PERSPECTIVE

When is resemblance mimicry?

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Abstract

1. Mimetic resemblance is extensive across the tree of life yet agreeing on what constitutes mimicry is challenging. One of the reasons for disagreement is a lack of unambiguous criteria to resolve whether a case of resemblance is a product of mimicry or alternative processes.

2. Mimicry occurs when an organism takes advantage of the perception and association that a receiver has with a model to gain adaptive benefits. Three conditions should be fulfilled to confirm mimicry: (1) characterising a model, (2) identifying a receiver with a percept of said model and (3) demonstrating that the receiver exerts selection on the mimic.

3. We suggest multiple lines of evidence, both experimental and correlative, to support each condition. These conditions help separate similarity due to crypsis and perceptual bias from mimetic resemblance. Furthermore, we explore forms of receiver-mediated selection on the mimic, what mimics need to resemble for successful mimicry to occur, and the evolution of imperfect mimicry.

4. We hope this perspective provides a functional pathway for biologists to confirm the existence of mimicry and serve as a guide for studying mimetic interactions across disciplines.

KEYWORDS
adaptation, convergence, fitness, mimic, perception, receiver, resemblance, selection

1 | INTRODUCTION

Mimicry provides some of the most compelling evidence for natural selection as a driver of biological adaptation (Joron & Mallet, 1998). Mimetic resemblance is remarkably common and has been reported in fish (Cheney & Côté, 2005), amphibians (Darst & Cummings, 2006), reptiles (Pfennig, Harcombe, & Pfennig, 2001), arachnids (Oliveira, 1988), hemipterans (Wignall & Taylor, 2011), butterflies (Kapan, 2001), angiosperms (Johnson, Alexandersson, & Linder, 2003) and birds (Davies, 2015). The evolution of mimicry also spans several sensory modalities: visual (butterflies avoid predation with wing patterns resembling toxic heterospecifics—Llaurens, Joron, & Théry, 2014), chemical (orchids are pollinated by copying the sex phero-mones of their pollinators' females—Schiestl et al., 2003), acoustic (butterfly larvae gain access to ant nests and food by mimicking the stridulations of ant queens—Barbero, Bonelli, Thomas, Balletto, & Schönrogge, 2009), and tactile (predatory assassin bugs attract spiders by vibrating webs to simulate captured prey—Wignall & Taylor, 2011).

Despite the prevalence of mimicry and its pivotal role in exemplifying natural selection (Darwin, 1869; Fisher, 1930; Malcolm, 1990; Wallace, 1865), defining what qualifies as mimetic resemblance remains ambiguous (Dalziell & Welbergen, 2016; Grim, 2005; Quicke, 2017; Ruxton & Schaefer, 2011; Wickler, 2013). This paradox is often due to a lack of decisive criteria for identifying mimicry (Grim, 2005; Ruxton & Schaefer, 2011). Many interpretations of mimicry are also exclusive and view mimicry in light of a specific ecological setting or taxon. For instance, the term "deception" when defining mimicry (Wickler, 1968, 2013) excludes Müllerian mimicry, one of the best-studied and longest recognized forms of mimicry.

While there have been numerous attempts to define mimicry functionally (Bates, 1862; Dalziell & Welbergen, 2016; Endler, 1981; Starrett, 1993; Vane-Wright, 1976; Wickler, 2013), most definitions overlap in key themes. These can be encapsulated as: mimics resemble models, as perceived by their receivers, to gain fitness benefits. This statement highlights the adaptive nature of mimetic resemblance (e.g., increased survival, feeding and reproduction), and the three entities recognized by all authors—mimics, models and receivers (Wickler, 1968). Consequently, to identify mimicry one should first confirm the existence of a model and a receiver and then demonstrate that resemblance between the mimic and the model is adaptive. It is worth noting that models, receivers and mimics need not be different species. For instance, in avian brood parasitism, receivers and models may be different life stages (adults vs. eggs) of the same species (Brooke & Davies, 1988).

Here we consider the roles played by each of these entities and propose a set of conditions that should be met for an interaction to be considered mimetic. These conditions provide a functional pathway towards the verification of mimicry. To demonstrate the utility of this approach, we apply these conditions to ambiguous cases of resemblance to determine whether they can be considered mimicry or not. This study thus functions as a theoretical treatise on the agents of mimicry and their interactions; and a practical guide for designing experiments and interpreting evidence to identify and confirm mimicry.

2 | CONFIRMING MIMICRY

Resemblance between organisms can have many origins, of which mimicry is one. For example, phenotypic similarity may also result from phylogenetic constraints shared among closely related taxa or from random chance (Table 1). Unlike phylogenetic constraints or chance, however, mimetic resemblance is adaptive and confers a selective advantage on the mimetic organism (Dalziell & Welbergen, 2016; Jamie, 2017; Starrett, 1993). This benefit can only occur when a receiver selects against the mimics it perceives to be distinct from their models. The receiver therefore needs to have a percept of the model that the mimic can exploit (Dalziell & Welbergen, 2016). A percept is a cognitive impression developed through use of the sensory system that is associated with an experience. Below we capture these fundamentals in a set of three conditions and tests that should be satisfied before mimicry is invoked as the cause of resemblance.

