

# Natural selection in mimicry

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## ABSTRACT

Biological mimicry has served as a salient example of natural selection for over a century, providing us with a dazzling array of very different examples across many unrelated taxa. We provide a conceptual framework that brings together apparently disparate examples of mimicry in a single model for the purpose of comparing how natural selection affects models, mimics and signal receivers across different interactions. We first analyse how model–mimic resemblance likely affects the fitness of models, mimics and receivers across diverse examples. These include classic Batesian and Müllerian butterfly systems, nectarless orchids that mimic Hymenoptera or nectar-producing plants, caterpillars that mimic inert objects unlikely to be perceived as food, plants that mimic abiotic objects like carrion or dung and aggressive mimicry where predators mimic food items of their own prey. From this, we construct a conceptual framework of the selective forces that form the basis of all mimetic interactions. These interactions between models, mimics and receivers may follow four possible evolutionary pathways in terms of the direction of selection resulting from model–mimic resemblance. Two of these pathways correspond to the selective pressures associated with what is widely regarded as Batesian and Müllerian mimicry. The other two pathways suggest mimetic interactions underpinned by distinct selective pressures that have largely remained unrecognized. Each pathway is characterized by theoretical differences in how model–mimic resemblance influences the direction of selection acting on mimics, models and signal receivers, and the potential for consequent (co)evolutionary relationships between these three protagonists. The final part of this review describes how selective forces generated through model–mimic resemblance can be opposed by the basic ecology of interacting organisms and how those forces may affect the symmetry, strength and likelihood of (co)evolution between the three protagonists within the confines of the four broad evolutionary possibilities. We provide a clear and pragmatic visualization of selection pressures that portrays how different mimicry types may evolve. This conceptual framework provides clarity on how different selective forces acting on mimics, models and receivers are likely to interact and ultimately shape the evolutionary pathways taken by mimetic interactions, as well as the constraints inherent within these interactions.

*Key words:* aggressive mimicry, Batesian mimicry, classification, coevolution, deception, fitness, Müllerian mimicry, purifying selection, resemblance, selection.

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## I. INTRODUCTION

*'Natural Selection' explains almost everything in nature, but there is one class of phenomena I cannot bring under it, — the repetition of the forms and colours of animals in distinct groups, but the two always occurring in the same country and generally on the very same spot.* Footnote of a letter from Wallace to Darwin (Wallace, 1860).

While an adaptive explanation for the close resemblance of unrelated species troubled and eluded Alfred Russel Wallace, uncanny resemblances between organisms have subsequently provided researchers with some of the most compelling evidence for the powers of natural selection (Joron & Mallet, 1998). A few years after the publication of *On the Origin of Species* (Darwin, 1859) and Wallace's letter to Darwin (Wallace, 1860), Henry Walter Bates proposed an adaptive explanation for the startling resemblance between unrelated, co-occurring butterfly species: by resembling unpalatable butterflies, palatable species gain a protective advantage when predators treat them as though they are distasteful (Bates, 1862). So taken was Darwin with this elegant solution to Wallace's conundrum that he included Batesian mimicry as an exemplar for the power of natural selection in all forthcoming issues of *On the Origin of Species*. Six years later, Fritz Müller provided an adaptive, Darwinian explanation for the close resemblance of unrelated, unpalatable butterfly species (Müller, 1878), now known as Müllerian mimicry. Through the first use of a mathematical model in evolutionary biology, Müller (1879) demonstrated that similarities in the colouration of unpalatable butterfly species could evolve because it hastens the learning process of predators, leading to fitness benefits for the butterflies (Joron & Mallet, 1998). Both cases of mimicry involve butterfly species (mimics) that evolve a resemblance to other butterfly species (models). In both cases, the predators (receivers) have a pre-existing, negative association with the distasteful models but avoid mimics because they appear similar to the models. Mimics consequently benefit by their resemblance to the models whenever receivers treat them and the models in a similar way. Following previous authors, we refer to the three protagonists as the mimic, model and receiver (Wickler, 1968; Vane-Wright, 1980; Pasteur, 1982; Dalziell & Welbergen, 2016). These two contrasting examples of classic butterfly mimicry highlight the possibility of differences in the selective pressures underpinning them. This review aims to examine and provide a conceptual framework for the types of selection that likely underpin all cases of mimicry.

## II. CLASSIFICATIONS OF MIMICRY

Since the first cases of butterfly mimicry, myriad other putative mimetic examples have been discovered spanning

an impressive array of taxa across the tree of life [fish (Cheney & Côté, 2005); insects (Wignall & Taylor, 2011); spiders (Oliveira, 1988); birds (Davies, 2015); amphibians (Darst & Cummings, 2006); reptiles (Harper & Pfennig, 2007); plants (Newman, Anderson, & Johnson, 2012); gender mimicry within species (Goncalves *et al.*, 1996)]. While its taxonomic replicability has cemented mimicry as an outstanding exemplar of natural selection (Joron & Mallet, 1998), many authors pointed out that its pervasiveness has also allowed a siloed and often taxonomically compartmentalized study approach (e.g. Vane-Wright, 1976; Dalziell & Welbergen, 2016; Johnson & Schiestl, 2016; Jamie, 2017).

Several authors have attempted to generate unity by breaking taxonomic barriers and classifying mimicry according to ecological/and or evolutionary criteria instead of their taxonomic affinities. For example, in an attempt to unify confusing terminology, Vane-Wright (1976) conceptualized a classification system determined by a host of characters including costs and benefits to models, mimics and receivers, whether receivers respond positively or negatively towards the model signal and whether the purpose of mimicry is to attack or defend. With 40 possible outcomes, the classification was able to show when different interactions had a full set of common traits, but the complexity of the system and the terminology made it very difficult to use practically. Later, Pasteur (1982, p. 169–170) attempted to 'supply the biological community with as comprehensive as possible a checklist of the kinds of mimicry systems that exist in the living world'. To this end, he used an assortment of ecological and evolutionary characters, each with multiple states. These characters included the function of mimicry (e.g. aggressive, reproductive or protective), how receivers react to models (e.g. attraction *versus* repulsion) and species composition (e.g. if all three species are different or if there are only two species involved, as in cuckoo egg mimicry). Pasteur recognized 18 different kinds of mimicry and coined 17 new names. The only name still in use is Batesian mimicry, which he did not coin. More recently, Jamie (2017, p. 2) attempted 'to uncover the criteria by which examples of mimicry are conceptually organized' by classifying interactions according to another set of criteria. Jamie's criteria included whether the mimic mimics signals or cues, whether the mimic attracts or repels the receiver, and whether the mimic's signal is deceptive or not. The result was an elegant classification system describing eight different kinds of mimicry.

The distinct outcomes of these classification systems exemplify the fact that there are many ways to classify mimetic interactions, which perhaps begs the question of which classification system is correct. We suggest there is no single, correct classification system, and that different classification systems are likely to serve different purposes (as argued by Vane-Wright, 1976 and Grim, 2013). For

example, an ecologist may broadly classify birds by their foraging strategies (e.g. wader, swimmer, runner) while a systematist may classify the birds by their evolutionary affinities. Neither classification system is wrong and both are useful for different reasons. Given that different classification systems may have different uses and aims, it is unlikely that a single classification system will unify the field. Consequently, classification systems should be custom designed to serve a particular role or purpose that needs to be clearly identified for the classification to be useful. While most previous classification systems have not outlined their purpose beyond ‘unifying the field’ or ‘providing terminology’, we have specifically created a classification framework for the purpose of describing and visualizing how natural selection is likely to affect the evolution of different kinds of mimicry. We show that mimetic interactions are moulded by a complexity of different selection pressures which also act (often differently) on interacting species, and the framework presented in this review helps to identify patterns within that complexity. In the first part of this framework, we focus solely on characters that directly affect the strength and direction of selection acting on the mimetic traits at the core of mimetic interactions. These characters are the costs and benefits experienced by protagonists as a result of model–mimic resemblance.

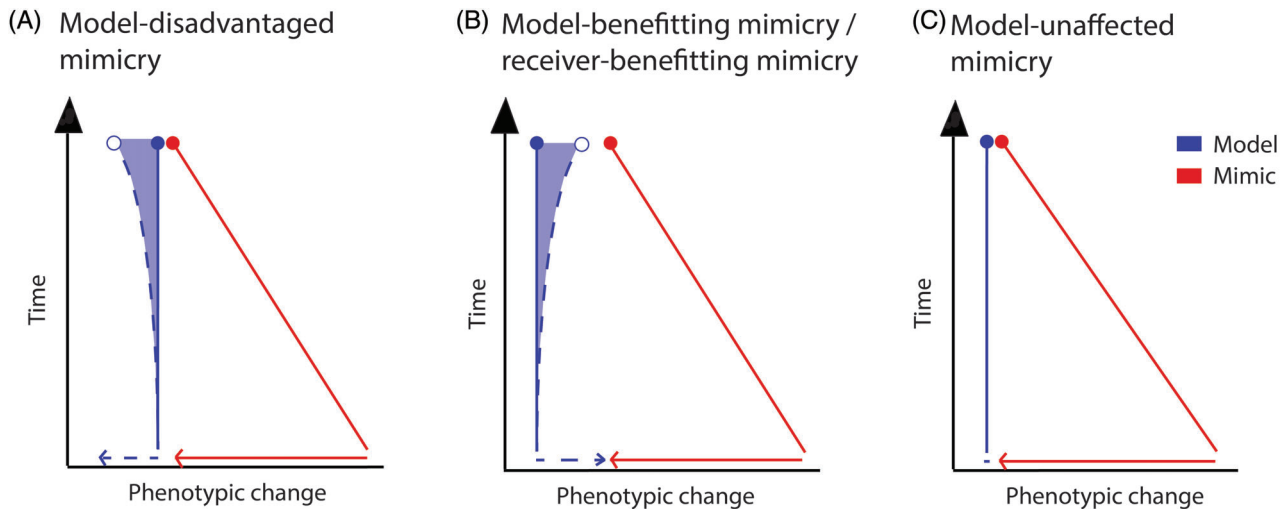
### (1) Mimetic resemblance affects selection on models, mimics and receivers

