

INSINCERE FLATTERY? UNDERSTANDING THE EVOLUTION OF IMPERFECT DECEPTIVE MIMICRY

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ABSTRACT

Mimicry is the phenotypic resemblance of one organism to another because the resemblance is favored by selection from a signal receiver who perceives the resemblance. We would expect mimics to resemble their models closely, yet the widespread existence of imperfect mimics confounds this expectation, and has led to a profusion of possible explanations for the phenomenon. Despite this, we still lack an understanding of what general evolutionary principles, if any, result in imperfect mimicry. A common approach to this problem is to test and compare several imperfect mimicry hypotheses with the aim of uncovering such general evolutionary principles. We suggest, however, that a better understanding of the hypotheses and clarification of the distinctions or similarities between them is necessary, since each hypothesis makes very different assumptions, requiring different analytical approaches. Therefore, this review aims to focus future studies into imperfect mimicry, and to aid in understanding how to test and compare hypotheses. First, we summarize and characterize hypotheses from the literature based on their types of explanation, subjects, and adaptive landscapes they predict for mimics. Next, we review evidence for the hypotheses, describe desirable characteristics of mimicry complexes for study, and finish by investigating mimicry complexes from past studies.

INTRODUCTION

M IMICRY is a phenotypic resemblance of one organism (the *mimic*) to another organism (the *model*) that has evolved because another organism perceives their similarity and changes its behavior in such a way that the mimic receives a selective advantage (Ruxton et al. 2004; Dalziell and Welbergen 2016). The organism that perceives the resemblance is referred to as the *signal receiver* (or receiver, the term we prefer here; Wickler 1965), *operator* (Vane-Wright 1980), *selective agent* (Reiskind 1977), or *dupe* (Pasteur 1982).

Mimics are broadly classified as to whether they are deceptive or honest (for a classification of mimicry types, see Jamie 2017). Deceptive mimicry, as the name suggests, deceives the signal receiver for the benefit of the mimic and at the cost of the receiver. Some intriguing examples of deceptive mimics include moths that are virtually indistinguishable from stinging wasps (Boppré et al. 2017), cuckoo eggs with the same size, color, and patterning as their host's eggs (de L. Brooke and Davies 1988), and orchid flowers that emit female wasp pheromones to induce pseudocopulatory pollination by male wasps (Nilsson 1992; Gaskett et al. 2008). Deceptive mimicry can be further separated into Batesian and aggressive mimicry; Batesian mimics signal a fitness cost to the receiver, while aggressive mimics signal a fitness benefit (Jamie 2017). The majority of research

on deceptive mimicry to date has addressed Batesian mimicry, and this is reflected in our review; however, aggressive mimicry is also addressed.

Early theoretical work predicted maximum benefits from a close resemblance between mimic and model (Nur 1970). Against this framework, the existence-and abundance-of imperfect mimics seems paradoxical (reviewed in Kikuchi and Pfennig 2013; Sherratt and Peet-Paré 2017), even to Henry Walter Bates, who recognized the existence of imperfect mimicry and that it required an explanation (Bates 1862). Later studies of mimicry investigated whether mimics and models were locked in an evolutionary arms race, since the presence of mimics reduces the effectiveness of model warning signalsthe chase-away hypothesis (Fisher 1930; Sheppard 1959; Nur 1970; Turner 1987). More recently, a wave of explanations has been proffered to explain the abundance and diversity of poor mimics, assuming they must result from evolutionarily stable mechanisms that are not addressed by traditional mimicry theory (Gilbert 2005). This multitude of explanations has led to the thinking that it is high-fidelity mimicry that requires explanation rather than imperfect mimics (Dalziell and Welbergen 2016; Ruxton et al. 2018). Nonetheless, explaining the physical differences between mimics and models remains a fundamental question for all mimicry complexes.