2.1 | Condition 1: There is a model

This is the logical starting point for any investigation into mimicry, because the existence of a model is required to initiate the evolution of mimetic resemblance. The model establishes a percept in the receiver that the mimic exploits for its own benefit (Dalziell & Welbergen, 2016). Consequently, the model must overlap geographically and temporally with the receiver, but not necessarily with the

TABLE 1 Different processes responsible for the occurrence of resemblance between taxa

Resemblance a result of	Process
Selection to resemble a receiver's percept of a model	Mimicry
Similar environmental conditions	Convergent evolution
Selection imposed by a receiver's sensory system	Exploitation of perceptual bias
Shared bauplan or developmental pathways	Developmental constraint
Common descent	Phylogenetic constraint
Shared environment through close geographic co-occurrence	Spatial autocorrelation
Interbreeding	Gene flow
Selection to avoid detection	Crypsis
By-product of selection on another trait	Genetic linkage/Pleiotropy
Coincidence when phenotypic variation among taxa is low	Random matching

mimic. Receivers may still facilitate the evolution and persistence of mimicry despite occasional geographic or temporal isolation from models and mimics, if they are highly mobile or long-lived (reviewed in Pfennig & Mullen, 2010). Nevertheless, the existence of a model is required to drive the evolution of mimicry by generating and maintaining a percept in the receiver. If interactions between receivers and models cease, receivers will have no experience of, or specific behavioural responses to the models that mimics can exploit, resulting in mimetic breakdown. Such a breakdown of mimicry has been documented in the well-studied coral snake (Harper & Pfennig, 2008) and admiral butterfly (Ries & Mullen, 2008) mimicry systems.

The necessity of a model excludes cases of resemblance that evolved due to perceptual bias in a receiver that is not the result of the receiver's interaction with a model. For instance, an insect receiver may be more likely to perceive certain signals than others (e.g., yellow instead of red), simply due to inherent constraints of its visual system (Kelber, 2001). Similarly, most insects perceive UV because their ancestors possessed UV sensitive photoreceptors millions of years before the appearance of flowering plants (Chittka, 1997). When plants evolve phenotypically similar flowers (for instance, yellow flowers or flowers that reflect UV) in response to such sensory limitations and preferences in a shared receiver, this can hardly be considered mimicry, because each plant attracts their receivers independently by exploiting behaviour that is not dependent on any model.

This scenario is different from a percept in the receiver, which is a complex, learned or evolved, cognitive association between a given outcome and interaction with a model. The strength of this association will vary based on the receiver's frequency of interaction with the model and the magnitude of the costs or benefits it experiences as a result. A percept is therefore flexible, as indicated by studies on floral mimicry that report variable floral preferences

and interactions with phenotypically distinct flower models across the ranges of widespread fly (Whitehead, Gaskett, & Johnson, 2018) and butterfly (Newman, Anderson, & Johnson, 2012) pollinator receivers. Mimics thus exhibit different floral phenotypes across the landscape to exploit divergent percepts within a shared receiver (Newman et al., 2012; Whitehead et al., 2018), as also found within butterfly mimicry complexes (Hines et al., 2011; Joron & Mallet, 1998).

In contrast, the exploitation of perceptual bias, when based on the limits of a receiver's sensory system, is less flexible, typically similar between populations, and independent of a specific model (Ruxton & Schaefer, 2011). If it can be demonstrated that perceptual bias in the receiver includes higher cognitive processing involving classification (i.e., a percept—Dalziell & Welbergen, 2016, or categorization—Chittka & Osorio, 2007), and is modified by its interaction with different models (Whitehead et al., 2018), such resemblance may grade into mimicry (Ruxton & Schaefer, 2011; Schaefer & Ruxton, 2009).

While the existence of a model is necessary for mimicry to evolve, there is no limit to the number of models that can exist. Some mimics are polymorphic and resemble different models in different parts of their range (Clark & Vogler, 2009; Darst & Cummings, 2006; Newman et al., 2012). More than one model species may also be responsible for generating the percept in the receiver that mimics exploit, as suggested for some orchids that mimic multiple, closely related models with highly conserved flower morphology (Papadopulos et al., 2013; Scaccabarozzi et al., 2018). Within Müllerian mimicry rings, several sympatric models may also co-exist, and it can be difficult to distinguish model from mimic (Hines et al., 2011). In such cases, it is best to refer to all resembling species that interact with the same receiver as co-mimics or co-models (Brown & Benson, 1974). Regardless of the details of the model(s), it is expected that their removal will reduce mimic fitness once the receiver's percept of the model deteriorates.

