkel näitab, millised on laialt levinud triaadiliste mimikrimudelite ja -tüpoloogiate piirid ning osutab ühtlasi, et nende seos looduses esinevate mimikrinähtustega on puudulik. Artiklis väidetakse, et mimikri koherentsemaks kirjeldamiseks on vaja dünaamilisemaid teoreetilisi vahendeid, mis võimaldaksid ühtlasi erinevate mimikrijuhtumite võrdlevat analüüsi. Selleks pakutakse artiklis välja viieosaline mudel, mis liidab endas klassikalist mimikriteooriat, Jakob von Uexkülli omailmateooriat ja semiootilist ning kommunikatsioonilist analüüsi. Selle uurimismudeli sisu võib väljendada viie küsimusena: 1) milline on mimikrisüsteemi formaalne struktuur; 2) millised on tajumuslikud ja toimimislikud vastavused mimikri osapoolte vahel; 3) millised on sarnasuse omadused; 4) kuidas on mimikrisüsteem reguleeritud ontogeneesis ja evolutsioonis; 5) kuidas on mimikrisüsteem seotud inimeste kultuuri-protsessidega. Antud semiootilise metodoloogia praktilise näitena analüüsitakse pesaparasitismi käo *Cuculus canorus* ja tema sagedamate perekonnaliikide vahel.