Underlying the idea of imperfect mimicry is the assumption that mimetic accuracy can be quantified. Accuracy can be measured using a variety of methods that can be broadly categorized as either *receiver responses* or *trait measurements*. Receiver response assessments deliberately take receiver senses, cognition,

measurements. Receiver response assessments deliberately take receiver senses, cognition, and/or assessment into account. By contrast, trait measurements aim to repeatably and objectively quantify the difference of a trait from its "optimal" value (i.e., the corresponding trait from a model), and are independent of receivers. The two types of measurement are complementary, and the differences between them can be exploited for hypothesis testing. We address methods of measurement in more detail after introducing the hypotheses for imperfect mimicry.

Although a multitude of explanations for imperfect mimicry has been proposed, the relationships among them is unclear. Some hypotheses overlap; some propose evolutionary effects that apply to mimics, while others apply to receivers; and some propose adaptive explanations and others invoke constraints. Additionally, some hypotheses are broadly applicable while others apply only to specific mimicry complexes. This review builds upon and extends previous work by Kikuchi and Pfennig (2013). Specifically, we identify additional hypotheses and characterize each hypothesis by identifying whether it invokes effects on mimics or receivers, whether the explanation is adaptive or a constraint, and describe the evidence for and against it. We subsequently evaluate which hypotheses overlap, are logically inconsistent or untestable, and make recommendations regarding them. Subsequently, we highlight the characteristics that might make a mimicry system most suitable for simultaneously testing multiple hypotheses. Finally, we describe the mimics and models that have been most studied over the last 30 years. This review focuses on imperfect deceptive mimicry, since receiver/mimic dynamics in deceptive mimicry complexes may differ from those in honest mimicry complexes. Here, we consider a mimic to be imperfect if one or more of its mimetic traits differs objectively from the model traits being mimicked.

Hypotheses: Summary and Characterization

To help clarify the relationships between the imperfect mimicry hypotheses, we summarize them, and identify various characteristics that group or differentiate them (Table 1; references for each hypothesis are given in Supplemental Table 1, available at http:// www.journals.uchicago.edu/loi/qrb). Hypotheses differ in whether their explanations are adaptive, nonadaptive, or whether they argue that mimicry no longer occurs. Although the subject of some hypotheses is the mimic, for others it is the signal receiver. We further illustrate the adaptive landscapes for mimics described by the hypotheses (or, more precisely, a "selection surface," which relates individual phenotypic traits to relative fitness; Arnold 2003; Table 1; Figure 1).

By an "adaptive" hypothesis, we mean that the imperfect mimetic resemblance (for hypotheses addressing mimics) or the receiver response to imperfect mimicry (for hypotheses addressing receivers) is solving a fitness maximization problem for the subject of the hypothesis (mimic *or* receiver) and can be considered optimal (Buss et al. 1998). Nonadaptive hypotheses, on the other hand, describe circumstances that result in mimetic resemblances or receiver responses that are not optimal for the subject of the hypothesis (i.e., mimic or receiver; Buss et al. 1998). Nonadaptive hypotheses are often labeled "constraints" (Dawkins 1982; Buss et al. 1998), but we have avoided this term as it is often used ambiguously or with a different meaning (e.g., Holen and Johnstone 2004).

TECHNICAL ERRORS

Two of the proposed hypotheses are "nonhypotheses" that describe classification errors by researchers rather than evolutionary explanations of imperfect mimicry. The first is that mimicry has been incorrectly attributed to an organism, and imperfect mimics are not functional mimics in nature (the "not a mimic" hypothesis; Dittrich et al. 1993). The second is that mimics are considered imperfect since they are being compared to the incorrect model (the "ugly duckling"