2.1.1 | Test 1: The fitness of mimics should decrease when models are removed

Experimental tests for model existence can take many variants. Increasing the distance between models and mimics provides strong evidence for mimicry when correlated with decreases in mimic fitness (Duffy & Johnson, 2017; Harper & Pfennig, 2008; Peter & Johnson, 2008). Similarly, a reduction in mimic fitness with decreasing model abundance reveals the existence of a model in rewardless flower mimics that resemble co-occurring, nectar-producing flowers (Anderson & Johnson, 2006). Demonstrating reduced fitness of mimetic phenotypes in areas where models are absent can likewise serve this purpose. Pfennig et al. (2001) demonstrated across two mimicry systems that non-venomous kingsnake mimics suffer increased attack rates in areas where their venomous coral snake models are absent. Within Müllerian mimicry, co-mimics/co-models also exhibit fitness reductions when separated from their resembling counterparts (Chouteau & Angers, 2011; Chouteau, Arias, & Joron, 2016; Kapan, 2001), although these fitness reductions will be

most apparent during the process of receiver learning (Chouteau & Angers, 2011).

Controlled learning experiments with naïve receivers can also illustrate the existence of a model. Naïve bat receivers consume highly noxious moth co-models at the start of a flight cage experiment, despite avoiding them under natural conditions (Barber & Conner, 2007). After exposure to these noxious moths, they avoid newly introduced noxious co-models and palatable mimics alike (Barber & Conner, 2007). The above-mentioned patterns of decreased mimic fitness are all a product of receivers lacking a strong percept of the model when too few, or no models are present.

Receiver life span and the frequency and intensity of its experience with the model may affect the evidence obtained for a model, especially when experiments are conducted over very small spatial and temporal scales. For example, we might expect an intense interaction with the model (e.g., a near fatality when vertebrate predators attempt to eat a toxic snake) to result in the long-term maintenance of a percept within long-lived receivers (Akcali & Pfennig, 2014). In contrast, a low-intensity interaction (e.g., increased nectar consumption when an insect pollinator visits a rewarding flower) may result in short-term maintenance of a percept in short-lived receivers (Duffy & Johnson, 2017). Nonetheless, we predict that benefits to the mimic will decrease, either immediately, or eventually, when there are no models to maintain the receiver's percept.

2.2 | Condition 2: There is a receiver

To benefit from its resemblance to a model, a mimic must exploit an established and predictable interaction between a receiver and the model (Starrett, 1993; Wickler, 1968). These interactions can broadly be grouped into receiver attracted to the model (e.g., most cases of aggressive mimicry), receiver repulsed by the model (e.g., Müllerian and Batesian butterfly mimicry) or receiver tolerating the model (e.g., competitive mimicry, where the model is permitted within the receiver's defended territory). Experiments with domesticated species can help reveal how receivers form these precepts of models. Investigations of mimicry in dendrobatid poison frogs, for example, used naïve domestic chickens to show how wild avian receivers form a percept of toxic models that extend to phenotypically similar mimics (Darst & Cummings, 2006). While studies of mimicry often identify a single receiver species, receivers may comprise several species that share a percept of the models (Akcali & Pfennig, 2014; Scaccabarozzi et al., 2018).

The requirement of a receiver rules out cases of resemblance where organisms are not perceived by receivers. Cryptic organisms escape receiver detection by concealing their signals among the backdrop (e.g., tree bark, leaves or soil) against which receivers view objects. Crypsis is thus not considered mimicry, because the signals of cryptic organisms are masked and not perceived by a receiver (Endler, 1981). Furthermore, the predators or prey of cryptic organisms typically have no specific interaction with the backgrounds on which cryptic organisms hide. Unlike mimics, cryptic organisms do not trigger specific behaviours (attraction, repulsion, tolerance) from

receivers (Grim, 2013; Vane-Wright, 1980). Instead, crypsis functions to suppress such responses in order to remain undetected.

Resemblance via masquerade, where detected organisms resemble specific inanimate or inedible objects, might be considered mimicry under this condition, should it be demonstrated that receivers perceive and interact with models and mimics. Masquerade has been experimentally explored in twig-mimicking caterpillars, where naïve avian receivers interact with twig models when first encountered by repeatedly pecking at them (Skelhorn & Ruxton, 2010). After receivers have been exposed to these unrewarding models, twig-mimicking caterpillars suffer less predation than before receiver exposure to models. This demonstrates that when receivers interact with twig models, they develop a percept of it, which mimics exploit with detectable signals resembling the models (Skelhorn, Rowland, Speed, & Ruxton, 2010).

Should receivers fail to detect masqueraders (e.g., if twig-mimicking caterpillars are viewed against a very dense background of twig models), this could be akin to crypsis because the signals of the resembling organisms may not be detectable by a receiver. Species that resemble inanimate or inedible objects may thus benefit from masquerade and crypsis (Skelhorn, Rowland, & Ruxton, 2010), making their inclusion in mimicry dependant on demonstrating that the receiver detects the resembling organism. Visual modelling of how specific receivers perceive colours and patterns (Stoddard, 2012) coupled with behavioural experiments can help determine whether receivers can detect resembling organisms in such cases.

