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Mimicry, Camouflage and Perceptual Exploitation: the Evolution of Deception in Nature

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Abstract

Despite decades of study, mimicry continues to inspire and challenge evolutionary biologists. This essay aims to assess recent conceptual frameworks for the study of mimicry and to examine the links between mimicry and related phenomena. Mimicry is defined here as similarity in appearance and/or behavior between a mimic and a model that provides a selective advantage to the mimic because it affects the behavior of a receiver causing it to misidentify the mimic, and that evolved (or is maintained by selection) because of those effects. Mimics copy cues or signals that are already in use as part of a stable communication system, but offer misleading information to receivers. Mimicry overlaps, both conceptually and evolutionarily, with camouflage and perceptual exploitation but the overlap is only partial, which may create some confusion. Certain types of camouflage (e.g. masquerade) conform to the definition of mimicry, while others (e.g. background matching) are not considered mimicry because they prevent detection rather than recognition of the camouflaged animal. Mimicry, on the other hand, works by exploiting peculiarities of the receiver at higher stages of sensory processing involving recognition and classification of stimuli. Perceptual exploitation models of trait evolution are also closely related to mimicry, and sensory traps in particular may act as a precursor for true mimicry to evolve. The common thread through these diverse phenomena is deception of a receiver by a mimic. Thus receiver deception (i.e. perceptual error) emerges as a key characteristic of mimicry shared with some types of camouflage and perceptual exploitation.

Keywords Mimicry · Deception · Communication · Camouflage · Perceptual exploitation

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"*Deception is a very deep feature of life*" (Trivers 2011)

Introduction

In nature, organisms may resemble each other for a number of reasons, including shared phyletic history, convergent evolution, and chance (Grim 2013). In some cases, however, resemblance is the product of selection favoring similarity between an organism (the mimic) and another organism of the same or a different species or an inanimate object (the model). We refer to the latter as mimicry, a complex and fascinating phenomenon embracing some of the most dramatic examples of biological adaptation.

Consider, for example, the spider-tailed viper, *Pseudocerastes urarachnoides*. This little-known snake species, endemic from Iran, has a unique appendage at the end of the tail that bears an uncanny resemblance to a spider, even to the point of displaying what appears to be a full complement of spidery legs. The tail ends with an oval, knob-like structure and is surrounded by drooping, elongated lateral scales that resemble arthropod legs. To add to the resemblance, the snake moves the spider-like tail tip back and forth along its own cryptically colored body in a rather convincing arachnid impersonation. The few recorded instances of interactions between spider-tailed vipers and their prey suggest that the peculiar tail appendage, initially thought to be a tumor or a parasite affecting the snake's tail, is actually a lure that the snake uses to attract unsuspecting prey, mainly birds (Bostanchi et al. 2006; Fathinia et al. 2009). Biologists marvel at the existence of this and other similar adaptations and have long struggled to understand the evolutionary processes shaping them.

Mimicry has been around for a long time. A recent study revealed an astonishing example of leaf mimicry in a katydid from the middle Permian, some 270 mya (Garrouste et al. 2016). The newly discovered katydid displayed modifications of the forewings closely resembling those of modern leaf-mimicking katydids. The leaf-like wings probably functioned, as in modern katydids, as an anti-predator adaptation (an example of masquerade, see below). Despite its antiquity, the first clear formulation of the phenomenon of biological mimicry is attributed to British naturalist-explorer Bates (1862), who offered an intriguing explanation for the resemblance among some Amazonian butterflies (for recent accounts of the history of mimicry research see Forbes 2009; Quicke 2017). Since then, research on mimicry and other types of adaptive resemblance has grown exponentially, with new and fascinating examples and new insights accumulating at an ever increasing pace.

However, the field of mimicry research is beset with debates and controversies regarding the proper definition of mimicry and its relationship with other, related phenomena (e.g. Quicke 2017). The aim of this essay is to critically assess recent attempts to bring terminological clarity and to provide unifying principles for the study of mimicry (e.g. Dalziell and Welbergen 2016; Weldon 2016; Jamie 2017), and to explore the conceptual and evolutionary links between mimicry, camouflage, perceptual exploitation, and deception. I will also highlight some largely overlooked links between mimicry and communication theory.

Problems of Definition

As explained by Dalziell and Welbergen (2016), the study of mimicry suffers from considerable terminological and conceptual confusion, and it is unclear how different types of mimicry relate to each other and to other forms of adaptive resemblance. In particular the debate regarding the proper definition of mimicry has been raging for many years (reviewed in Quicke 2017). Mimicry research is dominated by studies of the types of mimicry that function to avoid predators (i.e. Batesian and Müllerian mimicry), but mimicry phenomena are a diverse lot and it has proved difficult to come up with a definition that accommodates all generally accepted instances of mimicry and at the same time excludes related but non-mimetic phenomena.

Mimicry requires the participation of at least three parties ("the mimicry trinity"; Wickler 1968). In addition to a mimic and a model, a mimetic relationship engages a third party which is variously referred to as the receiver, operator, interpreter, dupe, detectee, or selective agent. Receivers and mimics are usually animals or at least living organisms, whereas models can be animate or, if we count masquerade as a type of mimicry (see below), inanimate objects. Although textbook examples of mimicry usually emphasize interactions in which mimic and model belong to different species, mimicry applies equally to intra-specific interactions (e.g. sex and age-class mimicry; see Weldon 2016).

