

Development and Natural Selection, the Historical Foundations of Mimesis in Animal and Plant Form

Alessandro Minelli

alessandro.minelli@unipd.it

In biology, mimesis includes imitation between individuals of the same species – the study object of behavioral sciences and neurophysiology – and mimicry between different species through traits or behaviours generally common to all individuals – to be analyzed from an evolutionary and morphogenetic perspective. Mimicry is widespread among representatives of many animal lineages, but has been also recorded among plants. Mimicry is very often adaptive, e.g. because of protection produced by the similarity of a harmless animal to a poisonous or otherwise dangerous one (Batesian mimicry, e.g., false vs. true coral snakes, or hoverflies vs. wasps), or by sharing of closely similar livery by animals protected by different weapons (Müllerian mimicry). Less conventional kinds of mimicry include the aggressive behaviour of some fireflies imitating the flashing of a different species on which they prey; the intraspecific Müllerian mimicry between larva and adult of some ladybirds; and the presence of identical compounds in the sexual pheromone produced by a female wasp and in the fragrance of the orchid species pollinated by the male. Morphological and biochemical similarity cannot be explained by selective advantage only. Even in cases of adaptive mimicry, shared developmental constraint may facilitate the evolution of similarity between model and mime.

Keywords: adaptation, developmental constraints, evo-devo, mimicry.

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alessandro.minelli@unipd.it

We humans, and the others

It is not easy to avoid lexical pitfalls when exporting a term from philosophy to the natural sciences or applying to other species (animals or even plants) terms that have a meaning consolidated in relation to human conditions or actions. This applies also to mimesis. In biology, mimesis can advantageously be split into imitation and mimicry. Imitation, when mimesis is exercised between individuals of the same species; mimicry when it instead takes on the connotation of similarity between different species. In biology, this distinction is fundamental. Imitation is the object of study of behavioral sciences and neurophysiology, while mimicry describes properties common (generally) to all individuals of the species and can be analyzed from an evolutionary and morphogenetic perspective.

Mirror neurons

A little over thirty years ago, a group of Italian researchers from the Institute of Human Physiology at the University of Parma, directed by Giacomo Rizzolatti, discovered in the macaque's brain a set of neurons that are activated every time the animal sees one of its fellows perform an action: those same neurons are activated when it is the animal itself that performs the same actions¹. Thanks to these cells, the observer identifies himself, so to speak, with the watched individual. A few years later, the same group of researchers

¹ G. di Pellegrino, L. Fadiga, L. Fogassi, V. Gallese, G. Rizzolatti, *Understanding motor events: a neurophysiological study*, in "Experimental Brain Research", XCI, 1992, pp. 176-180.

demonstrated the presence of this type of neurons in humans and gave them the suggestive and well-chosen name of mirror neurons². This discovery is probably the most important contribution of experimental science to the understanding of imitation phenomena. Within a few years, the existence of mirror neurons was ascertained not only in primates but also in some birds. In these animals, therefore, we know at least in part the morphological and functional basis of flexible behaviour, which allows an individual of one species to imitate the behaviour of a conspecific and perhaps, at least in some cases, of another species³.

However, in the living world, mimesis is not only the result of flexible behaviour of the individual, but also manifests itself in the more or less precise resemblance between species, even those that are phylogenetically very distant from each other, and in each of them it takes on the character of a species-specific structural or behavioural trait, essentially invariant within the species. To study this form of mimesis, we leave the sphere of behaviour and neurophysiology and venture into evolutionary biology and, as we shall see later, developmental biology.

Before addressing from an evolutionary and developmental biology perspective the complex case history of mimicry in the animal kingdom, it is necessary to devote some attention to plants.

Unexpected mimesis in plants

Boquila trifoliolata is a liana native to South America that appears to imitate the leaves of the trees on which it climbs. But these trees belong to different species, which means that the shape of the liana's leaves is not strictly determined genetically, but is modulated by imitation of the shape of the leaves of the plant on which each individual *Boquila* leans. If, in the course of its growth, it comes into contact with two or more different trees, the shape of its new leaves will adapt to that of the leaves of the new tree offering support⁴.