To introduce the approach used, let us consider contrasts in the ways that model–mimic resemblance is likely to affect selection on the protagonists involved in Batesian and Müllerian mimicry: Batesian mimicry always involves the evolution of a dishonest signal that deceives the receiver (Jamie, 2017). This produces an antagonistic interaction between the mimic and the receiver. In the case of Bates’ butterflies, the receiver is in theory affected negatively by the resemblance between the mimic and the model, because it misses out on potential feeding opportunities (see also Gaskett, Winnick, & Herberstein, 2008 who show negative consequences for male wasps which ejaculate after being attracted to orchids that emit female wasp-mimicking pheromones). Consequently, there may be selective pressures on receivers to evolve phenotypes that enable them to distinguish models better from mimics, while mimics may reciprocate by continuously evolving phenotypes that make it harder for receivers to recognise them. Evidence supporting this ‘escape and chase’ reciprocal selection (*sensu* Thompson, 2013) by receivers and mimics has mostly been theoretical (e.g. Oaten, Pearce, & Smyth, 1975; Holmgren & Enquist, 1999; Franks, Ruxton, & Sherratt, 2009; reviewed in Ruxton, Sherratt, & Speed, 2004; Kikuchi & Pfennig, 2013), suggesting a fruitful area for future experimental research. However, Spottiswoode & Stevens (2011) show empirically that cuckoo eggs match the egg phenotypes of their hosts and that host bird receivers may have responded to egg matching by increasing their discriminatory ability as well as by evolving phenotypic variation in eggs.

The phenotypic matching of host and parasite eggs described by Spottiswoode & Stevens (2011) (see also Brooke & Davies, 1988; Caves *et al.*, 2015) suggest similar ‘escape and chase’ coevolutionary races between the model and the mimic driven by antagonism (see Huheey, 1988; Thompson, 2013; Anderson, 2015). This putative race is a result of the cost suffered by the model and results in reciprocal evolution of host and parasite egg phenotypes. By definition, coevolution occurs when there is reciprocally driven evolutionary change, even if evolutionary change by the protagonists is asymmetric (Thompson, 2005, 2013). When selection is highly asymmetric, the coevolutionary race may simply occur at a slower rate, dictated by the protagonist which is evolving slowest [i.e. has the weakest reciprocal selection operating on it (Dawkins & Krebs, 1979; Anderson, Ellis, & Terblanche, 2010)]. Under some circumstances, coevolutionary races are elicited by reciprocal selection when mimics evolve phenotypes that match their models and models respond by diversifying their phenotypes (see Fig. 1; Huheey, 1988; Gavrillets & Hastings, 1998; Spottiswoode & Stevens, 2012). However, in aposematic systems (e.g. Batesian and Müllerian butterflies) the potential for coevolution may be constrained because changes in the model phenotype could elicit increased attack rates from predators which no longer recognise them as being noxious (Lindström, Alatalo, & Mappes, 1997; Mallet, 1999; see Section V). Such selection for conformity of model phenotypes is often referred to as purifying selection (e.g. Joron & Mallet, 1998; Mallet & Joron, 1999). Purifying selection will act on aposematic creatures irrespective of whether they are being mimicked or not.

Müllerian mimicry contrasts with Batesian mimicry, because Müllerian mimicry entails the evolution of an honest signal instead of a dishonest one (Jamie, 2017). In the case of Müller’s butterflies, resemblance reinforces the receiver’s association between a phenotype and unpalatability. This benefits the receiver, because fewer learning trials are required to learn that multiple species are toxic. This process also benefits the models and mimics, because fewer of each have to be consumed by receivers in the process of learning (Müller, 1879; Mallet, 1999). There is unlikely to be selection on the receiver to distinguish models better from mimics in Müllerian mimicry, because it should be more advantageous to group phenotypes of unpalatable species so that the general phenotype can be avoided. Since both model and mimic are expected to be consumed less frequently when sharing an unpalatable phenotype, we do not expect ‘escape and chase’ selection between model and mimic, as envisaged for Batesian mimicry. Instead, we expect reciprocal selection for the convergence of phenotypes (Fig. 1; Thompson, 2013; Anderson, 2015; Hoyal Cuthill & Charleston, 2012, 2015; Hoyal Cuthill *et al.*, 2019). However, reciprocal selection may not always result in coevolution, should change in the model phenotype be strongly opposed by purifying selection (Joron & Mallet, 1998; Sherratt, 2008; see Section V).

The next section uses the logic above to analyse the ways in which types of mimicry are likely to differ in terms of the



**Fig. 1.** Depictions of potential phenotypic changes in models and mimics over time under three different mimetic scenarios (modified with additions from Vane-Wright, 1976). (A) Batesian mimicry: models are negatively affected by being mimicked, and consequently, we may expect selection for phenotypic differentiation from mimics as time increases (dashed blue line). However, phenotypic change in models may not always be apparent, if opposed by other forces like purifying selection (Chouteau, Arias, & Joron, 2016). In aposematic mimicry systems, where model change is constrained by purifying selection, model phenotype may remain largely unchanged (solid blue line), despite the increasing costs of mimicry. The blue-shaded area represents a range of possible curve shapes depending on the relative strengths of purifying selection *versus* mimic-driven selection. (B) Müllerian and model-benefitting mimicry: models are positively affected by being mimicked and we may expect them to evolve phenotypic similarity to their mimics over time (coevolutionary convergence). However, purifying selection can also oppose phenotypic change in the model, leading to a range of possibilities for the model (blue-shaded area). (C) Model-unaffected mimicry: models are often non-living, as in carrion (van der Niet *et al.*, 2011) or faecal mimicry (Midgley *et al.*, 2015) and thus not able to evolve. Consequently evolution is always one-sided (advergence).

costs and benefits resulting from model–mimic resemblance. To do this, we group different types of mimicry by whether we expect model–mimic resemblance to produce a cost or a benefit to each of the protagonists. This outcome is likely to affect the direction of selection on the key traits (model–mimic signal similarity and perception of the receiver) involved in mimicry, which is clearly visualized for practical purposes in Section IV. By grouping different cases of mimicry according to the likely forms of (or lack of) natural selection operating on the protagonists, we can compare and contrast many of the important evolutionary processes involved in mimicry across the entire field, without confounding groupings with characters unrelated to selection. Section V examines other putative selective forces which are not the result of model–mimic resemblance (e.g. purifying selection), but which may also influence the net strength of selection and consequent evolution of model and mimic signals.

### III. COSTS AND BENEFITS ASSOCIATED WITH DIFFERENT KINDS OF MIMICRY

The approach used herein to group different types of mimicry has been influenced by the classic work of Vane-Wright (1976), who systematically used a combination of evolutionary and ecological characters to classify mimicry

in terms of the effects and roles of all three participants. While Vane-Wright's (1976) objective was to classify different kinds of mimicry, using the evolutionary and ecological characters at his disposal, our objective is to provide a specific framework to enable comparison of the different types of selection pressures that shape documented mimetic interactions. While many of Vane-Wright's characters may be useful for a general classification system (e.g. whether the receiver is attracted or repelled by the mimetic signal), they may be unrelated to differences in selection and hence not suited to our objectives. For example, receivers like small predatory fish attracted to the lures of angler fish and predatory birds repelled by the bright colours of a tasty butterfly respond differently to the signal of the mimic (one is attracted and the other repelled). However, both receivers are negatively affected by being deceived, and selection is therefore likely to operate in the same way on both receivers – increase discriminatory ability – despite differences in the type of response they exhibit towards the mimic.

Since many of Vane-Wright's (1976) characters are not appropriate for our objectives, we have focussed on just a few of his characters which relate directly to selection resulting from resemblance. Here, we have also taken inspiration from the well-established tradition of classifying symbiotic relationships into mutualisms, antagonisms and commensalisms, as first proposed by Haskell (1947). Haskell's method is based on deciding whether the net outcome of an interaction



is beneficial or costly (also used by Vane-Wright, 1976 in addition to other characters) for each interacting species, and is usually visualized as a two-dimensional interaction grid (Haskell, 1947) where plus and minus signs represent costs and benefits. While there has been occasional criticism of Haskell's (1947) system, the foundations of employing costs and benefits remain supported and unchanged (see discussion by Bronstein, 2015). Measuring selection strengths and directions are ideally required to confirm the existence of mimicry (de Jager & Anderson, 2019), but may be difficult or time consuming. As used in Haskell's (1947) classifications, the perceived costs and benefits of protagonists may be considered as selection surrogates when exploring the evolution of mimicry. We view perceived costs and benefits as the most useful characters for a framework designed specifically to make predictions about putative selection differences acting on different kinds of mimetic relationships. Furthermore, the experience of a cost *versus* a benefit is also likely to influence the subsequent behaviour of organisms (Anderson, Johnson, & Carbutt, 2005; de Jager & Ellis, 2014; Dalziell & Welbergen, 2016) which will govern mimetic interactions.