Humans are sometimes part of the mimicry trinity in their interactions with other animals, as receivers or, less often, as mimics. Catania (2008) reports the intriguing example of so-called "worm grunting". Locals in some areas of the southeastern United States collect giant earthworms used as fishing bait by vibrating a wooden stake driven into the soil. In response to the vibrations the earthworms exit their burrows and emerge to the surface where they can easily be collected by the hundreds. Unbeknown to the bait collectors, the vibrations produced by worm grunting mimic those produced by digging moles that are the natural predators of earthworms, thereby eliciting an out-of-context antipredator response that exposes the earthworms and facilitates their capture.

Modern definitions of mimicry are based on Vane-Wright's (1980) definition which states that "mimicry involves an organism (the mimic) which simulates signal properties of a second living organism (the model) which are perceived as signals of interest by a third living organism (the operator), such that the mimic gains in fitness as a result of the operator identifying it as an example of the model" (p. 4). There have been several attempts to amend or improve Vane-Wright's definition. Dalziell and Welbergen (2016), for example, assert that "mimicry evolves if a receiver perceives the similarity between a mimic and a model and as a result changes its behaviour in a manner that provides a selective advantage to the mimic" (p. 612). However, there seems to be no universally accepted definition and disagreement abounds about the sort of phenomena that should be included under the mimicry label (see Quicke 2017).

Mimicry as Deceptive Resemblance

Throughout this review I will contend that all mimicry phenomena share two key characteristics: resemblance to a model and receiver deception (see also Maran 2011, 2017). Thus, mimicry is best characterized as a type of deceptive resemblance. That mimicry involves some sort of resemblance to a model is uncontroversial. Starrett (1993) coined the all-inclusive term adaptive resemblance to refer to “any resemblance that has evolved or is maintained as a result of selection for the resemblance” (p. 301). Adaptive resemblance therefore encompasses most examples of mimicry discussed here but also cases of resemblance due to other evolutionary processes, such as some forms of camouflage which are not considered mimetic (e.g. cryptic coloration, background matching). Although mimicry and camouflage are often discussed together, possibly because of their prevalence as anti-predator adaptations, they are different phenomena and much effort has been devoted to establishing clear criteria to distinguish them (see below).

Things are different with the deception criterion. In fact, whether or not mimetic phenomena are deceptive has been one of the most contentious issues in the study of mimicry (Quicke 2017). Where some traditional definitions (e.g. Wickler 1968; Edmunds 1974; Pasteur 1982) consider receiver deception a key ingredient of mimicry, others have argued that deception should not be a defining characteristic of mimicry (e.g. Vane-Wright 1976). Dalziell and Welbergen (2016) in particular have recently asserted that “deception is not necessary for mimicry to evolve” (p. 613).

Controversy surrounding the role of deception in mimicry may have arisen because of an underlying confusion regarding deception itself. First, use of the term deception does not imply (nor preclude) intentionality or conscious awareness in the deceiving agent, and therefore does not depend on the mimic’s known or presumed behavioral or cognitive complexity. Second, different authors have characterized deception in different ways. Some define deception in mechanistic terms, as a receiver mistake or perceptual error (Mitchell 1986; Searcy and Nowicki 2005; Christy and Rittschof 2011). Others, however, use a functional definition and propose instead that deception occurs when the receiver incurs a fitness cost for responding to a signal that provides incomplete or misleading information (Semple and McComb 1996). To further complicate things, some definitions combine both elements and describe deception as the kind of perceptual error that benefits senders at the expense of receivers (e.g. Bradbury and Vehrencamp 2011; Ruxton and Schaefer 2011; Mokkonen and Lindstedt 2016).

Dalziell and Welbergen (2016) are clearly using a functional definition when they explain that, given that the costs incurred by a receiver can be partial, context dependent or transient, receiver deception should not be part of the definition of mimicry. But mimetic signals can still be deceptive in a mechanistic sense, as receiver perceptual error, whether or not this error entails any fitness costs for the receiver. In fact, Christy (1997) offered two valid reasons why receiver costs should not be considered a necessary condition for deception generally. First, even though receivers may sometimes suffer a cost from responding to deceptive signals, it must be remembered that these are effective because they mimic authentic signals that the receiver benefits from responding to in a different context. Therefore, costs and benefits should be judged considering all the different contexts in which the receiver responds to the signal (see also Carazo and Font 2014). Second, the requirement that there be receiver costs would exclude the possibility of deception in many essentially cooperative, mutually beneficial interactions that entail little or no costs to receivers, such as those taking place between genetic relatives (e.g. parents and offspring), or between individuals with overlapping evolutionary interests (e.g. members of a mated pair).