Type of explanation	Applies to	Hypotheses	Adaptive landscape for imperfect mimics	Explanation	References
Adaptive	Mimic	Selection trade- offs, multiple predators, mul- tiple models, character dis- placement	Life-history tradeoffs result in an adaptive peak for imperfect mimicry (Fig- ure 1B)	Inaccurate mimicry is the result of life-history trade- offs for other functions that are affected by the mimetic traits. Specific hypotheses propose differ- ent life-history tradeoffs, and include functions such as thermoregulation, camouflage, sexual se- lection, predation by predators of nominities and predators of models, and competition with models resulting from phenotypic similarity. Alternatively, imperfect mimics may be generalized mimics that are phenotypically intermediate between multiple different models.	Reiskind (1977); Edmunds (2000); Sherratt (2002); Holen and Johnstone (2004); Pekär et al. (2011); Pfemig and Kikuchi (2012); Taylor et al. (2016)
		Kin selection	Imperfect mimicry is an adaptive peak (Figure IC)	In populations with closely related individuals, and at high relative frequencies of mimics to models, or when the benefits afforded by mimicry are rela- tively small, there is a net cost to improving mi- metic accuracy since it increases total predation in the population.	Johnstone (2002)
	Receiver	Cone-of- protection, information limitation, speed-accuracy tradeoffs	Relaxed selection—the adaptive peak encompasses both perfect and imperfect mimicry (Figure 1D)	Suboptimal detection of mimics is optimal receiver behavior. Behavior may be optimal when consid- ering factors such as: cost of mistaking a model for a mimic, benefit from correctly detecting a mimic, receiver motivation, modelmimic ratio, availability of alternatives to mimics (cone-of-protection hypothesis, information limitation); complex rules are required to discriminate mimics from models (information limitation); and discrimination is time constunion (speed-accuracy readeoffs)	Duncan and Sheppard (1965); Nonacs (1985); Hetz and Slobodchikoff (1988); Sherratt (2003); Chittka and Osorio (2007); Pekár and Jarab (2011b); Ab- bott and Sherratt (2013); Kikuchi and Sherratt (2015); Sherratt and Peet-Paré (2017)
Nonadaptive	Mimic	Developmental constraints	Imperfect mimics are not at an adaptive peak, and are currently constrained and unable to evolve greater accuracy (Figure 1E)	Developmental or genetic constraints in mimics limit the evolution of greater mimetic accuracy, even though more accurate mimics would be better adapted.	Maynard Smith et al. (1985); Holloway et al. (2002); Gilbert (2005)

TABLE 1 vbotheses explaining imberfect deceptive mim

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		Evolutionary lag	Imperfect mimics are not at an adaptive peak, but are evolving toward it (Figure 1A)	Mimics are in the process of evolving greater accu- racy. Dynamic equilibrium may result in persistent imperfection if mimics are unable to evolve faster than the rate at which models evolve a dissimilar appearance (the chase-away hypothesis).	Nur (1970); Nesse (2005); Pekár (2014)
	Receiver	Eye-of-the- beholder, stim- ulus salience, increased de- ception, aide mémoire	Relaxed selection—the adaptive peak encompasses both perfect and imperfect mimicry (Figure 1D)	Receiver discrimination of imperfect mimicry is not optimal. Different hypotheses propose different mechanisms explaining why the behavior is not optimal. Eye-of-the-beholder merely suggests such a mechanism exists, without specifying what it is. We consider aide mémoire to be untestable and recommend it should be dismissed.	Carter (1948); Duncan and Sheppard (1965); Rothschild (1984); Dittrich et al. (1993); Green et al. (1999); Hebets and Papaj (2005); Chittka and Osorio (2007); Kazemi et al. (2014); Penney et al. (2014); Quicke (2017); Kikuchi and Dornhaus (2018)
		Perceptual bias exploitation, satyric mimicry	Imperfect mimicry is an adaptive peak (Figure 1F)	Imperfect mimics benefit from a perceptual bias, or else from a slowdown of the "perceptual process" when signal receivers interpret the imperfect mi- metic signal (satyric mimicry).	Howse and Allen (1994); Vereecken and Schiestl (2008); Howse (2013); O'Hanlon et al. (2014)
		Other factors	Relaxed selection—the adaptive peak encompases both perfect and imper- fect mimicry (Figure 1D)	Various additional reasons have been suggested ex- plaining why receiver behavior may relax selection for mimetic accuracy. These include environmen- tal factors that affect signal receiver perception, the sensory system of the signal receiver, signal receiver preferences, community diversity, and prey characteristics unrelated to mimicry (such as prey size or speed of locomotion) that affect re- ceiver decisions.	Ihalainen et al. (2007); Cheney and Marshall (2009); Pekár and Jarab (2011b); Penney et al. (2012); Wilson et al. (2013); Kemp et al. (2015)
Nonmimic	Mimic	Mimetic break- down	Mimicry does not affect fit- ness, or has a fitness cost	Mimicry was historically adaptive but no longer is due to a loss of models or receivers. The breakdown occurred before accurate mimicry had evolved or else accurate mimicry has degraded because of a lack of selection for mimic fidelity. Mimetic breakdown may result in persistent imperfection if the remaining mimetic resemblance is selectively neutral or the resemblance is maintained by gene flow from nearby geographic regions where mim- icry is active.	Bates (1862); Brower (1960); Harper and Pfennig (2008)