² V. Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., *Action recognition in the premotor cortex*, in "Brain", CXIX, 1996, pp. 593–609; G. Rizzolatti, L. Fadiga, V. Gallese, L. Fogassi, *Premotor cortex and the recognition of motor actions*, in "Social Cognitive and Affective Neuroscience", III, 1996, pp. 131-141.

³ V. Gallese, M.A. Gernsbacher, C. Heyes, G. Hickok, M. Iacoboni, *Mirror neuron forum*, in "Perspectives on Psychological Science", VI, 2011, pp. 369–407; C. Heyes, C. Catmur, *What happened to mirror neurons?*, in "Perspectives on Psychological Science", XVII, 2022, pp. 153–168. G. Rizzolatti, C. Sinigaglia, *So quel che fai, Il cervello che agisce e i neuroni specchio*, Raffaello Cortina Editore, Milano 2006.

⁴ E. Gianoli, F. Carrasco-Urra, *Leaf mimicry in a climbing plant protects against herbivory*, in "Current Biology", XXIV, 2014, pp. 984-987.

How this polymorphism comes into being is still unclear, the proposed explanation that the leaves of the liana are able to ‘see’ what the leaves of the tree on which the plant leans look like and grow by imitating the shape of these⁵ being problematic. It is possible, however, that this similarity may have adaptive value, reducing the consumption of *Boquila* leaves by phytophages. This remains to be verified in nature, but it is at least certain that the production of very different leaves by the same plant can actually reduce the risk of these being used by phytophagous animals.

This is known for some species of passion flowers, mostly vines or lianas, that are the feeding plants for the caterpillars of the showy *Heliconius* butterflies. Several *Passiflora* species have evolved preventive defence mechanisms against butterflies, with strategies that reduce the risk of *Heliconius* laying the eggs on their leaves. In *Passiflora cyanea*, for example, there are yellow outgrowths at the base of the leaves that look very much like the eggs of some *Heliconius*, including *H. ethilla*, which is the most frequent visitor to this plant⁶. Unlike many other lepidopterans, the females of these butterflies avoid laying an egg close to another already present on a leaf, so by egg laying they will also keep their distance from the false eggs developed by the *Passiflora*; as a result, the overall number of eggs laid on one *Passiflora* plant will be reduced. An example, we might say, of deterrent mimesis. To the same category we can ascribe the production, by the same plant, of very differently shaped leaves, as in *Passiflora tenuiloba*⁷, a condition that can reduce the risk of being recognised as an optimal site for oviposition by the *Heliconius*. Gilbert⁸, noting the high degree of visual acuity and behavioral sophistication of *Heliconius*, speculated that different passion vines have diverged in their appearance and even come to mimic the leaves of other groups of common tropical plants to escape detection by these butterflies. The ability of the latter to choose the oviposition sites based

⁵ J. White, F. Yamashita, *Boquila trifoliolata* mimics leaves of an artificial plastic host plant, in “Plant Signaling & Behavior”, XVII, 2022, 17, 1977530.

⁶ W.W. Benson, K.S. Brown, Jr., L.E. Gilbert, *Coevolution of plants and herbivores: passion flower butterflies*, in “Evolution”, XXIX, 1975, pp. 659-680; L.E. Gilbert, *Ecological consequences of a co-evolved mutualism between butterflies and plants*, in L.E. Gilbert, P.R. Raven (eds.), *Coevolution of animals and plants*, University of Texas Press, Austin 1975, pp. 210-240.

⁷ K. Porter-Utley, *A revision of Passiflora L. subgenus Decaloba (DC.) Rchb. supersection Cieca (Medik.) J.M. MacDougal & Feuillet (Passifloraceae)*, in “PhytoKeys”, XLIII, 2014, pp. 1-224.

⁸ L.E. Gilbert, *Ecological consequences of a co-evolved mutualism*, cit.

on their perception of leaf shape had been repeatedly suggested based on field observations⁹, and has recently been demonstrated experimentally¹⁰.