Thus, labeling a mimetic signal as deceptive does not imply, as some have inferred, that responding to the signal necessarily carries fitness costs for the receiver. As Weldon (2016) puts it, deception "denotes that receivers fail to distinguish between authentic and counterfeit cues" (p. 723). Thus, deception, construed as receiver perceptual error, is not necessarily costly for receivers and may benefit both mimic and receiver. In fact, many mutually beneficial relationships are maintained by deception (Weldon 2016). A case in point are male courtship signals that mimic stimuli that females are selected to respond to in a different context and which are beneficial to both males and females (e.g. sensory traps, see below). Mimetic signals are deceptive in the mechanistic sense because they elicit receiver errors, i.e. misperceptions or categorical mistakes, not because they are costly (Christy 1997; see also Weldon 2016). Therefore, I argue that deception (understood as perceptual error) is a hallmark of mimetic relationships and offer the following updated definition:

> Mimicry is resemblance/similarity in appearance and/or behavior between a mimic and a model that provides a selective advantage to the mimic because it affects the behavior of a receiver causing it to misidentify the mimic and that evolved (or is maintained by selection) because of those effects.

This definition is modelled after recent adaptationist definitions of communication (Maynard Smith and Harper 2003; Scott-Phillips 2008; Carazo and Font 2010; Font and Carazo 2010). The requirement that the resemblance is favored by selection due to the benefits it accrues to the mimic allows the distinction between mimicry and other causes of resemblance, such as shared ancestry, resemblance as a by-product of selection for other traits, chance, or other forms of convergent evolution that do not involve a model-mimic relationship. The definition does not make any assumptions as to how mimetic signals develop and therefore does not explicitly address the role of learning in mimicry. Although learning could operate on receivers, mimics and models, the case in which the mimetic resemblance is learned has been considered especially problematic (e.g. vocal mimicry; Dalziell et al. 2015). Pasteur (1982), for example, rejected vocal mimicry as a form of mimicry because it is learned. However, vocal mimicry is not necessarily learned (Kelley et al. 2008). Burrowing owls (*Athene cunicularia*) imitate the sounds produced by rattlesnakes without having ever encountered a rattlesnake and without the need to learn those sounds from other burrowing owls. In any event, the definition above easily accommodates both genetic and cultural modes of acquisition of the mimetic phenotype. Selection will in some cases be responsible for development of an unlearned resemblance, while in others it will be responsible for the development and maintenance of the neural machinery necessary for learning the mimetic signal.

Müllerian Mimicry

Definitions, however, are rarely watertight. In particular, the stipulation that mimicry should deceive receivers would seem to exclude cases of Müllerian mimicry. Müllerian mimicry is resemblance between members of a guild of unpalatable species, and is considered mutualistic because co-mimics reduce the per capita predation risk and share the costs of predator education. This type of mimicry is problematic because receivers failing to discriminate between the Müllerian co-mimics apparently are not deceived. Stevens (2016) deliberately eschews discussion of Müllerian mimicry in his excellent book on deception, because this type of mimicry "does not involve deception" (p. 292). Similarly, Weldon (2016) acknowledges that Müllerian mimicry is, compared to other types of mimicry, exceptional because it "is not deceptive" (p. 719). However, receivers of Müllerian mimetic signals are deceived in the sense that they are unable to discriminate among the members in a ring of Müllerian mimics (i.e. a perceptual error) (see also Vane-Wright 1976). Further, under some realistic scenarios the deception could also be costly to the receiver. In particular, it has been argued that, where Müllerian mimics differ in toxicity or unpalatability, receivers selecting weakly unpalatable prey may incur a fitness cost in the form of missed opportunities (Ruxton et al. 2004; Sherratt 2008). Following Müller (1879), who first described the phenomenon, it is usually assumed that all co-mimics in a Müllerian mimicry ring are equally unpalatable, but this is an unlikely situation. In fact, it has been shown that co-mimics often differ in their toxicity or unpalatability (e.g. Bowers and Farley 1990). Under these circumstances, weakly unpalatable mimics can become Batesian mimics of more unpalatable models, particularly when resources are scant and predators are prone to accepting weakly distasteful prey (called quasi-Batesian mimicry; Speed 1999; Ihalainen et al. 2008; Rowland et al. 2010). Indeed, it has been proposed that Batesian and Müllerian mimicry should be considered as two extremes of a mimicry continuum, rather than purely parasitic and mutualistic alternative phenomena. As the edibility of a prey item is to a large extent dependent on predator hunger, the status of a certain mimetic resemblance may change and it may be difficult to determine the extent to which a given relationship is Batesian or Müllerian (Ruxton et al. 2004; Sherratt 2008).

Mimicry for all Sensory Modalities

Although mimicry research originated as an attempt to explain visual similarities among organisms, it has expanded to include signals in every known sensory modality, including visual, chemical, acoustic, tactile, even electric signals (Stoddard 1999; Maran 2017). For example, assassin bugs (*Stenolemus bituberus*) lure the web-building spiders on which they feed by plucking the web's silk threads to produce vibratory cues that mimic the frequency, duration, amplitude and temporal structure of the vibrations generated by insect prey (Wignall and Taylor 2011). The relationship between ants and aphids provides an example of chemical mimicry as well as an unexpected twist on a familiar story. Ant-aphid relationships are often described as mutualistic: ants eat the sugar-rich honeydew excreted by the aphids and, in return, provide them with protection and hygienic services. However, during part of its life cycle, the aphid *Paracletus cimiciformis* produces two wingless morphs that differ in morphology and behavior: a whitish flat morph and a greenish round morph. Individuals of the round morph maintain a "conventional", mutualistic relationship with *Tetramorium* ants, their main tending ants. In contrast, individuals of the flat morph induce ants to pick them up and transport them to the ants' brood chamber, where they feed by piercing ant larvae and sucking their haemolymph. The flat morph aphids accomplish their trick by imitating the cuticular hydrocarbons of *Tetramorium* ant larvae