Although costs *versus* benefits are likely to differ in their directions of selection on a trait, not all costs are equal, and similarly, not all benefits are equal. This realization led to a large conceptual advance on Haskell's original symbiosis classification system (Haskell, 1947): costs and benefits are continuous, not categorical variables, and the differences in the relative strengths of costs and benefits are poorly visualized in a tabular format (Haskell, 1949). Instead, a compass was used to visualize the asymmetries and differing strengths of costs and benefits which characterized different kinds of interaction. Similar to Haskell (1949), we visualize the asymmetries of mimetic interactions as continuous variables in a novel three-dimensional graph, discussed in Section IV. For example, the net benefits for Batesian mimetic butterflies are likely to be much greater than the net costs incurred by the receivers.

To employ cost–benefit thinking in mimicry, we created a data set based on a single question, which was posed to each of the three protagonists in a mimetic system: does the protagonist experience a cost or a benefit as a result of model–mimic similarity? There are three possible answers to this question: (i) the protagonist experiences a cost; (ii) the protagonist experiences a benefit; (iii) the protagonist experiences neither a cost nor a benefit. Thus, there are three different characters (one question for each protagonist), each with three possible character states (i, ii or iii). Similar to the classification of symbiotic relationships, these questions can be applied as a simple thought experiment. For example, in a Batesian mimicry system involving butterflies, it is rationally clear that the resemblance between the mimic and the model may be costly for the model and the receiver, but beneficial for the mimic. Costs to the model would include mistaken identity and consequent consumption. Costs to the receiver may include missed feeding opportunities, while benefits to the mimic would include reduced predation. We selected 24 reported cases of mimicry from the literature, aiming to

cover as many mimicry types and taxa as possible (Table 1) and coded each relationship accordingly. The similarities between different kinds of mimicry were visualized using a simple clustering technique on the characters and character states used. The data set was subjected to a Bray Curtis similarity analysis without applying transformations, which served as the input for a cluster analysis using group averages in PRIMER 5 (version 5.2.9), a multivariate analysis tool (Clarke & Warwick, 2001). Based on costs and benefits, we can divide all examples of mimicry into two groups and several subgroups depending on whether the receivers benefit or not as a result of model–mimic resemblance (Fig. 2). Model–mimic resemblance is likely to have different selection effects on the protagonists involved in these different interactions, and selection is likely to operate in similar directions within groups and different directions among groups. Below we discuss selection from two broad groupings, as well as from the subdivisions within groupings.

### (1) Receiver-disadvantaged mimicry

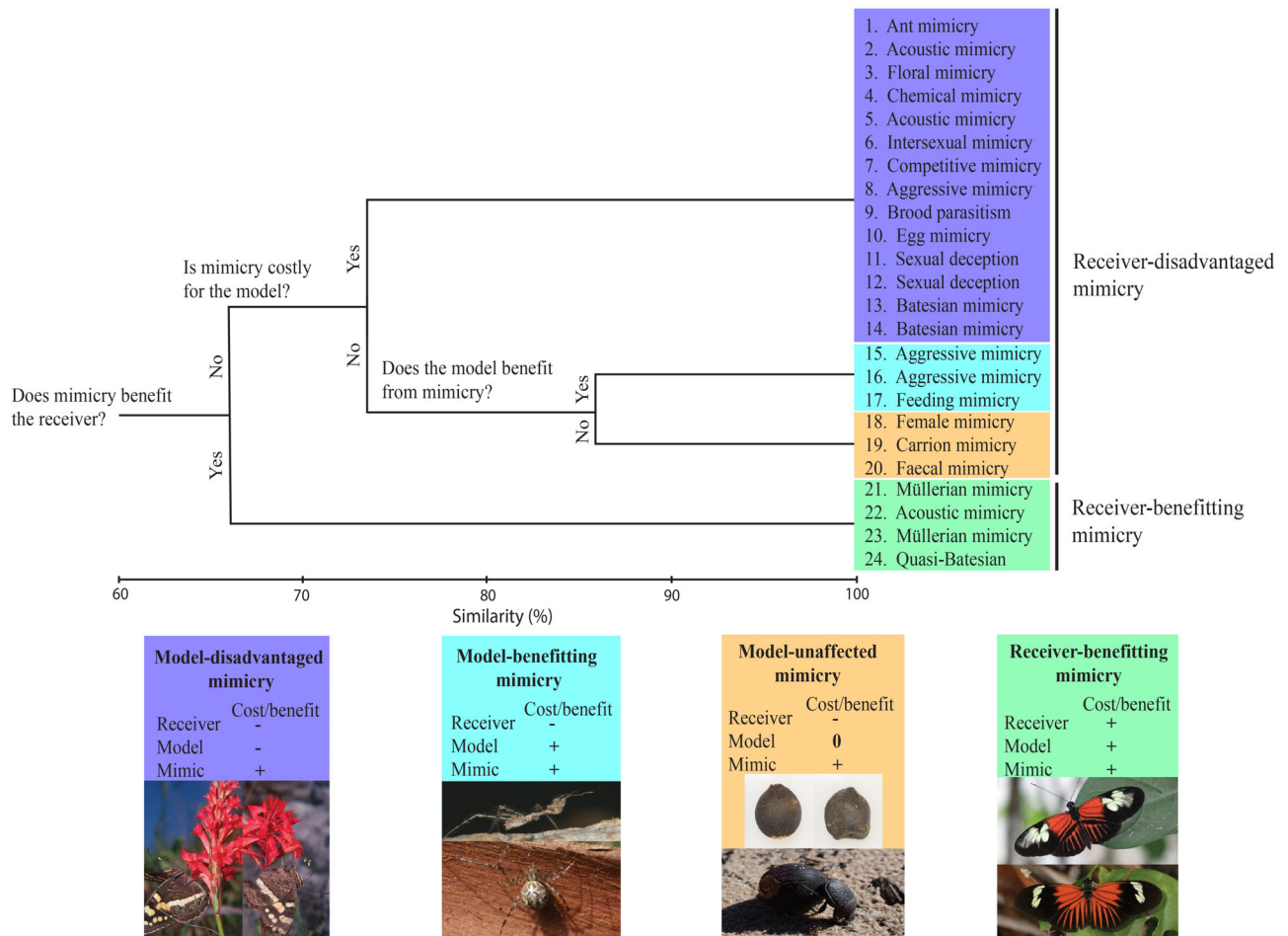
In most cases examined, mimics deceive receivers by producing a dishonest signal with a negative impact (cost) on the receivers. This cost could arise for multiple reasons. For example, model–mimic similarity could cause: mating attempts between the wrong species [e.g. male wasps attempting to mate with non-rewarding orchids have lower success in finding mates (Wong & Schiestl, 2002) and waste sperm (Gaskett *et al.*, 2008)], attempts to forage from non-rewarding mimics [e.g. nectar-seeking pollinators waste energy visiting flowers without nectar (Newman *et al.*, 2012)], consumption/death of receivers [e.g. snakes consume receivers after luring them with tail movements resembling prey (Reiserer & Schuett, 2008)] or missed feeding opportunities [e.g. birds do not consume edible butterflies because they appear distasteful (Jeffords, Sternburg, & Waldbauer, 1979)]. The receiver-disadvantaged group can be further divided into three subgroups, based on whether the model experiences a cost (model-disadvantaged) or a benefit (model-benefitting), or neither (model-unaffected).

#### (a) Model-disadvantaged mimicry

The first subgroup contains all the classic examples of Batesian mimicry where mimicry imposes a cost on the model, as well as the receiver (Table 1, Fig. 2). For example, distasteful model butterflies may be consumed more regularly when they are mimicked by palatable butterflies leading predatory birds (receivers) to perceive them as palatable (Jeffords *et al.*, 1979). This group also contains examples like floral Batesian mimicry, which is sometimes perceived as different from Batesian mimicry in butterflies (Vane-Wright, 1976; Little, 1983; Jamie, 2017), because flowers attract receivers (pollinators), whereas butterflies repel receivers (predators). Under Jamie's (2017) classification, floral Batesian mimicry would be considered a case of aggressive mimicry because the signal produced by flowers is deceptive and it attracts receivers. However, it is clear that the strength

Table 1. Mimetic interactions grouped using costs and benefits to mimics, models and receivers. Each interaction is designated a category (Mimicry type) based on how it was described in the relevant publication. The identities of mimics, models and receivers are listed. Based on the cost–benefit analysis, we assign each interaction an evolutionary affinity corresponding to Fig. 2