FIGURE 1. PREDICTED ADAPTIVE LANDSCAPES FOR MIMICS DESCRIBED BY IMPERFECT MIMICRY HYPOTHESES Each plot represents the relationship between objective mimetic accuracy and evolutionary mimic fitness. Objective mimetic accuracy is treated here as a single phenotypic dimension along the x-axis. The vertical dotted line at the right-most extent of the x-axis indicates the model phenotype that is "perfect" accuracy. The y-axis represents increasing fitness for the mimic (Wright 1988). Organisms are expected to evolve to maximum possible fitness. Asterisks mark adaptive peaks for mimetic accuracy. A. The adaptive landscape predicted by traditional mimicry theory, which does not predict the existence of imperfect mimics. Selection is expected to drive ever improving mimetic accuracy, resulting in all mimics being accurate mimics (Mappes and Alatalo 1997). The evolutionary lag hypotheses position mimics below the adaptive peak, but assume they are climbing toward the peak over time. B. Under tradeoff hypotheses (e.g., Holen and Johnstone 2004; Pekár et al. 2011; Pfennig and Kikuchi 2012), selective pressure for greater accuracy is competing with selective pressure for reduced accuracy. The hypothesis; Sherratt and Peet-Paré 2017). Rather than describing these as hypotheses, we argue that studies of imperfect mimicry should take care to avoid these errors (Reiskind 1977; Dittrich et al. 1993; Ruxton and Schaefer 2011; Grim 2013; Wilson et al. 2013). We have thus excluded these two explanations from Table 1.

Hypotheses: Discussion and Evidence

Here we discuss the hypotheses in greater detail, together with the available supporting evidence. Hypotheses are grouped by type of explanation (adaptive, nonadaptive, nonmimic) and to whom the hypothesis applies (mimic or receiver; columns 1 and 2 in Table 1).

REASONS WHY IMPERFECT MIMICRY IS ADAPTIVE FOR MIMICS

If costs associated with mimicry increase with mimetic accuracy, then some level of inaccuracy may be more adaptive than greater accuracy (Figure 1B). Evolutionary game theory and signal detection theory have been used to predict the effects of the cost of mimicry on mimetic accuracy, which varies with ecological factors such as the selection pressure imposed on receivers by mimics, and the selection pressure imposed on mimics by failure to deceive an operator (Holen and Johnstone 2004). Evidence that mimetic traits carry a cost exists in a number of systems. For example, mimicry can lead to reduced mating success, presumably due to a lack of recognition of suitable mating partners (Estrada and Jiggins 2008; Bybee et al. 2012). Further, phenotypic convergence can lead to increased competition for resources between

mimic and model, as similar body structures may lead to similar diet and habitat requirements (character displacement hypothesis; Pfennig and Kikuchi 2012).

Morphological constraints could also make imperfect mimicry adaptive. Support for this idea comes from spiders that mimic ants. Changes in body shape that are required for ant mimicry limit the number of eggs in female spiders, resulting in a tradeoff between mimicry and fecundity (Gilbert 2005; Pekár and Jarab 2011a). Similarly, hoverflies in temperate regions may need to compromise between mimicry of hymenopterans, which requires bright colors, and thermoregulation, which favors melanization (Taylor et al. 2016). Other morphological constraints on mimics may include limitations on specific foraging and mating behaviors as a result of emulating model behavior (Cushing 2012).