(Salazar et al. 2015). Their relationship with ants is therefore best described as one of aggressive or parasitic mimicry. While these examples focus on a single sensory modality, there is increasing evidence that many cases of mimicry involve resemblance across several modalities. Sexually deceptive orchids, for example, attract specific male insects that are fooled into attempting to mate with the flowers and inadvertently act as their pollinators. Recent research has stressed the role of chemicals in the mimetic resemblance, but flower shape, color, size, texture and other close-range tactile cues may also be important (Gaskett 2011).

Mimicry Is in the Eye of the Beholder

Since mimetic signals are tailored to the perceptual systems of their intended receivers, human perception is generally inadequate to assess the extent to which mimics in a mimetic relationship resemble models. Often we find that mimics are not, to our senses, very good copies of the models they mimic. But our perception is often radically different from the perception of the true actors in a mimetic relationship. Where a human researcher appreciates only superficial resemblance, there may be a close match from the receiver's perspective (see Kikuchi and Pfennig 2013). For example, most myrmecophilous staphylinid beetles that live inside ants nests bear very little resemblance, to our eyes, to their ant hosts. However, recognition of nest mates in ants is primarily by means of chemical stimuli and the myrmecophilous beetles produce cuticular hydrocarbons that faithfully imitate, as in the flat morph aphids described above, the ants' hydrocarbons to deter or placate ants (Hölldobler and Wilson 1990).

Resemblance to the model has thus to be judged from the perspective of the intended receiver, not from that of a human observer. In fact, it has been argued that many examples of mimicry probably go undetected because to our eyes the mimic does not offer a reasonable facsimile of the model. Recent technological and methodological advances (e.g. the use of reflectance spectrophotometry and visual modelling in the study of visual mimicry) offer improved tools to assess the resemblance between mimic and model, and to advance in the quest to discover how receivers perceive the similarities between them (e.g. Stoddard and Stevens 2011). Still, to fully understand the evolution of mimetic phenomena it may be necessary to probe beyond sensory and perceptual mechanisms to address the cognitive processes involved in prey recognition and predator attack decisions (Rönkä et al. 2018).

Recent work with crab spiders (genus *Thomisus*) illustrates some of the complexities involved. Crab-spiders are sit-and-wait predators often found on flowers from which they stalk prey such as honeybees and other pollinating insects. The spiders' body color is a very good match to the white and yellow color of the flowers on which they sit, at least to the eyes of a human observer. However, the relevant receivers in this case are not humans, but honey bees and birds (who are spider predators). In contrast to humans, both honeybees and birds have extended visual sensitivity into the UV part of the spectrum, to which humans are blind. Using visual modeling techniques, Théry and Casas (2002) were able to determine that the reflectance in the UV spectrum of *Thomisus onustus* from France matches that of the flower petals on which they sit, making the spiders relatively inconspicuous to both honeybees and birds (Fig. 1). Australian crab spiders (*T. spectabilis*) also sit on white and yellow flowers but, in contrast to European *Thomisus*, their body reflects more UV than flowers do. Australian crab spiders are therefore as cryptic as European crab spiders to human eyes, but to the eyes of a honeybee they contrast strongly against the flower petals on which they sit (Fig. 1). Interestingly, Heiling et al. (2005) have shown that European honeybees are more attracted to flowers with Australian crab spiders than to flowers without them. Thus it seems that where European *Thomisus* rely on crypsis (extending into the UV) to capture prey, their Australian cousins lure prey by taking advantage of their preference for flowers with highly contrasting markings (Heiling et al. 2003).

Cue Mimicry and Signal Mimicry

Some influential definitions of mimicry describe mimics as imitating the communicative signals of models (e.g. Vane-Wright 1980; Robinson 1981; Wickler 2013). Semiotic approaches in particular emphasize the links between communication and mimicry, which is considered a formal communication structure (Maran 2017). However, as recently stressed by Jamie (2017), the model's traits that mimics copy can in fact be signals ("signal mimicry") or cues ("cue mimicry"). Cues are features of an individual's phenotype (or the environment) that incidentally provide information to an unintended receiver (Maynard Smith and Harper 2003; Stevens 2013). Signals represent traits that have been

Fig. 1 Crab spiders (*Thomisus*) ambushing prey on daisies. The top photographs (**a**, **b**) are of a European crab spider, while those in the bottom (**c**, **d**) are of an Australian *T. spectabilis* (**c** and **d** from Heiling and Herberstein 2004, with permission). The photographs on the left (**a**, **c**) were taken using normal (human) visible light; those on the right (**b**, **d**) were taken through a UV-transmitting filter, which lets through only UV and excludes all human-visible wavelengths. Note that, when viewed in the UV, the European crab spider is relatively inconspicuous against its background compared to its Australian counterpart (compare **b** and **d**), which reflects much more UV light than the flower and therefore stands out sharply to receivers capable of UV vision, such as honeybees

under selection specifically for their communicative function, whereas cues are potentially informative traits that have not been under such selection (Carazo and Font 2010; Font and Carazo 2010; Stevens 2013). Responding to cues is usually beneficial to receivers, but may be costly to senders (the individual producing the cue).