#	Mimicry type	Mimic	Model	Receiver	Reference	Affinities
1	Ant	Salticid & clubionid spiders	Various Amazonian ant species	Vertebrate predators	Oliveira (1988)	<i>Model-disadvantaged</i>
2	Acoustic	<i>Maculinea</i> butterfly larvae	<i>Myrmica</i> ant queens	<i>Myrmica</i> worker ants	Barbero <i>et al.</i> (2009)	<i>Model-disadvantaged</i>
3	Floral	<i>Hymenopus</i> mantises	Sympatric flowers	Bee pollinators	O'Hanlon, Holwell, & Herberstein (2014)	<i>Model-disadvantaged</i>
4	Chemical	<i>Maculinea</i> butterfly larvae	<i>Myrmica</i> ant larvae	<i>Myrmica</i> worker ants	Akino <i>et al.</i> (1999)	<i>Model-disadvantaged</i>
5	Acoustic	<i>Euchaetes</i> moths	<i>Cyenia</i> moths	<i>Lasius</i> and <i>Eptesicus</i> bats	Barber & Conner (2007)	<i>Model-disadvantaged</i>
6	Intersexual	<i>Jacaratia</i> female flowers	<i>Jacaratia</i> male flowers	Sphingid moth pollinators	Bawa (1980)	<i>Model-disadvantaged</i>
7	Competitive	<i>Acanthurus</i> juvenile fish	<i>Centropyge</i> fish	<i>Plectrogriffithodon</i> fish	Rainey & Grether (2007)	<i>Model-disadvantaged</i>
8	Aggressive	<i>Plagiobremus</i> fish	<i>Labroides</i> fish	Various client fish species	Cheney & Côté (2005)	<i>Model-disadvantaged</i>
9	Brood parasitism	<i>Cacabus</i> bird eggs	Bird eggs of various species	Adult birds of the model species	Brooke <i>et al.</i> (1988)	<i>Model-disadvantaged</i>
10	Egg	<i>Passiflora</i> leaves	<i>Heliconius</i> butterfly eggs	<i>Heliconius</i> female butterflies	Williams & Gilbert (1981)	<i>Model-disadvantaged</i>
11	Sexual deception	<i>Meloe</i> larvae	<i>Habropoda</i> female bees	<i>Habropoda</i> male bees	Saul-Gershenz & Millar (2006)	<i>Model-disadvantaged</i>
12	Sexual deception	<i>Chiloglottis</i> flowers	<i>Neozeloberia</i> female wasps	<i>Neozeloberia</i> male wasps	Wong & Shiestl (2002)	<i>Model-disadvantaged</i>
13	Batesian	<i>Callosamia</i> butterflies	<i>Battus</i> butterflies	Bird predators	Jeffords <i>et al.</i> (1979)	<i>Model-disadvantaged</i>
14	Floral Batesian	<i>Disa</i> flowers	<i>Tritoniopsis</i> flowers	<i>Aenopetes</i> butterfly	Newman <i>et al.</i> (2012)	<i>Model-disadvantaged</i>
15	Aggressive	<i>Stenolemus</i> bugs	<i>Drosophila</i> flies and aphids	<i>Achaearanea</i> spider predators	Wignall & Taylor (2011)	<i>Model-benefitting</i>
16	Aggressive	<i>Acanthophtis</i> snakes	Lizard prey	Lizard predators	Hagman, Phillips, & Shine (2008)	<i>Model-benefitting</i>
17	Feeding	<i>Sistrurus</i> snakes	<i>Rana</i> frog prey	<i>Rana</i> frog predators	Schuetz, Clark, & Kraus (1984)	<i>Model-benefitting</i>
18	Female	<i>Salaria</i> sneaker male fish	<i>Salaria</i> female fish	<i>Salaria</i> territorial male fish	Goncalves <i>et al.</i> (1996)	<i>Model-unaaffected</i>
19	Carrion	<i>Satyrium</i> flowers	Animal carrion	Sarcophagidae fly pollinators	van der Niet <i>et al.</i> (2011)	<i>Model-unaaffected</i>
20	Faecal	<i>Ceratocaryum</i> seeds	Antelope dung	<i>Epirinus</i> dungbeetle	Midgley <i>et al.</i> (2015)	<i>Model-unaaffected</i>
21	Müllerian	<i>Heliconius</i> butterflies	<i>Heliconius</i> butterflies	Bird predators	Kapan (2001)	<i>Receiver-benefitting</i>
22	Acoustic	<i>Syntomea</i> moths	<i>Cyenia</i> moths	<i>Lasius</i> and <i>Eptesicus</i> bats	Barber & Conner (2007)	<i>Receiver-benefitting</i>
23	Müllerian	<i>Ceroglossus</i> beetles	<i>Ceroglossus</i> beetles	Bird predators	Munoz-Ramirez <i>et al.</i> (2016)	<i>Receiver-benefitting</i>
24	Quasi-Batesian	<i>Brownelea</i> flowers	<i>Scabiosa</i> flowers	<i>Proseca</i> and <i>Philolichia</i> flies	Johnson <i>et al.</i> (2003)	<i>Receiver-benefitting</i>



**Fig. 2.** Cluster analysis displaying Bray Curtis similarity of published mimicry examples using costs and benefits as grouping variables. Numbers at tips correspond to different examples provided in Table 1 with the classifications given by these authors. We describe four mimicry classes based on groupings derived from costs and benefits. Mimicry classes are colour-coded, and we indicate whether each protagonist experiences a cost (–), a benefit (+) or neither cost nor benefit (0). Using three simple hypothetical questions (written on the cluster analysis), we can navigate the cluster analysis as a dichotomous key and quickly assess what mimicry group a system likely belongs to. Photographs below (left to right): butterfly receiver *Aeropetes tulbaghia* pollinating the rewarding model, *Tritoniopsis triticea* (right) and the rewardless mimic *Disa ferruginea* (left); assassin bug, *Stenolemus bituberus* (top), mimics the vibrations of captured model prey to lure species of the spider receiver *Achaearanea* (bottom), which instead becomes its prey; seeds of *Ceratocaryum argenteum* (top left) mimic the dung of the antelope *Damaliscus pygargus* (top right) to attract the dung beetle receiver, *Epirinus flagellatus* (bottom) for seed dispersal; the unpalatable mimic *Heliconius melpomene aglaope* (top) mimics the phenotype of the unpalatable *H. erato emma* (bottom), reducing predation from bird receivers. Photograph credits (left to right): Steven Johnson, Ken Harris and Anne Wignall, Steven Johnson (top) and Joseph White (bottom), receiver-benefitting mimicry: <http://katyscornertx.deviantart.com>.

and direction of selection is not dependent on whether a receiver is attracted or repelled by a mimic’s signal: in the cases of butterfly-eating birds and pollinating insects, both are affected negatively by the mimic’s signal and hence both may be subject to similar forms of underlying selection.

Some definitive examples of aggressive mimicry are also likely to share these evolutionary similarities with Batesian mimicry. For example, bluestriped fangblennies (*Plagiotremus rhinorhynchos*) benefit by resembling cleaner wrasse (*Labroides dimidiatus*) models, to which large fish (receivers) are attracted for parasite-removal services. Instead of eating ectoparasites from the receiver, fangblennies negatively affect them by

taking bites of their flesh or scales. While Cheney & Côté (2005) distinguished aggressive mimicry from Batesian mimicry based on the fact that aggressive mimics exploit mutualisms (e.g. between a client fish and a cleaner fish), whereas Batesian mimics exploit predatory relationships (e.g. between butterfly prey and a bird predator), this distinction is not universal (e.g. floral Batesian mimics do not exploit predators). Here we demonstrate some potentially important similarities in terms of costs, benefits and resultant selection gradients on protagonists across butterfly mimics, floral mimics, bird egg mimics and aggressive fish mimics – key considerations for the study of evolution (Holland & Rice, 1998; Franks & Noble, 2004).

*(b) Model-benefitting mimicry*

This subgroup is distinct from other kinds of mimicry within the ‘receiver-disadvantaged’ clade, because the model potentially benefits from its resemblance to the mimic. Examples include some cases labelled as ‘aggressive mimicry’ where angler fish and caudal-luring snakes move elaborate bodily extremities (e.g. tails or fin rays) in an alluring manner to attract small predators searching for prey. Once these small predators are within range, the mimic strikes and consumes it. The models in these cases are the intended prey of the receiver, and these models likely benefit from the mimicry to some degree by the reduction of their own predators’ populations (i.e. the consumed receivers). Contrast this to aggressive mimicry by bluestriped fangblennies, where model cleaner fish are likely to be negatively affected by mimics exploiting the mutualism between cleaner fish and client fish, through a reduction in client fish response and thus decreased foraging success on ectoparasites. Here we show that the models in different examples of aggressive mimicry are likely to experience contrasting patterns of selection as a result of model–mimic similarity. This distinction is significant, as costs to the model are likely to exert selective pressures on the model to diverge from the mimic phenotype, while benefits to the model may result in the model converging on the mimic phenotype (Fig. 1).

*(c) Model-unaffected mimicry*

The last subgroup comprises interactions where models are not affected by their resemblance to mimics. For example, flowers (van der Niet, Hansen, & Johnson, 2011) and seeds (Midgley *et al.*, 2015) can attract pollinating or dispersing receivers by mimicking carrion or faeces, respectively. Models in these examples are unable to undergo any evolutionary response to being mimicked, making model–mimic coevolution an impossibility. This class can also include cases where the models are alive and able to respond, but are unlikely to do so because the resemblance of the mimic does not affect them, making this a kind of commensalism. For example, in female mimicry, small, but highly fertile sneaker male blennies resemble females, allowing them to gain access to the territories of larger males where they can mate (Goncalves *et al.*, 1996). Although the larger males (receivers) are likely negatively affected through a reduction in siring success, there is no evidence that conspecific females (models) are negatively affected by mating with sneaker males (Goncalves *et al.*, 1996).

**(2) Receiver-benefitting mimicry**

This group, where receivers benefit from model–mimic resemblance contains all clear cases of Müllerian mimicry. Receivers benefit because mimic signals are honest. While Müllerian mimicry is usually thought of in the context of noxious prey items (mimics and models) that repel a receiver or predator (e.g. the *Heliconius* butterflies first noticed by Müller), receiver-benefitting mimicry may also contain

examples of mimics and models which attract receivers. For example, nectar-producing plants may evolve similar colouration if similarity facilitates higher visitation rates or faster learning by pollinators (Benitez-Vieyra *et al.*, 2007). In the system outlined by Benitez-Vieyra *et al.* (2007), it was unclear whether the rare mimics have a slightly positive (e.g. slightly higher visitation rates) or a slightly negative (e.g. less-pure pollen loads) effect on the more common models (they were unable to detect an effect in terms of female fitness). If we assume that the effect becomes slightly positive as mimic density increases (e.g. higher visitation), then this inclusion to Müllerian mimicry can be considered similar to the addition of aggressive mimicry to Batesian mimicry discussed above.