Mimicry – adaptive or not

If the robust insect that has just entered our room through the window has a conspicuous black-and-yellow livery, we should not treat it with confidence: it is likely to be a wasp, whose venomous sting would be very painful and possibly dangerous. The advantage the insect obtains from being immediately recognised is not difficult to discover: the fear of a sting will induce the observer (a human or an insectivorous animal) to keep distance and the wasp will avoid a conflict that could still harm it and it will conserve its supply of venom for a possible later occasion.

It is not certain, however, that the black-and-yellow insect is really a wasp. It could be instead a hoverfly, i.e. a two-winged insect (a member of the Diptera, like houseflies and mosquitoes), which, due to its wasp-like livery, is likely to be kept at a distance from the observer despite its inoffensive nature. This insect is therefore protected by its resemblance to a dangerous insect such as a wasp, but it spends nothing on offensive tools such as the wasp's sting and venom. Naturalists describe this similarity between the two insects as a case of mimicry, where the wasp is the model and the hoverfly is its mime. In similar terms we can describe the similarity between two American genera of snakes, the highly venomous coral snakes (*Micrurus*) and the inoffensive false coral snakes (some species of the genus *Lampropeltis*, e.g. the scarlet kingsnake (*L. elapsoides*) and the milk snake (*L. triangulum*), have coloration and patterning that can cause them to be confused with the highly venomous coral snakes, with which they share the unmistakable and very conspicuous livery with yellow and black rings on a red background.

Our suspicions about the adaptive value of this similarity must always be verified experimentally, but there are general criteria that can support, or deny, its plausibility. Firstly, the two species must live in the same geographical region and, essentially, in the same environments: if the hypothetical mime is not seen with the hypothetical model, the similarity would produce advantage for the former. For this reason, the similarity between

⁹ K.S. Brown, *The biology of Heliconius and related genera*, in “Annual Reviews of Entomology”, XXVI, 1881, pp. 427-456.

¹⁰ D.D. Dell’Aglia, M.E. Losada, C.D. Jiggins, *Butterfly learning and the diversification of plant leaf shape*, in “Frontiers in Ecology and Evolution”, IV, 2016, 81.

the livery of coral snakes (true and false), which are exclusive of the Americas, and that of some species of terrestrial free-living flatworms of the genus *Bipalium* living in Borneo cannot be considered an example of mimicry. Secondly, the mime can only benefit from its resemblance to a model protected from venom or other forms of defence if the abundance of the mime is modest, compared to the model. Only under these circumstances their livery will be a reliable signal of danger to other animals. However, if the alleged mime is as abundant as or more than its alleged model, it too is likely to represent a source of annoyance, if not danger, to other animals. If so, we move from Batesian mimicry, where the harmless mime looks like the venomous model, to Müllerian mimicry, in which the same livery is shared by two or more different species, each of which is equipped with its own weapons: in this way, the same visual image corresponds to a set of dangers, for example the venomous bite of a spider and the toxic substances present in a similarly coloured beetle or butterfly¹¹.

Mimicry can therefore have adaptive value, at least for one of the partners, but on other occasions this is not true. The resemblance to true penguins, which live only in the Southern hemisphere, did not save from extinction a Northern sea bird, the great auk (*Pinguinus impennis*), superficially similar to them to the point of giving them their name: penguin was originally one of the names for the great auk, only later applied to the similarly looking birds eventually met by sailors in the Southern seas, which however belong to a different order¹².

Sometimes, even the presence of both species in the same territory is not sufficient to explain their similarity, as in the case of the stinging nettle (*Urtica dioica*) and the dead nettle (*Lamium purpureum*), whose leaves are singularly similar, and likewise between the false helleborine (*Veratrum album*) and the great yellow gentian (*Gentiana lutea*); a similarity that has repeatedly caused fatal poisoning of people who have picked and used the former, which is very poisonous, instead of the latter, whose roots are good for making tonic and stomachic infusions and still used to produce a number of bitter liqueurs.

Thus, an explanation of mimicry in Darwinian terms may be convincing in some cases, but would fail in others.

¹¹ For an overview of the diversity of mimicry scenarios in the living world, see G. Pasteur, *A classificatory review of mimicry systems*, in "Annual Review of Ecology and Systematics", XIII, 1982, pp. 169-199.