Jamie (2017) asserts that, regardless of whether the model's trait it copies is a signal or a cue, the mimetic phenotype is always a signal, since it evolved specifically to affect the behavior of the receiver (see also Grim 2013). While this may be generally true, it does not take into account the full definition of communicative signal. According to current definitions (Maynard Smith and Harper 2003; Scott-Phillips 2008), for a phenotypic trait to be a signal the trait must have evolved for the purpose of affecting the receiver, but the receiver's response must have also evolved to be affected by that trait. The extent to which the response to a mimetic signal that imitates a cue has been specifically selected for that function is debatable. Responses to cues (mimetic or not) may depend on general properties of the sensory/perceptual systems rather than on selection for responsiveness to specific stimuli.

Jumping spiders (genus *Portia*) provide examples of both cue and signal mimicry. These spiders prey on other web-building spiders that they lure by imitating the vibrations produced when prey (e.g. flies) become ensnared in their webs. This is an example of cue mimicry since the fly-produced vibrations are cues that clearly did not evolve to attract spiders. *Portia fimbriata*, an Australian species, deceives females of another salticid spider by creating vibrations in their webs, but in this case the vibrations imitate the courtship vibrations produced by courting males (Jackson and Wilcox 1990). As the courtship vibrations evolved in the context of communication between males and females of the prey species, they are signals and their use by *P. fimbriata* in a predatory context is an example of signal mimicry.

According to Jamie (2017), a key difference between signal and cue mimicry is that mimic and model share the same receiver in signal mimicry, but not in cue mimicry, where mimic and model have different intended receivers. This distinction, however, is of little practical use given that cues do not, by definition, have intended receivers, i.e. they are incidental effects of traits that did not evolve for that purpose. But even assuming, for the sake of argument, that cues can have intended receivers, it is possible to point to cases of cue mimicry in which mimic and model have the same potential receiver. The intended receiver of the worm-like lure of an anglerfish, one of the examples of cue mimicry discussed by Jamie (2017), is presumably a smaller fish. But the same small fish may on a different occasion (provided it survives the encounter with the anglerfish) be the receiver of cues provided by the real worms on which it feeds. Thus both real and fake worms share one and the same receiver that acts as predator in one relationship and as potential prey in the other.

Jamie (2017) provides a framework for classifying the different types of mimicry based on two criteria: 1) the deceptiveness of the mimic's signal (high or low), and 2) the fitness consequences signaled by the mimic in order to manipulate receiver behavior (positive or negative). This results in four types of mimicry: the three traditional categories of Batesian, Müllerian and aggressive mimicry, plus a fourth category termed "rewarding mimicry" (essentially, a type of Müllerian mimicry in which mimics signal fitness rewards to manipulate receiver behavior). However, this classification scheme seems overly restrictive and puts familiar types of mimicry in unexpected categories. For example, food-mimicry by non-rewarding plants, which most authors consider a type of Batesian mimicry (Schaefer and Ruxton 2009), is classified as aggressive mimicry. Likewise, masquerade, a term reserved for organisms that closely resemble an inedible or uninteresting object (see below), is classified by Jamie (2017) as Batesian or aggressive mimicry.

The possibility that communicative signals become the target of selection for mimicry has been discussed previously (e.g. Vane-Wright 1981; Carazo and Font 2014). Signals are the result of a coevolutionary arms race between senders and receivers. One consequence of this arms race is that, for a communication system to be stable, signals must confer net fitness benefits to senders and receivers, which means that some aspect of the signals' design must correlate with a quality that receivers benefit from knowing about. In order to manipulate receiver behavior, senders must make available information to receivers, and the information has to be honest (on average) or else receivers will stop responding to the signal and the communication system will collapse (Searcy and Nowicki 2005; Font and Carazo 2010; Ruxton and Schaefer 2011). Deception, however, can invade a stable communication system in two ways: incomplete honesty and signal parasitism (Carazo and Font 2014). Incomplete honesty refers to situations in which a signal exaggerates (or attenuates) the quality about which the sender is signaling (e.g. body size). Mimicry epitomizes the other way in which deception can corrupt a communication system. When mimics copy signals that are already in use as part of a stable communication system, they become parasitic senders and their signals are considered parasitic. Parasitic signals (i.e. mimetic signals) are similar enough to model signals that they are mistaken by receivers for the legitimate model signals that they copy, and they work because they are relatively rare compared to the model signals they imitate (e.g. Lindström et al. 1997). In contrast to legitimate signal senders, mimics always offer misleading information to receivers about their identity (species, sex, age-sex class) or about the fitness consequences of responding to the signal. Parasitic senders fail to deliver their end of the communication bargain: they emit a signal that affects the receiver's behavior, but what they offer in return is counterfeit information. Misinformation is therefore responsible for the receiver's perceptual error. In a stable communication system, both senders and receivers benefit, on average, from their interaction. When such a system is invaded by parasitic senders, receivers often (but not always) incur costs for responding to the fake signals. But note that we still refer to signal mimicry as communication because, even though it may be costly for receivers to respond to mimetic signals, it is the average expected net fitness payoffs that count, i.e. receivers are exposed to legitimate and parasitic signals and responding to them will continue to benefit receivers, on average, provided that parasitic signals are relatively rare (Stevens 2013; Carazo and Font 2014; Nelson 2014).