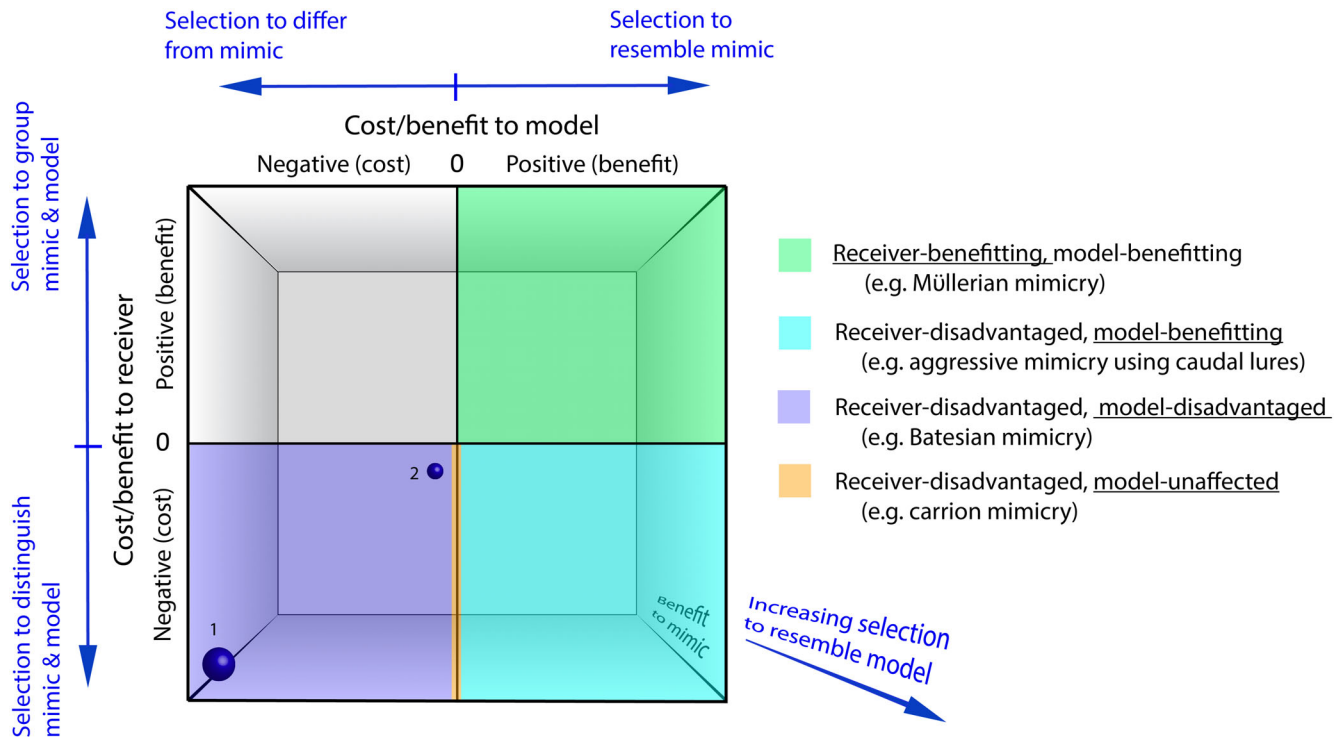
Some putative examples of Quasi-Batesian mimicry may also fall within this group, while others may function more like classic examples of Batesian mimicry (receiver-disadvantaged). Speed (1993) introduced the idea of Quasi-Batesian mimicry to describe distasteful mimics that function as Batesian mimics because, despite their distastefulness, they still provide a nutritive benefit to predators. Consequently, less-noxious, but still distasteful butterflies, may retard the learning ability of predators (i.e. receiver-disadvantaged). However, it is also possible that less-noxious butterflies may help reinforce the learned association of predators with a more noxious model. For example, if a receiver experiences a small negative net effect of consuming a mildly noxious butterfly, this negative effect could reinforce the greater negative experience of consuming a more noxious model. In such cases, the signal employed by the mimic would be considered honest and its resemblance to the model would benefit the receiver (model-benefitting mimicry), because learning that a general colour pattern is toxic would come at lower cost (it may consume fewer highly toxic individuals). The idea of Quasi-Batesian mimicry has been very controversial (e.g. Mallet & Joron, 1999), however, viewing interactions in terms of net costs and benefits does away with semantics surrounding the classification of mimics that lie along a palatability spectrum (see Benson, 1977).

The distinction between two broad groups herein (i.e. receiver-disadvantaged and receiver-benefitting mimicry) corresponds exactly to two groups distinguished by Jamie (2017). Jamie (2017) distinguished between the groups based on whether the signal of the mimic was honest or dishonest, while we distinguish based on whether the receiver benefits or is disadvantaged. These are clearly different sides of the same coin, each highlighting a different perspective (signal honesty *versus* selection), but in the end providing complementary frameworks.

**IV. VISUALIZING SELECTION RESPONSES ASSOCIATED WITH MIMICRY**

In the previous section, we placed primary emphasis on the costs and benefits (whether selection is negative or positive) that arise due to the perceived resemblance between mimic and model. We focussed on costs and benefits





**Fig. 3.** Conceptual model of three-dimensional space occupied by mimetic interactions as measured by costs or benefits to protagonists resulting from perceived model–mimic resemblance. Blue arrows depict how costs or benefits are likely to affect selection on model/mimic phenotype and receiver perception. Colours represent zones of interaction space: grey space is where mimetic interactions are not expected to exist. The model-unaffected zone (orange) has been enlarged beyond zero costs or benefits to models to make it visible. We depict two hypothetical points within the ‘model-disadvantaged’ quadrant. Size of the points illustrate proximity to the viewer along the ‘benefit to mimic’ axis. Point 1 could be an example of bird egg mimicry where mimics have very high costs on models/receivers (parasitic birds kill host chicks). High resemblance is also likely to have large benefits to the mimics because detection will result in death. This interaction is likely to lie far from the central axis with strong selective pressures acting on all protagonists. By contrast, point 2 could represent floral Batesian mimicry. Here, costs to the receiver are likely to be comparatively low (missed feeding opportunities *versus* direct offspring death) and costs to the model (reduced visitation *versus* direct offspring death) are also likely to be low (see Anderson & Johnson, 2006). We expect that many floral Batesian systems will be characterized by weak selection on models and receivers, but moderate selection on mimics, placing this interaction closer to the central axes than most avian egg mimicry interactions.

because these dictate how resemblance may affect the direction of selection on key traits involved in mimicry: resemblance and perception (Figs 1 and 2, Table 1; see also Anderson *et al.*, 2005; Dalziell & Welbergen, 2016). For example, in butterflies that resemble one another, costs should select for decreased similarity between models and mimics, while benefits should select for increased similarity (Joron & Iwasa, 2005). Costs and benefits may also alter the behaviour of models and mimics, for instance, avoidance behaviour *versus* attraction. Furthermore, costs and benefits are likely to provide a selective force acting on a receiver’s perception and the way it learns (de Jager & Ellis, 2014; Lindström *et al.*, 1997). For example, if model–mimic similarity causes receivers to miss potential meals (i.e. a cost), selection should favour increased discriminatory power.

Importantly, changes in the direction of selection (e.g. a switch from selection for increased to decreased model–mimic resemblance) occur at a precise point: the

point where there is neither a cost nor a benefit. On either side of this point, costs and benefits should select for opposing traits (increased resemblance *versus* decreased resemblance). We can visualize this as a square, divided into four parts by two bisecting lines (points where there are no costs or benefits, see Fig. 3). While mimics always experience a benefit from mimicry (Wickler, 1965, 1968), that benefit is likely to differ between examples in terms of degree or strength. Similarly, costs, benefits and the strength of selection on models and receivers are also continuous rather than categories. Consequently, we can visualize all interactions on a simple set of continuous, three-dimensional  $x,y,z$  axes, where one set of axes is the cost/benefit to the receiver, and another is the cost/benefit to the model. The last axis (benefit to the mimic) does not have a negative or cost component, because mimicry always benefits mimics (Fig. 3).

Jamie (2017) classified mimicry using a set of two-dimensional, continuous axes. However, the axes used were

the information content of a mimic's signal (i.e. is the signal used to indicate a reward or a punishment for the receiver?) and the degree of signal deceptiveness (signal honesty), thus only partially overlapping with our own. While signal honesty is likely to have cost/benefit implications for receivers, information content is unlikely to have any consistent association with costs or benefits. Like Vane-Wright's (1976) use of operator response (attraction or repulsion) to a signal, distinguishing whether a mimic is signalling a reward or punishment does not have any bearing on the direction of selection operating on the receiver. Consequently, for the purposes of our framework, this character is not useful. While Jamie's (2017) classification highlights some key distinctions between different kinds of mimicry, unlike our own, its purpose was not to evaluate the selection pressures that likely mould mimetic interactions. Instead the graphic framework provides an excellent visualization of mimicry's fluidity and how one form can transition into another. This fluidity was emphasized by the fact that the classification system provides no precise points where one kind of mimicry transitions to another, although one drawback of this is that it makes practical classification difficult. Similar to Jamie (2017), we also make use of continuous axes (although ours are three-dimensional) to emphasize the fluidity of mimicry. However, we provide precise points of transition (points of no cost/benefit) which allows for a more practical application of the framework, and we also contemplate costs and benefits to models and mimics in addition to receivers.