¹² Auks are currently classified with the Charadriiformes, whereas penguins are placed in an order of their own (Sphenisciformes).

Before shifting our attention to the developmental processes that result in the production of these similar phenotypes, it is worth mentioning kinds of mimicry other than those which concern the morphological similarity between two species, as considered so far.

Intraspecific mimicry

Let's first focus on one of those infrequent examples of *intraspecific mimicry*, evolved through an increasing and sometimes surprising similarity between larva and adult, in lineages where these stages are nevertheless separated by a radical metamorphosis. We will look for them within holometabolous insects, where precisely the presence of larvae and adults radically different in morphology and ecology has facilitated an extraordinary adaptive radiation of unsurpassed success.

In most major groups of holometabolous insects, e.g. beetles and flies, we recognise a trend towards the evolution of larval types increasingly diverging from adult morphology. The maggots, that is, the larvae of the flies, are an example: lacking a recognisable head, legs or other appendages, their metamorphosis is accomplished through a veritable dismantling of larval structures and the simultaneous building of the adult from specialised groups of cells (histoblasts and imaginal discs). In other insects, the metamorphosis is less dramatic than in the true flies, but the great morphological and biological discontinuity separating the larva from the adult are nearly universal among the holometabolans.

There are, however, some examples of newly evolved similarity (convergence) between the larva and its adult. These include a small ladybird common in our regions, the small *Psyllobora vigintiduopunctata*, which is often found on the leaves of pumpkins and courgettes. These are not the insect's foodplants, however, but are regularly visited by it as soon as the leaves or the stems are attacked by a microscopic fungus¹³ that cover its leaves with a white coating on which the *Psyllobora* graze, feeding on the fungus' spores. Larva and adult live together and feed on the same food. Although the larva has a soft elongated body, while the adult has the typical stiffness and compact shape typical of beetles, the observer does not hesitate an instant to recognise that the two yellow animals on the gourd leaves are two different stages of development of the same animal:

¹³ Usually, either *Golovinomyces cichoracearum* or *Podosphaera xanthii*.

both share the same shade of yellow as the adult and, like the latter, is sprinkled with small black dots. Very similar is also the livery of the pupa. Distasteful or even poisonous as ladybirds generally turn out to be, as advertised by their showy livery, the different developmental stages of *Ps. vigintiduopunctata* deserve be described as a case of *intraspecific Müllerian mimicry*¹⁴.

Behavioural mimesis

In the case of the similarity between wasps and hoverflies and, in general, in all cases of Batesian or Müllerian mimicry, the similarity takes on adaptive significance only if the different species involved fall into the visual field of the same external observer. In other situations, however, the mime benefits precisely from being perceived by its model. This occurs when the mime interferes into the communication between members of the other species, using signals that make it indistinguishable from those used by the latter. This allows, for example, insects of different species to be tolerated within an ant nest, as their cuticle contains molecules that the hosts cannot distinguish from those borne by their sisters¹⁵.

Sometimes, this form of mimicry, which allows for a real manipulation of communication between members of the other species, takes on a decidedly aggressive character, allowing the mime to feed at the expense of a victim lured by a misleading signal.

Other than among ants, where the most important communication channel is the chemical one, fireflies mainly rely on visual cues. Each species has its own language made up of flashes of light of different duration and emitted at characteristic time intervals, which enables a dialogue between males and females and thus the formation of reproductive pairs. But this is not always the case. In North America, the females of some fireflies of the genus *Photuris* emit light signals very similar to those of a species of the

¹⁴ M. Aslam, P. Veselý, O. Nedvěd O., *Response of passerine birds and chicks to larvae and pupae of ladybirds*, in "Ecological Entomology", XLIV, 2019, pp. 792-799.

¹⁵ T. Akino, *Chemical strategies to deal with ants: a review of mimicry, camouflage, propaganda, and phytomimesis by ants (Hymenoptera: Formicidae) and other arthropods*, in "Myrmecological News", XI, 2008, pp.173-181; P.E. Cushing, *Spider-ant associations: an updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders*, in "Psyche", 2012, 151989.

genus *Photinus*, and are thus able to attract males of the latter who, instead of a conspecific partner, find a predator ready to feed on them¹⁶.