Mimicry and Camouflage

A particularly nagging problem that has plagued mimicry studies is the distinction between mimicry and camouflage (Vane-Wright 1980; Endler 1981; Pasteur 1982; Starrett 1993). Although they are often conflated, mimicry and camouflage refer to different phenomena. Camouflage denotes all strategies used by organisms to avoid detection or recognition by other organisms, and includes several types of crypsis (i.e. colors and patterns that prevent initial detection), as well as masquerade, motion dazzle, and motion camouflage (Stevens and Merilaita 2009).

Background matching (a type of crypsis), is a widespread form of camouflage that involves resemblance of an organism to one or more background types in terms of coloration, luminance, texture, or pattern (Stevens and Merilaita 2009). Both mimicry and background matching involve adaptive resemblance, but in background matching the camouflaged organism resembles the background (an "undefined" model according to Wickler 2013) rather than a model proper. Background matching is generally not considered a form of mimicry for a number of reasons. While both are often concerned with protecting prey from predators (or concealing predators from prey), background matching and mimicry achieve the same function in different ways. Background matching functions by preventing detection and discrimination of the camouflaged individual from the background. In contrast, mimicry works by preventing recognition, rather than detection of the mimic. Vane-Wright (1976) expressed the difference as one between "failure of awareness" and "mistaken identification", and considered the latter an essential defining characteristic of mimicry. Background matching and other strategies that hinder detection presumably work by exploiting biases in the receivers' early stages of sensory processing. Mimicry, on the other hand, works by exploiting peculiarities of the receivers' sensory processes at higher stages of processing involving recognition and classification of stimuli (Stevens 2013). In mimetic interactions, receivers "undertake a recognition and classification task, which requires higher order cognitive processing that can be innate and/or learnt" (Dalziell and Welbergen 2016, p. 615). Thus background matching and mimicry address different processes in receivers, i.e. sensory in the case of background matching and cognitive in the case of mimicry. A background matching phenotype cannot be mimetic "because at these stages a receiver cannot yet 'perceive' similarity" (Dalziell and Welbergen 2016, p. 615). The difference is important, but in practice it may be difficult to distinguish between detection errors and recognition errors, and at least one type of camouflage (masquerade, see below) works, like mimicry, by preventing recognition.

Weldon (2016) likens the difference between detection and recognition errors to that between type I and type II errors in statistics (see also Christy and Rittschof 2011). In statistical hypothesis testing, type I errors consist of incorrectly rejecting a true null hypothesis, whereas type II errors consist of incorrectly accepting a false null hypothesis. In this analogy, recognition errors are akin to type I errors (an error of commission) and detection errors to type II errors (an error of omission). Mimicry often causes type I receiver-errors (false positives/mistaken identifications) while crypsis, including background matching, is responsible for type II (false negatives/missed detections) receiver errors. Note that the definition of mimicry presented above specifies that the mimetic phenotype should cause a recognition error in receivers, and thus allows for the distinction between mimicry and crypsis.

It has been argued that a further distinction between mimicry and background matching (and masquerade, see below) is that in the latter, mistakes made by the receiver have no effect on the population/evolutionary dynamics of the model (Endler 1981; Vane-Wright 1981). In contrast, receiver mistakes caused by mimics often affect the population/evolutionary dynamics of their models. For example, in Batesian mimicry there is a cost to the model species because predators that sample the mimic do not learn to recognize and avoid the model. Both costs and benefits are frequency-dependent, which explains why Batesian mimics tend to be rare compared to their models (Ruxton et al. 2004).

Still, there is a grey area and the decision whether a particular relationship involves mimicry or camouflage often relies on our perception rather than that of the intended receivers. Edmunds (1974) discussed the example of several nudibranchs that resemble the sponges and anemones upon which they feed. As Quicke (2017) rightly points out, "whether such cases are mimetic or cryptic depends crucially on whether a potential predator, say a fish, ignores the sponges or hydroids because they are not suitable food, or actively avoids them because they represent a threat" (p. 5). The nudibranchs could in fact be both cryptic and mimetic if they are exposed to different predators that avoid them for different reasons.