## V. STRENGTH, BALANCE AND OPPOSING FORCES OF SELECTION

Our classification of an interaction (Fig. 2) is associated with the quadrant in which an interaction is found (Fig. 3) and this is the result of whether receivers and models are ultimately experiencing net costs or net benefits due to model–mimic resemblance (i.e. the sign of selection). However, the specific position within a quadrant (depicted in Fig. 3) is a function of selection strengths (not sign of selection) on the three protagonists. In particular, selection strengths determine how far an interaction is found from the centre of the three-dimensional space (the point where there is no cost/benefit on any of the protagonists). The position within each quadrant is likely to affect the speed, symmetry and likelihood of (co)evolution. The strength of selection acting on the three protagonists and the degree of selection symmetry can be influenced by multiple ecological factors, some of which are unrelated to model–mimic resemblance. In the following subsections, we discuss how four different ecological factors (relative abundance, ecological effect size, absolute abundance and phenotypic inertia, and spatio-temporal context), may affect the net strength of selection on a protagonist in a mimicry interaction.

### (1) Relative abundance

The effects of mimicry on the three protagonists are expected to be strongly affected by their relative abundance. For example, avian egg mimicry is likely to have a large selection effect size on models if parasitic mimics are common (relative to the models), while the selection effect may be negligible if mimics are relatively rare (see Huheey, 1980, Lindström *et al.*, 1997, Anderson & Johnson, 2006 and Pfennig, Harcombe & Pfennig, Harcombe, & Pfennig, 2001 for frequency dependence on Batesian models and mimics). Similarly, Müller's (1878) mathematical model demonstrated that the mortality of Müllerian mimics should be inversely related to the square of their abundances (also see Mallet, 1999). Consequently, if one species is three times more common than another, the rare species will gain nine times as much protection from mimicry as the more common species (Joron & Mallet, 1998). In the initial stages of mimicry, the rare mimic is therefore unlikely to generate a strong selective force on the more common model and selection may be unilateral (sometimes termed advergent), (Sheppard *et al.*, 1985; Turner, 1995; Mallet, 1999). However, when the rare mimic's abundances increases and mimetic matching improves, as one may expect when the mimic establishes itself, selection imposed by the mimic on the model is likely to increase, and consequently the chance of coevolution between model and mimic increases (Franks & Sherratt, 2007; Sherratt, 2008; Fig. 1). In a recent study using methods employing machine learning, Hoyal Cuthill *et al.* (2019) demonstrated that the symmetry of evolutionary change was associated with abundance: in a classic Müllerian mimicry system involving noxious butterflies, the less-abundant *Heliconius melpomene* appeared to converge more than the abundant *Heliconius erato*.

### (2) Ecological effect size

For Müllerian mimics, differences in palatability are also likely to affect selection strengths in the same way as numeric differences (Mallet, 1999), so the less noxious species gains more advantage from mimicking a more noxious species than *vice versa*. Similarly, selection effects may also be much greater if mimicry leads directly to the death of receiver offspring (e.g. Batesian egg mimicry by cuckoos), compared to the selection effect size when receivers only suffer reduced foraging efficiency (e.g. floral Batesian mimicry). For example, Lindström *et al.* (1997) found greater survivorship of Batesian mimics as the distastefulness of the models increased. While differences in the selection effects or consequences of model–mimic similarity would place Batesian egg mimicry further from the dividing axes than floral Batesian mimicry, they would nevertheless both be found within the same quadrant (see Fig. 3). The differences in relative selection strengths on models and receivers in Batesian egg mimicry *versus* floral Batesian mimicry are expected to affect the degree of symmetry in coevolutionary races, as well as the speed, tempo and likelihood of coevolution (Anderson, 2015). However, because both interactions are found within the

same quadrant, receivers and models in Batesian egg mimicry and floral Batesian mimicry are both expected to be adversely affected by model–mimic similarity, and the direction of selection, not necessarily the strength, is likely to be the same.

### (3) Absolute abundance and phenotypic inertia

Since aposematic species gain protection from having high absolute abundances, novel or rare phenotypes are likely to be poorly protected if predators do not recognise them as aposematic (Nur, 1970; Turner, 1984; Kapan, 2001; Langham, 2004; Chouteau & Angers, 2011). This purifying selection may frequently counteract model–mimic coevolutionary races because purifying selection against rare model phenotypes (phenotypic change) opposes the selection driven by Batesian mimics for novel model phenotypes (Turner, 1984; Joron & Mallet, 1998; Mallet, 1999). For example, in localities with abundant Batesian mimics, Akcali, Kikuchi, & Pfennig (2018) found no evidence in support of a coevolutionary chase between venomous model and harmless mimic snakes. They attributed this to the fact that predators selected strongly against novel model phenotypes. Similarly, selection for the phenotypic *status quo* is also likely to oppose selection for common or well-defended Müllerian mimics to converge in phenotype with rare or poorly defended Müllerian mimics (Mallet, 1999; Sherratt, 2008). Hence, for a coevolutionary race to occur between mimics and models, selection on models to differ from their general form needs to be stronger than opposing purifying selection (Gavrilets & Hastings, 1998). Coevolutionary races may therefore be less likely when a mimicry system lies close to the centre of the axis (Fig. 3), or if purifying selection on models or mimics is strong.

The evolutionary ‘push-back’ against phenotypic change may not be driven solely by predators that select against novel forms. For example, extreme phenotypes may have reduced success at finding mates, or novel floral forms may be visited less regularly by pollinators. Given the vastly different sources of selection opposing evolutionary change, it is likely that balancing or purifying selection will be very variable in strength. For example, selection against phenotypic change is expected to be strong in aposematic mimicry, such as Müllerian and Batesian butterflies (Kapan, 2001), and this may account for an historic paucity of evidence for coevolution between models and mimics in these systems (Mallet, 1999; Sherratt, 2008; but see Hoyal Cuthill & Charleston, 2012, 2015). On the other hand, the paucity of empirical evidence for coevolution in Müllerian mimicry systems may simply be due to the fact that coevolution is notoriously difficult to demonstrate. Perhaps the most compelling evidence for coevolutionary convergence in Müllerian mimicry used machine learning and phylogenetic methods to demonstrate colour and pattern matching across multiple co-occurring populations of *Heliconius erato* and *Heliconius melpomene* butterflies (Hoyal Cuthill *et al.*, 2019). In one focussed case study, they demonstrate that the wing colour of *H. erato* has remained unchanged from the ancestral form while the wing colour of its *H. melpomene* co-mimic has

changed to match that of *H. erato*. But for a different wing trait (band thickness), the trait has remained unchanged in *H. melpomene* while in this case *H. erato* has changed to match *H. melpomene*. If these two traits were analysed in isolation, we would only see two cases of divergent evolution. But taken together it demonstrates reciprocal convergence and suggests that selection for convergence in Müllerian systems can be stronger than purifying selection, despite assertions to the contrary (Mallet, 1999).

In contrast to aposematic mimicry systems, purifying selection is not expected in avian egg mimicry, and this may allow model eggs more easily to undergo rapid and continuous diversification to escape the costs of mimicry (Spottiswoode & Stevens, 2012). Coevolution in avian egg mimicry may consequently be facilitated by a lack of purifying selection constraining phenotypic change in models (Akcali *et al.*, 2018). While this review has emphasized the roles played by the costs *versus* the benefits of model–mimic resemblance in driving phenotypic change, it is also clear that to understand how mimicry evolves and diversifies, we also need to understand how phenotypic change is constrained (often by forces unrelated to mimicry).

Since the strength of selection acting on different protagonists is likely to affect the distance of a mimicry system from the central axes (Fig. 3), we argue that the axes of zero cost/benefit mark the points of transition from one kind of mimicry to another. The strength of selection is thus also expected to affect the likelihood of transitions from one mimicry type to another. Batesian and Müllerian mimicry examples that lie very close to the centre of the axes may be able to transition easily. For example, the point where it becomes disadvantageous for a predator to avoid a slightly noxious butterfly in a mimicry complex marks an important threshold where Müllerian mimicry can become Batesian mimicry. Such a transition from Müllerian to Batesian mimicry could occur if prey densities or mimic toxicity decreases, making it more disadvantageous for predators to avoid mildly noxious prey items.

### (4) Spatio-temporal context

The effects of mimicry on protagonists may also vary temporally and geographically (Sherratt, 2008; Dalziell & Welbergen, 2016). These kinds of temporal and geographic mosaics in selection make it important for biologists to consider interactions at the level of populations rather than species, as selection mosaics are the foot soldiers of diversification. This view recognizes the possibility that the outcomes of interactions can fluctuate in space and time, and hence their classifications may also change spatio-temporally (Thompson & Cunningham, 2002; Thompson, 2005, 2013). We stress that the same is true of mimicry where different populations could be viewed differently, depending on whether protagonists experience net costs or benefits due to model–mimic similarity.

Establishing net costs and benefits for protagonists in different interactions would enable researchers to determine

and compare how close different interactions lie to points of transition, and how those positions may potentially vary in space and time. As yet, we are unaware of studies outside of egg mimicry in birds where the costs and benefits of mimicry to all protagonists have been calculated in terms of reproductive output – the currency of selection. However, there are some excellent experimental proofs of concept in Batesian systems involving snakes (Pfennig *et al.*, 2001; Pfennig & Mullen, 2010), plants (Johnson, Alexandersson, & Linder, 2003), bats (Barber & Conner, 2007), flies (de Jager & Ellis, 2014) and wasps (Wong & Shiestl, 2002), where the costs and benefits have been determined for one or two of the protagonists. Furthermore, we suggest that disentangling the components of selection resulting from the costs/benefits of mimicry *versus* purifying selection will give much more insight into how mimicry evolves.