Molecular mimesis

Mimesis is not restricted to morphology or behaviour it may involve instead the production of particular molecules, e.g. those that enable a flowering plant to obtain visits from a particular species of insect that can ensure its pollination. How close this relationship between plant and insect can be, especially in certain genera of orchids, has long been known: in particular, it was the subject of a monographic study by Charles Darwin¹⁷. However, it was not possible to seriously tackle the study of this relationship until precise analytical techniques were available to identify the substances (often numerous, even hundreds) that make up the scent emitted by the flower and the electrophysiological techniques that enable the study of the insect's perception of these substances. In the absence of this information, it was legitimate to believe that the specificity of the attraction exerted by the plant would lay in the particular blend of hundreds of different molecules mixed in its fragrance, rather than to one of those substances. But this is not the case.

The flowers of some genera of orchids, deceptively similar to an insect, are visited exclusively by the males of one species (or very few species) of hymenopterans. In a few instances at least, the flower is broadly similar to the female of the same wasp species, to the point that the insect-flower relationship has been often described as a pseudocopulation¹⁸. It seems thus useful to compare the scent of the plant with the sexual pheromone produced by the females of these insects, assuming that the males head for the flower following the same chemical clue that would lead them to a female of their species. An in-depth analysis will then make it possible to establish whether the efficacy of the lure is due to the mixture of the different molecules present in both the pheromone and the scent of the orchid, or to one or a few specific substances.

¹⁶ J.E. Lloyd, *Aggressive mimicry in Photuris: firefly femmes fatales*, in "Science", CXLIX, 1965, pp. 653-654; Id., *Aggressive mimicry in Photuris fireflies: signal repertoires by femmes fatales*, in "Science", CLXXXVII, 1975, pp. 452-453.

¹⁷ C. Darwin, *On the various contrivances by which British and foreign orchids are fertilised by insects: and on the good effect of intercrossing*, John Murray, London 1862.

¹⁸ H.F. Paulus, *Deceived males – Pollination biology of the Mediterranean orchid genus Ophrys (Orchidaceae)*, in "Journal Europäischer Orchideen", XXXVIII, 2006, pp. 303-353.

The studies by Florian P. Schiestl and co-workers on an Australian orchid (*Chiloglottis trapeziformis*) and its pollinator, the male of the typhiid wasp *Neozeleboria cryptoides*, deserve close attention. These researchers analysed both the scent of the flower and the attraction pheromone of the female wasp using the gas chromatography technique. They then exposed males of the same species to molecules present in the two natural mixtures and found that only one of them triggers a reaction when it is perceived by the insect with its antennae. This is a volatile compound (2-ethyl-5-propylcyclohexan-1,3-dione, more friendly called chiloglottone), which is present, in very modest quantities, in both the *Chiloglottis* perfume and the *Neozeleboria* pheromone¹⁹.

Why similar? An evo-devo perspective

Caleana major is the scientific name of an orchid whose flower, observed from a suitable angle, bears an extraordinary resemblance to a bird in flight, which is why the plant is known as the flying duck orchid. In this case, the resemblance, although extraordinary to our eyes, admits no rational explanation in terms of adaptation. However, while in this case we can limit ourselves to registering our visual perceptions, and avoid setting out in search of explanations that cannot be based on the mechanisms of biology or ecology, this example perhaps helps to remind us that every case of mimesis deserves to be addressed jointly both in terms of a possible adaptive explanation and in terms of the evolvability of the morphogenetic mechanisms involved.

In the case of Batesian mimicry, for example, the selective advantage of the similarity between model and mime is hardly disputable, and is in any case experimentally verifiable, but this does not help us understanding its origin. The similarity, in fact, could result from a complex interweaving of causes, both instructive and selective. That is, it is possible that the evolution of mimicry between distantly related groups, irrespective of the selective canalization due to its adaptive advantage to at least one of the partners, was also facilitated by the availability, for both models and mimes, of similar pattern units that are more likely to be expressed and modified in parallel ways due to shared developmental constraints.