2.2.1 | Test 2: The receiver interacts with the model and the mimic

In cases of receiver attraction, this condition may not require an empirical test, because attraction can be deduced through simple observations. Interactions based on receiver repulsion or tolerance may be more difficult to document, because these responses could be confounded with non-interaction or non-detection. For example, it may be hard to distinguish whether a bird fails to attack a butterfly phenotype because of negative prior experiences, no prior experience, or failure to detect it. Using naïve receivers in experiments can address this problem by demonstrating that exposure to a model causes a change in the receiver's behavioural interaction with the model (Barber & Conner, 2007; Darst & Cummings, 2006; Skelhorn & Ruxton, 2010), thereby distinguishing a lack of interaction as a result of learning from no interaction due to non-detection.

2.3 | Condition 3: The receiver exerts selection on the mimic to resemble its percept of the model

Demonstrating that resemblance between the mimic and the receivers' percept of the model benefits the mimic is essential to confirm mimicry, because it provides the mechanism whereby mimetic traits evolve. Since mimics benefit from copying specific signals and cues of their models (Jamie, 2017), which have specific meanings to the receiver (Vane-Wright, 1976; Wickler, 1968), we may expect

receivers to select for more accurate mimics over time. Although such receiver-mediated selection can produce very precise mimicry, as in the visual mimicry (wing colouration—Llaurens et al., 2014) and locomotory mimicry (wing-beat frequency—Srygley, 1999) of *Heliconius* butterflies, there are cases where mimicry appears incomplete (Penney, Hassall, Skevington, Abbott, & Sherratt, 2012; Ruxton, Sherratt, & Speed, 2004; Thurman & Seymoure, 2016). Nonetheless, when approximate resemblance to a model is functional, receivers will still exert selection on mimics to maintain existing resemblances (de Jager, Newman, Theron, Botha, & Anderson, 2016; Kikuchi & Pfennig, 2010).

2.3.1 | Test 3: The receiver exerts selection on the mimic

Resemblance to the model need not be perfect for mimics to gain adaptive benefits (Kikuchi & Pfennig, 2010, 2013). Receivers, for example, may not be able to perceive differences between models and mimics beyond a given threshold (Dyer & Chittka, 2004a). Furthermore, the strength of selection on the mimic to improve resemblance decreases as it approaches the model's phenotype, producing incrementally smaller adaptive benefits over time (Kikuchi & Pfennig, 2013). Consequently, an increase in the resemblance between model and mimic may not always lead to greater mimic fitness, but a decrease in resemblance is expected to result in fitness reductions for the mimic as a result of receiver-mediated selection (Barber & Conner, 2007; Johnson et al., 2003; Kikuchi & Pfennig, 2010).

Two avenues of evidence can be used to support selection exerted on the mimic. Firstly, direct empirical evidence can be obtained through experimentation. This method is preferred (Grim, 2013), because it reveals causality by controlling other parameters that could influence results. Experimental approaches, however, are labour intensive and often only applied in one or a few populations (but see Harper & Pfennig, 2007; Kikuchi & Pfennig, 2010). While experiments should ideally use direct measures of reproductive success or survival in mimics, analogous measures that are easier to record can be used if they correlate with increased reproduction (e.g., pollen deposition on the stigmas of mimetic plants—Duffy & Johnson, 2017) or survival (e.g., lack of predator bite marks on plasticine replicas of mimetic snakes—Pfennig et al., 2001).

The second approach employs indirect, correlative methods. This often involves measuring traits from specimens without studying the impact of receiver responses on mimic fitness. While correlations do not imply causality, making it difficult to distinguish mimicry from other causes of resemblance (Table 1), trait measurements can easily be done across populations (Newman et al., 2012), time periods (Spottiswoode & Stevens, 2012) and taxa (Penney et al., 2012). Correlative approaches are useful for investigating putative cases of resemblance between taxa (Gaskett & Herberstein, 2010; O'Hanlon, Holwell, & Herberstein, 2014b) and extrapolating the consequences of mimicry beyond a single, well-studied population (Newman et al., 2012; Spottiswoode & Stevens, 2012). Studies should preferably

employ both experimental and correlative approaches to obtain strong evidence for the existence of mimicry (Harper & Pfennig, 2007; Newman et al., 2012; Spottiswoode & Stevens, 2011).

A rigorous experimental approach for detecting receiver-mediated selection is to decrease the existing resemblance between mimic and model (Kikuchi & Pfennig, 2010). This can be achieved by manipulating key aspects of the mimic's phenotype that receivers are known to respond to. This method was elegantly demonstrated by removing the tymbals used by palatable moths to mimic ultrasonic clicks produced by noxious tiger-moth models (Barber & Conner, 2007). Mimics without tymbals were unable to mimic the sounds of their models and bat receivers consumed them more frequently than mimics with intact tymbals.

Similarly, Johnson et al. (2003) demonstrated receiver-mediated selection by manipulating the unique flat-topped inflorescences of mimetic orchids to resemble their ancestral erect inflorescence shape. This produced poorer resemblance to their flat-topped flower models, resulting in less pollinator visits that negatively impact plant reproduction. Altering floral colour in realistic replicas of mimetic orchids likewise revealed that mimics displaying the least similarity to their models suffer reduced pollinator visitation rates, relative to replicas closely resembling their models (Jersáková, Jürgens, Šmilauer, & Johnson, 2012; Newman et al., 2012).