## VI. CONCLUSIONS

(1) Based on the effects (costs *versus* benefits) of perceived model–mimic resemblance on the different protagonists involved in mimetic interactions, we draw attention to four broad evolutionary pathways which can be taken by any mimetic interaction: (i) both model and receiver are disadvantaged; (ii) the model benefits, but receiver is disadvantaged; (iii) the receiver is disadvantaged and the model is unaffected; and (iv) both receiver and model benefit.

(2) The direction of selection acting on key mimetic traits (model–mimic resemblance and receiver perceptible abilities) depends on whether different protagonists experience a cost *versus* a benefit as a result of model–mimic similarity. Consequently, each of the four pathways is characterized by differences in the way that protagonists are expected to evolve in response to one another, and the direction of selection on key mimetic traits.

(3) Depending on whether models, mimics and signal receivers experience costs or benefits as a result of model–mimic resemblance, interactions between mimics, models and receivers are likely to vary between different evolutionary forms. For example, benefits to one protagonist but costs to the other may result in reciprocal ‘escape and chase’ selection – e.g. Batesian mimicry. Alternatively, benefits to both protagonists could result in reciprocal selection for convergence (e.g. Mullerian mimicry), while benefits to one protagonist and no cost/benefit to the other is expected to result in advergence (one-sided evolution – model-unaffected mimicry).

(4) Overlaid on top of the four broad evolutionary pathways are differences in the symmetry and strength of (co)evolution between the three protagonists which are likely to be influenced by basic ecology, such as relative densities of models, mimics and receivers, as well purifying selection. Differences in the strength of selection acting on the protagonists is expected to result in variation in the

probability of transitions between different kinds of mimicry and the probability of coevolution.

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## VIII. REFERENCES

- AKCALI, C. K., KIKUCHI, D. W. & PFENNIG, D. W. (2018). Coevolutionary arms races in Batesian mimicry? A test of the chase-away hypothesis. *Biological Journal of the Linnean Society* **124**, 668–676.
- AKINO, T., KNAPP, J. J., THOMAS, J. A. & ELMES, G. W. (1999). Chemical mimicry and host specificity in the butterfly *Maculinea rebeli*, a social parasite of *Myrmica* ant colonies. *Proceedings of the Royal Society of London Series B: Biological Sciences* **266**, 1419–1426.
- ANDERSON, B. (2015). Coevolution in mutualisms. In *Mutualism* (ed. J. BRONSTEIN). Oxford University Press, Oxford.
- ANDERSON, B. & JOHNSON, S. D. (2006). The effects of floral mimics and models on each others' fitness. *Proceedings of the Royal Society of London Series B: Biological Sciences* **273**, 969–974.
- ANDERSON, B., JOHNSON, S. D. & CARBUTT, C. (2005). Exploitation of a specialized mutualism by a deceptive orchid. *American Journal of Botany* **92**, 1342–1349.
- ANDERSON, B., ELLIS, A. G. & TERBLANCHE, J. (2010). Predictable patterns of trait mismatches between interacting plants and insects. *BMC Evolutionary Biology* **10**, art. 204.
- BARBER, J. R. & CONNER, W. E. (2007). Acoustic mimicry in a predator-prey interaction. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 9331–9334.
- BARBERO, F., BONELLI, S., THOMAS, J. A., BALLETO, E. & SCHÖNRÖGGE, K. (2009). Acoustical mimicry in a predatory social parasite of ants. *Journal of Experimental Biology* **212**, 4084–4090.
- BATES, H. W. (1862). Contributions to an insect fauna of the Amazon valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society of London Zoology* **23**, 495–566.
- BAWA, K. (1980). Mimicry of male by female flowers and intrasexual competition for pollinators in *Jacaratia dolichaula* (D. Smith). Woodson (Caricaceae). *Evolution* **34**, 467–474.
- BENITEZ-VIEYRA, S., HEMPEL DE IBARRA, N., WERTLEN, A. M. & COCUCCI, A. A. (2007). How to look like a mallow: evidence of floral mimicry between Turneraceae and Malvaceae. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2239–2248.
- BENSON, W. W. (1977). On the supposed spectrum between Batesian and Müllerian mimicry. *Evolution* **31**, 454–455.
- BRONSTEIN, J. L. (2015). *Mutualism*. Oxford University Press, Oxford.
- BROOKE, M. DE L. & DAVIES, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* **335**, 630–632.
- CAVES, E. M., STEVENS, M., IVERSEN, E. S. & SPOTTISWOODE, C. N. (2015). Hosts of avian brood parasites have evolved egg signatures with elevated information content. *Proceedings of the Royal Society of London Series B: Biological Sciences* **282**, 20150598.
- CHENEY, K. L. & CÔTÉ, I. M. (2005). Frequency-dependent success of aggressive mimics in a cleaning symbiosis. *Proceedings of the Royal Society of London Series B: Biological Sciences* **272**, 2635–2639.
- CHOUTEAU, M. & ANGERS, B. (2011). The role of predators in maintaining the geographic organization of aposomatic signals. *American Naturalist* **178**, 810–817.