Another reason that imperfect mimicry may be adaptive is that multiple model species change the selective surface so that phenotypes that are intermediate between them yield greater protection than an accurate resemblance to a single model (multiple models hypothesis; Edmunds 2000). Similarly, predators of models may impose costs on protective mimetic accuracy, selecting for less accurate resemblance, as poorer accuracy reduces predation by model specialists while still deterring model-averse predators (multiple predators; Pekár et al. 2011). The latter idea has experimental support from ant-mimicking spiders, where imperfect mimics have a higher chance of survival when confronted by multiple predators compared with more precise mimics (Pekár et al. 2011).

Signal detection theory has long been used to build theoretical models of how receivers impose selection on mimics (Duncan

result is a fitness peak at less than full accuracy. C. According to the kin selection hypothesis, individual selection favors improved mimetic resemblance, however, a net improvement in population accuracy may increase the total population attack rate, and this could result in selection for imperfect mimicry in a closely related population (Johnstone 2002). D. Relaxed selection hypotheses argue that there is no benefit to mimics from greater mimetic accuracy beyond a nominal threshold. E. Under the developmental constraints hypothesis, organisms are unable to attain optimal theoretical fitness due to a bias or limitation on phenotypic variation (Maynard Smith et al. 1985). The dashed vertical line in the plot represents a developmental barrier to the evolution of improved accuracy. In this case, the asterisk represents a *reachable* fitness peak. F. Under perceptual exploitation hypotheses, imperfect mimicry is more effective than perfect mimicry due to signal receiver bias (Howse and Allen 1994; Vereecken and Schiest 2008). See the online edition for a color version of this figure.

and Sheppard 1963; Oaten et al. 1975; Getty 1985; Sherratt 2002). Counterintuitively, signal detection theory predicts that higher accuracy in a Batesian mimic can lead to a larger proportion of individuals in a population being attacked (Oaten et al. 1975) since predators who cannot reliably distinguish mimics from models may be less cautious in sampling prey (Penney et al. 2012). If individuals within such a population are closely related, kin selection can lead to selection for less accurate mimicry (the kin selection hypothesis; Johnstone 2002; Figure 1C). This hypothesis leads to several predictions: a population of inaccurate mimics with rare/ weakly aversive models will suffer fewer attacks than a population of accurate mimics; imperfect mimicry is more likely to occur in species with weakly aversive or uncommon models; and imperfect mimicry will be favored in species with limited dispersal ability or which live in family groups (Johnstone 2002). The kin selection hypothesis has little empirical support beyond the observation that poor mimics tend to be more abundant than both their models and accurate mimics (Edmunds 2000). Perhaps this lack of evidence reflects the difficulty of finding systems to which this hypothesis could feasibly apply.