¹⁹ F.P. Schiestl, R. Peakall, J.G. Mant, F. Ibarra, C. Schulz, S. Franke, W. Francke, *The chemistry of sexual deception in an orchid-wasp pollination system*, in "Science", CCCII, 2003, pp. 437-438.

This way, we shift attention away from the adaptational perspective on evolution, to tackle the dimension of morphogenesis.

This change of perspective characterises the biological discipline that goes by the name of evolutionary developmental biology, or evo-devo. Here, the focus is no longer on the adaptive value of a phenotype, but rather on its evolvability, the plausibility of its appearance in the evolutionary history of the lineages concerned. Taking an example that has become very popular in recent years, one can explain this change in perspective by emphasising the insufficiency of a purely adaptive explanation of, say, the giraffe's long neck. There is no reason to doubt the advantage conferred by this long neck on the animal, which thanks to it is able to find food in the foliage of the acacias scattered across the African savannah, but it cannot tell us whether this long neck is supported by a large number of short vertebrae like our cervicals, or by a few elongated cervicals, perhaps in the same number as ours. This can only be answered by developmental biology, which, in this case, has revealed the extreme resistance of mammals to producing a series of cervical vertebrae in numbers other than seven. Returning to mimicry, beyond its adaptive value, which can be verified (or ruled out) on a case-by-case basis, we cannot avoid tackling the complementary problem, i.e. the possible existence of morphogenetic constraints that may have channelled its evolution.

This hypothesis has been tested in a comparison between wasps and hoverflies, their Batesian mimics²⁰. Although they are insects belonging to different orders (wasps are hymenopterans, hoverflies are dipterans), it is possible to identify correspondences (homologies) between many elements of the exoskeleton (sclerites) of one and the other. One can therefore ask whether the black-and-yellow patterns of the models and mimics are constructed, predominantly at least, from homologous elements. In other words, whether a given sclerite that is habitually black in wasps corresponds to a homologous sclerite that is habitually black in wasp mimics, and so for the yellow elements of the shared livery. If this is so, the production of similar colour patterns could be partly conditioned by very ancient morphogenetic constraints, dating back to the evolutionary history of insects before the divergence of the lineages that led to wasps and hoverflies respectively, ca. 250 million years ago, between the Late Permian and the Early Triassic

²⁰ M. Marchini, D. Sommaggio, A. Minelli, *Playing with black and yellow: the evolvability of a Batesian mimicry*, in "Evolutionary Biology", XLIV, 2017, pp. 100-112.

period²¹. This would have facilitated the evolution of mimicry, obviously reinforced over time by the adaptive advantages provided. Data collected on a large sample of wasp and hoverfly species supports the plausibility of this hypothesis.

Evo devo – rescuing implausible mimicry

Development makes the evolution of similar structures more likely than a purely adaptationist argument might suggest²². This argument can tentatively be applied to the striking morphological similarity that sometimes exists between species belonging to evolutionarily remote lineages. For example, the unmistakable raptorial appendages into which the front legs of the praying mantis are modified are very similar to the front legs of the adults of the mantid lacewings (Mantispidae), a family belonging to a different insect order. Mantispids undergo a complete metamorphosis while mantises develop through a series of stages that are entirely similar to the adult (including the raptorial legs). Both true mantises and mantid lacewings use their raptorial appendages to catch their preys, but their common predatory habit per se does not explain their very detailed similarity. This is still truer of the similarity between the raptorial appendages of these two insect groups and the second thoracic legs of the mantis shrimps (Stomatopoda), a group of marine crustaceans, the second pair of thoracic limbs of which is strikingly similar to the raptorial legs of true mantises. To date, no studies have been carried out on the developmental genetics of all these appendages, and it is not easy to hazard a guess as to the possible presence of common mechanisms involved in the production of these very similar appendages in three groups of arthropods so distant from each other.

²¹ D. Grimaldi, M.S. Engel, *Evolution of the insects*, Cambridge University Press, Cambridge 2005.

²² A. Minelli, *An evo-devo perspective on analogy in biology*, in “Philosophies”, IV, 2019, 5.