The Problem with Masquerade

To complicate things further, there is a type of camouflage that according to most researchers qualifies also as a mimetic phenomenon. Masquerade involves resemblance to an inedible or uninteresting object such as a leaf, a thorn, a stick, a pebble or a bird dropping (Stevens and Merilaita 2009; Skelhorn et al. 2010a, b, Skelhorn 2015). Skelhorn et al. (2010a) define a masquerading species "as one whose appearance causes its predators or prey to misclassify it as a specific object found in the environment, causing the observer to change its behaviour in a way that enhances the survival of the masquerader" (p. 4). The leaf-mimicking katydids discussed above are a classic example of camouflage through masquerade (although, depending on circumstances, they could also be considered a case of background matching). Other examples include the familiar stick insects and the leafy sea dragon, an Australian sea-horse with bodily outgrowths that make it look like a seaweed. Masquerade has always been problematic because it seems to fall somewhat in between crypsis and mimicry. Unlike crypsis, masquerade acts by preventing recognition, not detection of the masquerading organism. In contrast to background matching, in which the camouflaged individual is mistaken for the background on which it rests, masquerading individuals are identified as specific – albeit uninteresting or undesirable – objects (Endler 1981). As Skelhorn et al. (2010a) put it, "the visual appearance of a cryptic species hinders its detection, whereas the visual appearance of a masquerading species hinders its correct identification" (p. 3). Thus a number of authors have argued that masquerade, preventing recognition, should be considered a type of mimicry (Endler 1981; Stevens 2013; Speed 2014; Dalziell and Welbergen 2016; Jamie 2017). However, unlike other cases of mimicry, many classical examples of masquerade involve resemblance to an inanimate object rather than to a living organism.

According to Endler (1981), masquerade differs from Batesian mimicry because masquerading species do not affect the population or evolutionary dynamics of the models being imitated. The presence of both masqueraders and Batesian mimics increases the rate at which models are attacked by predators, but only in Batesian mimicry does this increase in attack rate have an effect on the evolutionary dynamics of the model. However, Skelhorn et al. (2010a) have suggested that, excepting when they mimic inanimate objects, both masqueraders and Batesian mimics can have an influence on the population or evolutionary dynamics of their models, albeit in different ways. Batesian mimics affect the population dynamics of their models indirectly through their influence on the predator shared by mimics and models. Masqueraders, on the other hand, affect their models directly, either by damaging or consuming the models themselves (e.g. stick insects eating their host plants), or by killing animals that directly influence the reproductive success of the model (e.g. flower mantids eating seed-eating pests and/or pollinators).

Sensory Traps: Mimetic Courtship Signals

The receiver-precursor model of signal evolution posits that some communicative signals evolve by exploiting pre-existing features of the perceptual systems of receivers (Bradbury and Vehrencamp 2011). This model was originally developed in the context of mate choice, to explain the evolution of many displays that males use to acquire mates (Endler and Basolo 1998); however recent work has shown that the exploitation of pre-existing biases is a major route to the evolution of all kinds of signals used in many different contexts (Bradbury and Vehrencamp 2011). Most authors refer to this model of signal evolution as sensory exploitation, although perceptual exploitation may be a better term since it denotes a broader range of potential sensory, neural or cognitive biases (Schaefer and Ruxton 2009; Stevens 2013). The Australian crab spiders discussed above provide a well-documented example of perceptual exploitation, the spiders exploiting the honeybees' preference for flowers with highly contrasting markings. This preference is likely adaptive in a foraging context (i.e. an adaptive bias, see below), but has fatal consequences where a crab spider is involved.

Perceptual exploitation can be a source of resemblance, which raises the question to what extent similarities between a mimic and a model result from perceptual exploitation or from selection for mimicry. Is the mimic taking advantage of a pre-existing receiver bias or is the receiver mistaking the mimic for the model? The end result may be similar (i.e. adaptive resemblance), but the selective forces involved clearly are different. In the case of perceptual exploitation, there is no selection on the mimic to resemble a model and there is no receiver-error. In mimicry, the convergence between mimic and model depends on the costs associated with mistaking model and mimic. In perceptual exploitation, however, the perceptual bias determines the optimal signal design (Schaefer and Ruxton 2009; Stevens 2013, 2016). Therefore, signals evolved by perceptual exploitation are generally not mimetic, but there are exceptions (sensory traps, see below).

Perceptual biases can be latent or adaptive (Bradbury and Vehrencamp 2011). Latent biases are incidental and selectively neutral consequences of the design of sensory and cognitive systems. Adaptive biases and their associated responses, on the other hand, are selected because they are beneficial in other contexts. Adaptive biases include most examples of so-called sensory traps (Christy 1995). In many courtship interactions, males produce stimuli that imitate a model to which females are highly responsive in a non-courtship context. Male water mites (*Neumania papillator*), for example, move their legs in order to approach and mate with receptive females. The leg movements set up water vibrations similar to those produced by copepod prey. Females respond to the male vibrations as they would to copepods, initially grabbing the male, but then releasing it and picking up with her genital opening the spermatophores that the male deposits in front of her (Proctor 1991). Unlike perceptual exploitation of latent biases, sensory traps imply a model-mimic relationship and can therefore be considered mimetic (Stevens 2013, 2016; Dalziell and Welbergen 2016).