REASONS WHY POOR DISCRIMINATION IS ADAPTIVE FOR RECEIVERS

Receiver behavioral responses help shape mimetic signals, and so a fundamental evolutionary question is why do receivers exhibit behaviors that result in imperfect mimics? To answer this, we need to understand how mimetic signals affect receiver fitness. Many adaptive hypotheses for receiver behavior derive from mathematical models that make very specific assumptions. One of the most widely used models is signal detection theory, which predicts decision-making under uncertain signal reliability (Duncan and Sheppard 1965; Oaten et al. 1975; Getty 1985; Sherratt 2002; McGuire et al. 2006; Kikuchi et al. 2015). Critically, it operates before receivers make a choice. The theory makes a number of important assumptions. Receivers have complete knowledge of: the probability distributions of the signals of mimics and models; the relative frequencies of mimics and models; and the costs and benefits of attacking models and mimics, respectively (Oaten et al. 1975). Unfortunately for receivers, however, models and mimics cannot be told apart with certainty, either due to noise in the receiver's sensory or cognitive systems, or actual phenotypic overlap between models and mimics. To optimally resolve this problem, receivers must select a threshold in signal space that maximizes their expected payoff for responding to potential prey. Effectively, receivers classify all organisms of interest whose signals fall on one side of the threshold as models, and treat all those that fall on the other as mimics. Adjusting the threshold cannot eliminate errors, but it does alter the ratio of hits (e.g., predator correctly attacks a mimic) to false alarms (e.g., predator incorrectly attacks a model; Getty 1985). The theory calculates the probability that a given phenotype will be treated as a model, and shows that an imperfect resemblance is sufficient. Additionally, as the density of mimics decreases, or the cost of false alarms increases, lower accuracy in resemblance is required (Duncan and Sheppard 1965; Sherratt 2002). This approach provides the mechanistic basis of the cone-of-protection hypothesis for imperfect mimicry (Figure 1D).

Signal detection theory falls short when receivers cannot be assumed to have complete knowledge about mimics (Sherratt and Peet-Paré 2017). Incomplete knowledge gives rise to tradeoffs between information and accuracy, as information gathering has a cost (Abbott and Sherratt 2013; de Froment et al. 2014). Before sampling, receivers can choose to inspect mimics more closely thereby increasing their knowledge, but this requires either time or effort (Chittka and Osorio 2007; Chittka et al. 2009). Therefore, we categorize speed-accuracy tradeoffs as an adaptive hypothesis for the existence of imperfect mimicry. Signal detection theory can be used to model this, but must be augmented to include receiver inspection behavior and associated tradeoffs.

Other theories of receiver behavior deal with what happens *after* receivers make choices. For example, after sampling potential mimics by predators, receivers can update their estimates of the likelihood that prey of a given appearance are defended. Some models of learning are concerned with optimal investment in information (Sherratt 2011), so they describe adaptive behavior. For example, Kikuchi and Sherratt (2015) considered the question: When should a receiver learn about phenotypic differences between two unfamiliar prey, given the risk involved in sampling the unknown? Sherratt and Peet-Paré (2017) give a deep treatment of the logic behind what they call the information limitation hypothesis. They suggest that the optimal receiver behavior is to avoid sampling potentially risky mimics when possible, leading to relaxed selection for poor mimics (Figure 1D).

Poor discrimination by receivers (whether for adaptive or nonadaptive reasons) predicts a relaxed selection adaptive landscape for mimics. It may be indicated by the presence of high levels of variation in accuracy (Holloway et al. 2002) or it may be detected using circumstantial evidence (Penney et al. 2012). Empirical support for relaxed selection comes from hoverflies, where selection was found to be relaxed for smaller flies, perhaps due to a preference by predators for larger prey (Penney et al. 2012), and for hoverfly mimics of very noxious models (Holloway et al. 2002). However, later studies failed to support relaxed selection with no evidence of either greater variation in poorer mimics (Taylor et al. 2016) or of poorer mimetic fidelity in smaller-bodied mimics (Wilson et al. 2013). There is empirical support for relaxed selection in poison frog mimics (Darst and Cummings 2006), coral snake mimics (Harper and Pfennig 2007; Kikuchi and Pfennig 2010a; Akcali and Pfennig 2014), and ant mimics (Pekár and Jarab 2011b; Ramesh et al. 2016).

NONADAPTIVE REASONS WHY MIMETIC ACCURACY IS LIMITED

Various authors have listed reasons why any trait may be nonadaptive or suboptimal (e.g., Gould and Lewontin 1979; Dawkins 1982; Nesse 2005). Developmental constraints

on mimics may prevent the development of accurate mimicry (Figure 1E). The exact meaning of developmental constraints has not been well articulated in the context of imperfect mimicry. They are typically treated as a black box that prevents the evolution of an optimal value in one or more phenotypic traits by preventing the phenotypic variation required for selection to act on (e.g., Holloway et al. 2002). Mimics that are imperfect due to developmental constraints are predicted to exhibit little phenotypic variation since they are expected to be subject to strong purifying selection (Maynard Smith et al. 1985). Imperfect hoverfly mimics show large phenotypic variation, so are unlikely to be explained by developmental constraints (Holloway et al. 2002). If developmental constraints do not reflect a stable mechanism for maintaining imperfect mimicry (Gilbert 2005), then given sufficient time and strong selection, such constraints can be overcome and thus may be more appropriately considered an instance of evolutionary lag.