Natural variation in mimics can also be used in phenotypic selection analyses to detect receiver-mediated selection on mimetic phenotypes. Selection against extreme phenotypes with poor resemblance to the receivers' perception of the model can provide evidence of receiver-mediated stabilizing selection. This approach is seldom employed, and one study failed to detect selection against sexually deceptive orchid phenotypes that do not accurately match their insect models in shape (Benitez-Vieyra, Medina, & Cocucci, 2009). This finding may be the result of poor correlation between the model's phenotype and the receiver's perception of the model, or relaxed selection on traits unrelated to the receiver's percept.

Correlative approaches across multiple populations can help explore how geographic patterns of mimic variation are associated with model phenotype. In the coral snake-kingsnake mimicry system, Harper and Pfennig (2008) reported that mimic phenotypes in populations without models deviate from the mean mimetic phenotypic where models are present, suggesting a breakdown of receiver-mediated selection (Harper & Pfennig, 2008). However, without direct experimental evidence, this approach lacks the causality to irrefutably ascribe phenotypic variation in the mimic to model presence or absence.

Comparing the variance in traits that have been demonstrated to be involved in mimicry with traits unrelated to mimicry can also help indicate selection by the receiver. Within sexually deceptive orchids, scent compounds known to elicit strong attraction from pollinators are less variable than compounds with no effect on the receiver (Ayasse et al., 2000; Mant, Peakall, & Schiestl, 2005), suggesting receiver-mediated selection on mimetic traits. Similarly, in sexually deceptive daisies where mimetic signals are predominantly visual (de Jager & Ellis, 2012), suites of floral traits involved in female-fly

mimicry are under tighter phenotypic integration to form a convincing female mimic than suites of traits unrelated to female mimicry (Ellis et al., 2014).

The final correlative approach we discuss is comparing the traits of mimics with their closest non-mimetic relatives across a phylogeny. This method can help illustrate adaptive divergence between mimetic and non-mimetic phenotypes (Feeney, Troscianko, Langmore, & Spottiswoode, 2015; Johnson et al., 2003) by identifying derived traits in the mimic that likely evolved in association with models and receivers. Mimics may, however, exhibit pre-existing resemblance to a putative model that only becomes adaptive upon contact with a receiver. Consequently, phylogenetic comparisons can provide supportive evidence for mimicry, but may not be able to reject it. Pre-adaptations may play an important role in the evolution of mimicry because some pre-existing resemblance to models is likely necessary for receivers to initiate interaction with mimics. Pre-adaptations may also allow proto-mimics to cross adaptive valleys and exploit the percepts of novel receivers (Gamberale-Stille, Balogh, Tullberg, & Leimar, 2012).

3 | DETECTING RECEIVER-MEDIATED SELECTION ON MIMICS

Since mimics are expected to improve their match to receivers' perception of models over time, evidence of evolutionary change in the mimic can help confirm mimicry. Such evolutionary change in the mimic may be detected by investigating phenotypes at three hierarchical levels. At the broadest level, mimics may exhibit a divergent phenotype to their closest non-mimetic relatives due to receiver-mediated divergent selection (Figure 1a). This can be expected when the model is distantly related to the mimic, resulting in a relatively distinct mimetic phenotype (Feeney et al., 2015; de Jager et al., 2016; Johnson et al., 2003; Llaurens et al., 2014).

A phylogenetically derived mimetic phenotype was one of the original conditions that Alfred Russel Wallace suggested for identifying mimicry ("the imitators differ from the bulk of their allies"—Wickler, 1968, p. 47). However, since mimicry can only be initiated once the receiver perceives some overlap between a putative mimic and its model, mimics may often bear a degree of resemblance to the model prior to receiver-mediated selection (Gamberale-Stille et al., 2012). Depending on which traits of the mimic are being investigated, a derived phenotype may not always be apparent at the species level, rendering phylogenetic evidence insufficient to detect mimicry, if present.

If non-mimetic species with pre-adapted phenotypes become involved in mimetic interactions through range expansions, selection by receivers may be more easily detected at the population level (Figure 1b) than the species level. Mimetic populations may display evidence of stabilizing selection (low mimetic trait variation) relative to non-mimetic populations where trait variation is retained (Harper & Pfennig, 2008). Alternatively, fine-tuning directional selection in
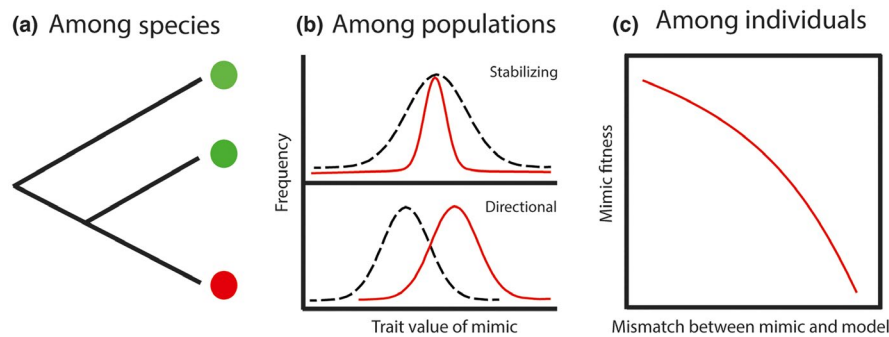
FIGURE 1 Lines of evidence for the evolution of mimicry across multiple hierarchical levels as a result of receiver-mediated selection on mimics. (a) Within a clade, mimics (red) may exhibit a divergent phenotype to its closest relatives (green), because of divergent selection imposed by the receiver to match a model. Similarly, associations with distinct models may also result in phenotypic divergence within mimetic clades. (b) Within a species, different populations may exhibit variation in phenotype, with mimetic populations (red) displaying reduced variation (stabilizing selection) or a shift in variation (directional selection), relative to non-mimetic populations (black, dotted). (c) Within a population, individuals that more closely match their receiver's perception of a model are generally expected to have higher fitness than mimics that poorly resemble models, leading to fitness peaks for mimetically accurate phenotypes