- CHOUTEAU, M., ARIAS, M. & JORON, M. (2016). Warning signals are under positive frequency-dependence in nature. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 2164–2169.
- CLARKE, K. R. & WARWICK, R. M. (2001). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. Primer-E, Ltd., Plymouth.
- DALZIELL, A. H. & WELBERGEN, J. A. (2016). Mimicry for all modalities. *Ecology Letters* **19**(6), 609–619.
- DARST, C. R. & CUMMINGS, M. E. (2006). Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature* **440**, 208–211.
- DARWIN, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- DAVIES, N. (2015). *Cuckoo: Cheating by Nature*. Bloomsbury Publishing, New York.
- DAWKINS, R. & KREBS, J. R. (1979). Arms races between and within species. *Proceedings of the Royal Society of London Series B: Biological Sciences* **205**, 489–511.
- DE JAGER, M. L. & ANDERSON, B. (2019). When is resemblance mimicry? *Functional Ecology* **33**, 1586–1596.
- DE JAGER, M. L. & ELLIS, A. G. (2014). Costs of deception and learned resistance in deceptive interactions. *Proceedings of the Royal Society of London Series B: Biological Sciences* **281**, 20132861.
- FRANKS, D. W. & NOBLE, J. (2004). Batesian mimics influence mimicry ring evolution. *Proceedings of the Royal Society of London Series B: Biological Sciences* **271**, 191–196.
- FRANKS, D. W. & SHERRATT, T. N. (2007). The evolution of multicomponent mimicry. *Journal of Theoretical Biology* **244**, 631–639.
- FRANKS, D. W., RUXTON, G. D. & SHERRATT, T. N. (2009). Warning signals evolve to disengage Batesian mimics. *Evolution* **63**, 256–267.
- GASKETT, A. C., WINNICK, C. G. & HERBERSTEIN, M. E. (2008). Orchid sexual deceit provokes ejaculation. *American Naturalist* **171**, E206–E212.
- GAVRILETS, S. & HASTINGS, A. (1998). Coevolutionary chase in two-species systems with applications to mimicry. *Journal of Theoretical Biology* **191**, 415–427.
- GONCALVES, E., ALMADA, V., OLIVEIRA, R. & SANTOS, A. J. (1996). Female mimicry as a tactic in males of the blennioid fish *Salarias pavo*. *Journal of the Marine Biological Association of the United Kingdom* **76**, 529–538.
- GRIM, T. (2013). Perspectives and debates: mimicry, signalling and co-evolution (Commentary on Wolfgang Wickler – understanding mimicry – with special reference to vocal mimicry). *Ethology* **119**, 270–277.
- HAGMAN, M., PHILLIPS, B. L. & SHINE, R. (2008). Tails of enticement: caudal luring by an ambush-foraging snake (*Acanthophis praelongus*, Elapidae). *Functional Ecology* **22**, 1134–1139.
- HARPER, G. R. & PFENNIG, D. W. (2007). Mimicry on the edge: why do mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society of London Series B: Biological Sciences* **274**, 1955–1961.
- HASKELL, E. F. (1947). A natural classification of societies. *Transactions of the New York Academy of Sciences* **29**, 186–196.
- HASKELL, E. F. (1949). A clarification of social science. *Main Currents in Modern Thought* **7**, 45–51.
- HOLLAND, B. & RICE, W. R. (1998). Perspective: chase-away sexual selection: antagonistic seduction versus resistance. *Evolution* **52**, 1–7.
- HOLMGREN, N. & ENQUIST, M. (1999). Dynamics of mimicry evolution. *Biological Journal of the Linnean Society* **66**, 145–115.
- HOYAL CUTHILL, J. & CHARLESTON, M. (2012). Phylogenetic codivergence supports coevolution of mimetic *Heliconius* butterflies. *Public Library of Science ONE* **7**, e36464.
- HOYAL CUTHILL, J. & CHARLESTON, M. (2015). Wing patterning genes and coevolution of Müllerian mimicry in *Heliconius* butterflies: support from phylogeography, cophylogeny and divergence times. *Evolution* **69**(12), 3082–3096.
- HOYAL CUTHILL, J. F., GUTTENBERG, N., LEDGER, S., CROWTHER, R. & HUERTAS, B. (2019). Deep learning on butterfly phenotypes tests evolution's oldest mathematical model. *Science Advances* **5**, eaaw4967.
- HUHEY, J. E. (1980). Studies in warning coloration and mimicry. VIII. Further evidence for a frequency-dependent model of predation. *Journal of Herpetology* **14**, 223–230.
- HUHEY, J. E. (1988). Mathematical models of mimicry. *American Naturalist* **131**, S22–S42.
- JAMIE, G. A. (2017). Signals, cues and the nature of mimicry. *Proceedings of the Royal Society of London Series B: Biological Sciences* **284**, 20162080.
- JEFFORDS, M. R., STERNBURG, J. G. & WALDBAUER, G. P. (1979). Batesian mimicry: field demonstration of the survival value of pipevine swallowtail and monarch color patterns. *Evolution* **33**, 275–286.
- JOHNSON, S. D. & SCHIESTL, F. P. (2016). *Floral Mimicry*. Oxford University Press, Oxford.
- JOHNSON, S. D., ALEXANDERSSON, R. & LINDER, H. P. (2003). Experimental and phylogenetic evidence for floral mimicry in a guild of fly-pollinated plants. *Biological Journal of the Linnean Society* **80**, 289–304.
- JORON, M. & IWASA, Y. (2005). The evolution of a Müllerian mimic in a spatially distributed community. *Journal of Theoretical Biology* **237**, 87–103.
- JORON, M. & MALLET, J. L. B. (1998). Diversity in mimicry: paradox or paradigm? *Trends in Ecology and Evolution* **13**, 461–466.
- KAPAN, D. D. (2001). Three butterfly system provides a field test of Müllerian mimicry. *Nature* **409**, 338–340.
- KIKUCHI, D. W. & PFENNIG, D. W. (2013). Imperfect mimicry and the limits of natural selection. *Quarterly Review of Biology* **88**, 297–315.
- LANGHAM, G. M. (2004). Specialized avian predators repeatedly attack novel color morphs of *Heliconius* butterflies. *Evolution* **58**, 2783–2787.
- LINDSTRÖM, L., ALATALO, R. V. & MAPPEL, J. (1997). Imperfect Batesian mimicry – the effects of the frequency and the distastefulness of the model. *Proceedings of the Royal Society of London Series B: Biological Sciences* **264**, 149–153.
- LITTLE, R. J. (1983). A review of floral food deception mimics with comments on floral mutualism. In *Handbook of Experimental Pollination Biology* (eds C. E. JONES and R. J. LITTLE), pp. 294–309. Van Nostrand Reinhold, New York.
- MALLET, J. (1999). Causes and consequences of a lack of coevolution in Müllerian mimicry. *Evolutionary Ecology* **13**, 777–806.
- MALLET, J. & JORON, M. (1999). Evolution of diversity in warning color and mimicry: polymorphisms, shifting balance, and speciation. *Annual Review of Ecology and Systematics* **30**, 201–233.
- MIDDLEY, J. J., WHITE, J. D. M., JOHNSON, S. D. & BRONNER, G. N. (2015). Faecal mimicry by seeds ensures dispersal by dung beetles. *Nature Plants* **1**, 15141.
- MÜLLER, F. (1878). Über die vorteile der mimicry bei schmetterlingen. *Zoologischer Anzeiger* **1**, 54–55.
- MÜLLER, F. (1879). Ituna and Thyridia; a remarkable case of mimicry in butterflies. *Transactions of the Entomological Society of London* **1879**, xx–xxix.
- MUNOZ-RAMIREZ, C. P., BITTON, P.-P., DOUCET, S. & KNOWLES, L. L. (2016). Mimics here and there, but not everywhere: Müllerian mimicry in *Ceroglossus* ground beetles? *Biology Letters* **12**, 20160429.
- NEWMAN, E., ANDERSON, B. & JOHNSON, S. D. (2012). Flower colour adaptation in a mimetic orchid. *Proceedings of the Royal Society of London Series B: Biological Sciences* **279**, 2309–2313.
- VAN DER NIET, T., HANSEN, D. M. & JOHNSON, S. D. (2011). Carrion mimicry in a South African orchid: flowers attract a narrow subset of the fly assemblage on animal carcasses. *Annals of Botany* **107**, 981–992.
- NUR, U. (1970). Evolutionary rates of models and mimics in Batesian mimicry. *American Naturalist* **104**, 477–486.
- OATEN, A., PEARCE, C. E. M. & SMYTH, M. E. B. (1975). Batesian mimicry and signal detection theory. *Bulletin of Mathematical Biology* **37**, 367–387.
- O'HANLON, J. C. O., HOLWELL, G. I. & HERBERSTEIN, M. E. (2014). Pollinator deception in the orchid mantis. *American Naturalist* **183**, 126–132.
- OLIVEIRA, P. S. (1988). Ant-mimicry in some Brazilian salticid and clubionid spiders (Araneae: Salticidae, Clubionidae). *Biological Journal of the Linnean Society* **33**, 1–15.
- PASTEUR, G. (1982). A classificatory review of mimicry systems. *Annual Review of Ecology and Systematics* **13**, 169–199.
- PFENNIG, D. W. & MULLEN, S. P. (2010). Mimics without models: causes and consequences of allopatry in Batesian mimicry complexes. *Proceedings of the Royal Society B: Biological Sciences* **277**, 2577–2585.
- PFENNIG, D. W., HARCOT, W. R. & PFENNIG, K. S. (2001). Frequency-dependent batesian mimicry. *Nature* **410**, 323–323.
- RAINEY, M. M. & GREYER, G. F. (2007). Competitive mimicry: synthesis of a neglected class of mimetic relationships. *Ecology* **88**, 2440–2448.
- REISERER, R. S. & SCHUETT, G. W. (2008). Aggressive mimicry in neonates of the sidewinder rattlesnake, *Crotalus cerastes* (Serpentes: Viperidae): stimulus control and visual perception of prey luring. *Biological Journal of the Linnean Society* **95**, 81–91.
- RUXTON, G. D., SHERRATT, T. N. & SPEED, M. P. (2004). *Avoiding Attack*. Oxford University Press, Oxford.
- SAUL-GERSHENZ, L. S. & MILLAR, J. G. (2006). Phoretic nest parasites use sexual deception to obtain transport to their host's nest. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 14039–14044.
- SCHUETT, G. W., CLARK, D. L. & KRAUS, F. (1984). Feeding mimicry in the rattlesnake *Sistrurus catenatus*, with comments on the evolution of the rattle. *Animal Behavior* **32**, 625–626.
- SHEPPARD, P. M., TURNER, J. R. G., BROWN, K. S., BENSON, W. W. & SINGER, M. C. (1985). Genetics and the evolution of Müllerian mimicry in *Heliconius* butterflies. *Philosophical Transactions of the Royal Society London Series B: Biological Sciences* **308**, 433–610.
- SHERRATT, T. N. (2008). The evolution of Müllerian mimicry. *Naturwissenschaften* **95**, 681–695.
- SPEED, M. P. (1993). Müllerian mimicry and the psychology of predation. *Animal Behavior* **45**, 571–580.
- SPOTTISWOODE, C. N. & STEVENS, M. (2011). How to evade a coevolving brood parasite: egg discrimination versus egg variability as host defences. *Proceedings of the Royal Society of London Series B: Biological Sciences* **278**, 3566–3573.
- SPOTTISWOODE, C. N. & STEVENS, M. (2012). Host-parasite arms races and rapid changes in bird egg appearance. *American Naturalist* **179**, 633–648.
- THOMPSON, J. N. (2005). *The Geographic Mosaic of Coevolution*. University of Chicago Press, Chicago, IL.
- THOMPSON, J. N. (2013). *Relentless Evolution*. The University of Chicago Press, Chicago.
- THOMPSON, J. N. & CUNNINGHAM, B. M. (2002). Geographic structure and dynamics of coevolutionary selection. *Nature* **417**, 735–738.

- TURNER, J. R. G. (1984). The palatability spectrum and its consequences. In *The Biology of Butterflies* (eds R. I. VANE-WRIGHT and P. ACKERY). Princeton University Press, Princeton.
- TURNER, J. R. G. (1995). Mimicry as a model for coevolution. In *Biodiversity and Evolution* (eds R. ARAI and M. KATO), pp. 131–150. National Science Museum Foundation, Tokyo.
- VANE-WRIGHT, R. (1976). A unified classification of mimetic resemblances. *Biological Journal of the Linnean Society* **8**, 25–56.
- VANE-WRIGHT, R. I. (1980). On the definition of mimicry. *Biological Journal of the Linnean Society* **13**, 1–6.
- WALLACE, A. R. (1860). *Darwin Correspondence Project*. University of Cambridge, Cambridge.
- WICKLER, W. (1965). Mimicry and the evolution of animal communication. *Nature* **208**, 519–521.
- WICKLER, W. (1968). *Mimicry*. Wiedenfeld and Nicholson, London.
- WIGNALL, A. E. & TAYLOR, P. W. (2011). Assassin bug uses aggressive mimicry to lure spider prey. *Proceedings of the Royal Society of London Series B: Biological Sciences* **278**, 1427–1433.
- WILLIAMS, K. S. & GILBERT, L. E. (1981). Insects as selective agents on plant vegetative morphology: egg mimicry reduces egg laying by butterflies. *Science* **212**, 467–469.
- WONG, B. B. M. & SCHIESTL, F. P. (2002). How an orchid harms its pollinator. *Proceedings of the Royal Society of London Series B: Biological Sciences* **269**, 1529–1532.

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