Schaefer and Ruxton (2009) have suggested that perceptual biases could act as precursors for the evolution of mimetic relationships (see also Stevens 2013). The spider-tailed viper provides a potential example of this evolutionary transition. Many snakes wriggle the tip of their tail to attract potential prey, mainly small insectivorous lizards. This behavior, known as caudal-luring, has traditionally been described as aggressive mimicry (Vane-Wright 1976; Schuett et al. 1984). However, an equally likely interpretation is that this behavior originated as a sensory trap, exploiting the known propensity of lizards to approach small wriggling objects (Desfilis et al. 2003). In this alternative scenario, lizards would not be misidentifying the snake's tail for an insect or some other suitable wriggling prey item; they would simply be responding to a stimulus to which their perceptual systems are particularly sensitive (Nelson (2014) reviews the evidence in support of alternative scenarios for the evolution of caudal-luring in snakes). But increased discrimination by the lizards could trigger a coevolutionary arms race resulting in further elaboration of the snake's tail tip to make it more similar to the lizards' actual prey. In the end, such a process could lead to the production of a mimetic phenotype as astonishing as that of the spider-tailed viper. A similar proposal has been made to explain how signals that originate as sensory traps could evolve into honest signals of mate quality in intraspecific interactions (Macías-García and Ramirez 2005; Stuart-Fox 2005).

Deception: The Common Thread

The evidence reviewed above shows that mimicry overlaps, both conceptually and evolutionarily, with camouflage and with perceptual exploitation. However, the overlap is only partial, which may explain the difficulties in providing clear, unambiguous diagnostic criteria (Fig. 2). Often the same phenomenon can be classified into two or more discrete categories depending on perspective and the proclivities of the researcher doing the classification.

I contend that the common thread through these diverse phenomena is deception. Deception emerges as a strategy that cuts across different ecological interactions and taxonomic groups (Mokkonen and Lindstedt 2016). However, as stated above, different authors use the term deception to mean different things. These definitional ambiguities hamper fruitful interaction between mimicry research and communication theory. I suggest that deception can usefully be seen as receiver perceptual error that does not, despite claims to the contrary, necessarily carry an associated fitness cost for the deceived individual. Signal senders (e.g. mimics) must, by definition, benefit from deception, but receivers of deceitful signals also may benefit from some, perhaps many interactions (Weldon 2016). Restricting the use of deception to cases in which receivers incur a fitness cost would at the very least force us to find a new term to describe interactions in which receivers do not pay a cost or even benefit from responding to deceptive signals. This seems unnecessary.

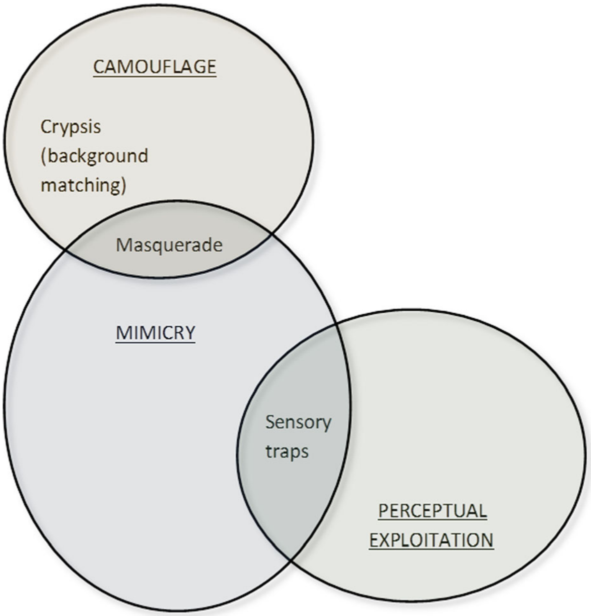

Fig. 2 Idealized representation of areas of overlap between mimicry, camouflage, and sensory exploitation

Once thought to be a primarily human trait, deception is rife among many taxa (Trivers 2011). Discussions of animal deception have traditionally been restricted to the realm of interspecific interactions. Classical ethologists did not think that deception (lying, faking and bluffing) was important to understand most cases of intraspecific communication: rather communication was widely seen as an essentially cooperative interaction between sender and receiver for their mutual benefit, and most animals were in fact thought to lack the cognitive underpinnings necessary for deception. Smith (1977), in one of the books that best summarizes the classical ethological perspective on communication, asserted that "Ethologists have not yet caught nonhuman animals in intentional acts of lying with display behavior" (p. 264). In the wake of the sociobiology revolution, however, both deception and mimicry gained prominence in discussions of intraspecific communication (Mitchell 1986; Searcy and Nowicki 2005). Dawkins and Krebs (1978; Krebs and Dawkins 1984) proposed an alternative view of communication centered on the idea of manipulation of receivers by senders and of senders by receivers. Since the interests of senders rarely align exactly with those of receivers, lying and deception should be, according to this new paradigm, the rule rather than the exception. Animals should use every trick in the book to lie, cheat and deceit hetero- and conspecifics alike. Yet, contrary to expectations, the available evidence reveals that signals are usually honest. In the words of Brockmann (2006) "As with human communication, "truth in advertising" appears to be the rule" (p. 850). But honest communication provides fertile ground for the emergence of deceptive strategies, including mimicry. The current outlook on communication sees deception as an important ingredient of every communicative interaction and an evolutionarily stable strategy within many, perhaps most communication systems, particularly in situations where senders and receivers have conflicting interests (Searcy and Nowicki 2005; Greenfield 2006; Rowell et al. 2006).

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