mimetic populations may allow mimics to more accurately resemble the receiver's percept of the model (Gamberale-Stille et al., 2012) relative to non-mimetic populations.

Within a given population, evidence of mimicry may also be detectable at the individual level (Figure 1c). Mimics that most closely match their receiver's perception of the model can be expected to exhibit higher fitness than mimics that poorly resemble models. This line of evidence may be undetectable if there is too little variation in a population, or if perfect mimicry is not adaptive (Kikuchi & Pfennig, 2013). However, manipulative experiments can reveal receiver-mediated selection by generating the needed trait variation for selection studies and decreasing mimic-model resemblance below the thresholds required to elicit receiver discrimination (Barber & Conner, 2007; Johnson et al., 2003; Kikuchi & Pfennig, 2010).

4 | WHAT DO MIMICS NEED TO RESEMBLE TO GAIN FITNESS BENEFIT?

Organisms display multiple traits, which can be perceived via multiple sensory modalities. Receivers are unlikely to utilize all the available signal information of mimics (Bain, Rashed, Cowper, Gilbert, & Sherratt, 2007; Chittka & Osorio, 2007). This provides opportunity for mimics to resemble only the model signals that contribute the most to the receiver's subjective perception of the model, especially when signals are costly to produce. Untangling which of the mimic's traits receivers are responding to may be instrumental in explaining patterns of resemblance, or the lack thereof.

For instance, a series of increasingly complex binary choice tests were used to demonstrate that pollinating male fly receivers respond only to the most elaborate dark, fly-mimicking, floral spots (de Jager & Ellis, 2012). Floral traits that do not inform the receiver's perception of the model (a female fly) can thus be shaped by other selective agents or drift and are not constrained to match the model. Other flowering plants pollinated by this same fly species exhibit rudimentary floral spots (Ellis & Johnson, 2009; de Jager & Ellis, 2017) and additional fly (Eisikowitch, 1980; Johnson & Dafni, 1998), bee (de Jager, Willis-Jones, Critchley, & Glover, 2017) and beetle (de Jager & Ellis, 2014; Van Kleunen, Nänni, Donaldson, & Manning, 2007) species are also attracted to these rudimentary spots, suggesting that simplistic dark spots may exploit a general perceptual bias in insect receivers. The exploitation of a perceptual bias in a receiver could therefore act as a precursor to the evolution of mimicry (Schaefer & Ruxton, 2009).

Within mimetic systems comprising a specific model, there are nevertheless numerous instances where mimics do not precisely match their models (Edmunds, 2000; Kikuchi & Pfennig, 2010; Ruxton et al., 2004). Such imperfect mimicry can occur for various reasons (Kikuchi & Pfennig, 2013), not least because human researchers may perceive mimics to be imperfect copies of their models, that is the eye-of-the-beholder hypothesis (Edmunds, 2000). Even when considering resemblance as perceived by the receiver—the only agent whose perception matters in mimicry—there are instances when mimics do not closely resemble their models (Thurman & Seymoure, 2016).

A meta-analysis of 38 hoverfly mimics of stinging Hymenoptera revealed substantial variation in phenotype between models and mimics, likely as a result of relaxed selection by receivers where mimics are not under selection to evolve greater resemblance (Penney et al., 2012). One reason why this imperfect mimicry continues to work is that receivers might only respond to a few salient traits, such as a black and yellow striped pattern, and ignore other traits, like body shape and size (Bain et al., 2007; Chittka & Osorio, 2007). Likewise, within the coral snake mimicry system, receivers place non-venomous mimics under selection to match the proportion of red and black of their venomous models, but not the order in which the colours occur (Kikuchi & Pfennig, 2010).

To assess the accuracy of mimicry, it is important to identify which traits receivers use to classify objects (Chittka & Osorio, 2007; Gamberale-Stille et al., 2012; Kikuchi & Pfennig, 2010),

and what their sensitivity is towards these signals (Llaurens et al., 2014; Thurman & Seymoure, 2016). This knowledge will help unlock the percept of receivers that mimics need to resemble to benefit. Unfortunately, we have limited insights into receivers' percepts, a situation that will hopefully improve with technological advances (Dalziell & Welbergen, 2016). Notable progress in this area has been made in the visual sensory systems of animals. Breakthroughs in colour coding via opponent mechanisms, for instance, have enabled researchers to investigate how distinctly

bees perceive different colours (Chittka, Beier, Hertel, Steinmann, & Menzel, 1992).

Behavioural tests can be crucial for confirming models of receiver perception, because they reveal how information is processed and acted upon by receivers. For instance, coupling of perception modelling with behavioural experiments has uncovered the colour discrimination threshold for bees (Dyer & Chittka, 2004b). Discrimination thresholds can illustrate when colours are indistinguishable, as demonstrated in hymenopteran receivers that are
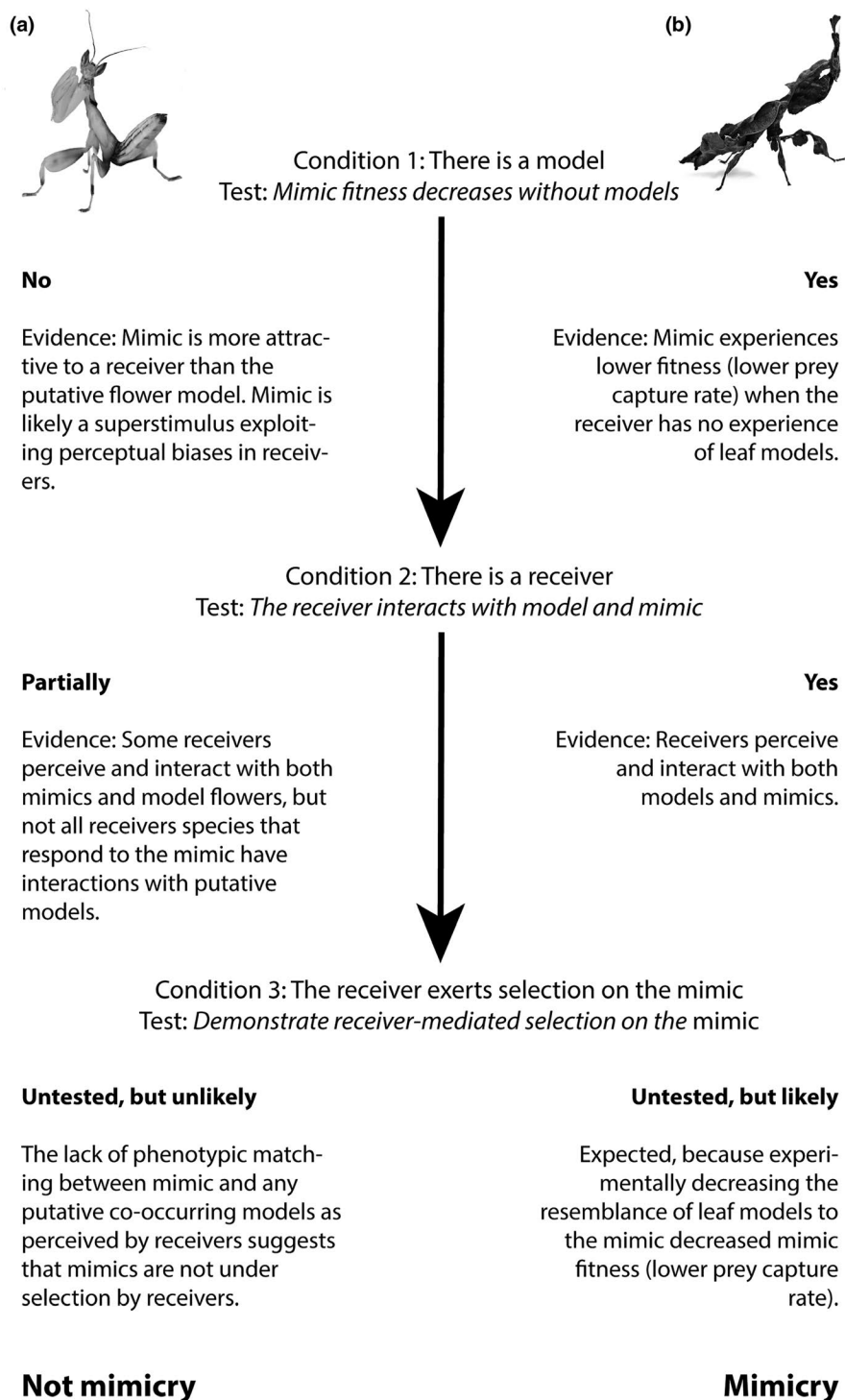
(a)

(b)

Condition 1: There is a model
Test: *Mimic fitness decreases without models*

No

Evidence: Mimic is more attractive to a receiver than the putative flower model. Mimic is likely a superstimulus exploiting perceptual biases in receivers.

Yes

Evidence: Mimic experiences lower fitness (lower prey capture rate) when the receiver has no experience of leaf models.

Condition 2: There is a receiver
Test: *The receiver interacts with model and mimic*

Partially

Evidence: Some receivers perceive and interact with both mimics and model flowers, but not all receivers species that respond to the mimic have interactions with putative models.

Yes

Evidence: Receivers perceive and interact with both models and mimics.

Condition 3: The receiver exerts selection on the mimic
Test: *Demonstrate receiver-mediated selection on the* mimic

Untested, but unlikely

The lack of phenotypic matching between mimic and any putative co-occurring models as perceived by receivers suggests that mimics are not under selection by receivers.

Untested, but likely

Expected, because experimentally decreasing the resemblance of leaf models to the mimic decreased mimic fitness (lower prey capture rate).

Not mimicry

Mimicry

FIGURE 2 A tale of two mantises. Applying our conditions for confirming mimicry to two ambiguous cases of resemblance: (a) the predatory orchid mantis Hymenopus coronatus, which putatively resembles flowers to capture flower visitors (Hanlon et al., 2014a, 2014b), and (b) the predatory ghost mantis Phyllocrania paradoxa, which putatively resembles dead leaves to appear harmless to prey (Skelhorn, 2018). Each system is evaluated by considering the evidence for the presence of three specific conditions to determine whether the observed resemblance is a product of mimicry

unable to discriminate the colours of rewarding flowers from their nectarless floral mimics (de Jager & Peakall, 2016; Peter & Johnson, 2008). Similar advances in lepidopteran, dipteran and avian vision modelling have allowed exploration of mimetic colours as perceived by receivers spanning various taxa (de Jager et al., 2016; Spottiswoode & Stevens, 2012; Stoddard, 2012; Théry & Casas, 2002; Whitehead et al., 2018).

Another area where receiver perception has been elucidated is olfaction. By measuring neuronal responses of hymenopteran receivers to floral bouquets of sexually deceptive flowers, gas chromatography and electroantennographic activation confirmed that male pollinators perceive and react similarly to physiologically active compounds in the flowers they pollinate and the sex pheromones of their females' (Bohman et al., 2014; Schiestl et al., 1999, 2003). Floral compounds not physiologically active in the receiver may be free to differ from the female model's sex pheromones (Schiestl, 2005), and traits of the mimic perceived via less relevant sensory modalities in the receiver might differ considerably from their models (Phillips & Peakall, 2018; Phillips, Xu, Hutchinson, Dixon, & Peakall, 2013).

5 | EMPLOYING THIS FRAMEWORK TO CONFIRM MIMICRY

In Figure 2, we demonstrate the utility of the conditions outlined in this manuscript by employing them to determine whether two ambiguous cases of mimetic resemblance should be considered mimicry. The first case is floral resemblance in the predatory orchid mantis *Hymenopus coronatus*, which putatively resembles flowers to attract pollinators as prey (Figure 2a). First recorded by Wallace (1877), these mantises often bear a resemblance to co-occurring flowers. However, there appears to be little evidence to support this as an example of mimicry, because the mimic is more successful at attracting pollinators than the putative model (Hanlon, Holwell, & Herberstein, 2014a), some receivers responding to the mimic have no interaction with flower models, and there is a lack of phenotypic matching between the mimic and putative flower models as perceived by receivers (Hanlon et al., 2014b), thus rejecting the three conditions required to confirm mimicry (Figure 2). Furthermore, alternative forces may play stronger roles in shaping mantis phenotypes (e.g., potential camouflage from bird predators) than resemblance to putative flower models (Hanlon et al., 2014b).

Next, we investigate a recently reported case of masquerade in the ghost mantis *Phyllocrania paradoxa* (Skelhorn, 2018), which resembles dead leaves to appear innocuous to potential prey (Figure 2b). This system is highly likely to qualify as mimicry, based on experimental evidence that the mimic has lower fitness when the receiver has no experience of model leaves, and evidence that receivers interact with models and mimics, satisfying the first two conditions required to confirm mimicry. Although the final condition of demonstrating receiver-mediated selection on the mimic is untested, this is very likely to be fulfilled, because experimental evidence reveals that decreasing the resemblance of the leaf models

to the mimic decreased mimic fitness through a reduction in prey capture rate (Skelhorn, 2018). In addition, the study clearly demonstrates that receivers form a percept of the model and change their behaviour towards it by documenting that naïve receivers learn to ignore harmless model leaves with experience.

While we provide useful guidelines for determining when resemblance is mimicry, further exploration of the initial stages of resemblance, as well as the perception of receivers will shed much needed light on the evolution of mimetic resemblance. We hope this manuscript provides functional guidelines for mimicry research and helps to separate it from other processes that can generate resemblances between species. We highlight that the existence of a model and a receiver is crucial for mimicry to occur. Furthermore, the receiver selects for, and maintains mimetic traits that match its percept of the model. We stress the importance of taking experimental approaches to validate these conditions, because experiments are often the only way to demonstrate the mechanisms that are responsible for the evolution of mimicry.

AUTHORS' CONTRIBUTIONS

The manuscript was conceptualized through discussions between M.L.D.J and B.A. M.L.D.J took the lead role in the writing. Both authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

This manuscript does not use data.

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