Mimic species may be poor simply due to a lack of evolutionary time required to evolve more accurate mimicry (evolutionary lag; Figure 1A). The evolutionary lag hypothesis predicts that poor mimics are ancestral to good mimics (Pekár 2014), and that populations of accurate mimics should contain lower levels of phenotypic variation since they have been subject to selection for increased accuracy for a longer period of time (Holloway et al. 2002). Evidence supporting the perfecting hypothesis comes from some ant mimics (McIver and Stonedahl 1993; Pekár 2014), although it has not been supported in coral snake mimics (Kikuchi and Pfennig 2010b) or hoverflies (Holloway et al. 2002). The "chase-away" model describes a possible outcome of the evolutionary lag hypothesis. It argues that mimics and models are locked in an evolutionary arms race, with the fitness of models decreased by the presence of mimics, resulting in selective pressure on models to decrease the resemblance between mimic and model. The result is that imperfect mimics cannot evolve fast enough to catch their models (Nur 1970; Gavrilets and Hastings 1998). No evidence

of chase-away selection has been found in a studies of ant-mimicking jumping spiders (Ceccarelli and Crozier 2007) or coral snake mimics (Akcali et al. 2018); however, evidence of chase-away selection was found in mimetic brood parasite eggs (Spottiswoode and Stevens 2011). It is generally thought that Batesian mimics are under greater pressure to evolve a close resemblance than their models are to evolve a distinct resemblance, so chaseaway selection is unlikely to apply to most cases of Batesian mimicry (Nur 1970; Gilbert 2005).

NONADAPTIVE REASONS WHY RECEIVER DISCRIMINATION IS LIMITED

Since the seminal works of Ryan et al. (1990), Guilford and Dawkins (1991), and Endler and Basolo (1998) on receiver psychology and the evolution of signals, research in this area has exploded (Rodd et al. 2002; Fuller et al. 2005; Fuller 2009; Zuk et al. 2014), leading to recent studies on the perceptual biases of receivers of imperfect mimicry (Bain et al. 2007; Kikuchi and Pfennig 2010a; Penney et al. 2012; Kazemi et al. 2014, 2015; Sherratt et al. 2015; Kikuchi et al. 2016). Multiple layers of perceptual processes impinge on the way that receivers interact with the signals of mimics. The most fundamental of these processes are sensory adaptations for acquiring information from the environment, whatever the sensory modality. Mimetic signals only need resemble those of their models to the extent that their shared receivers are unable to detect differences between them (Ford 1953).

Even if sensory mechanisms can detect elements of signals, cognitive mechanisms may not be able to integrate the signal elements. To illustrate this point, predators of coral snakes probably have innate aversions to their colored rings (Gehlbach 1972; Smith 1975, 1977). However, how the colored rings are ordered does not affect attack rates (Kikuchi and Pfennig 2010a). As a result, imperfect coral snake mimicry can probably be explained by a simple, innate bias or cognitive limitation on the part of at least some predators. Innate biases can also result in inaccurate mimics with higher fitness than perfect mimics. An example of an innate receiver bias is provided by sexually deceptive *Ophrys* orchid flowers, which are pollinated by male bees in the act of pseudocopulation. The flowers are imperfect chemical mimics of female bees, yet the male bees actively prefer the orchid's floral odor over the sex pheromone of the female bees (perceptual bias exploitation; Figure 1F; Vereecken and Schiestl 2008). Similarly, the flower-mimicking orchid mantis *Hymenopus coronatus* attracts pollinators (its prey) at a higher rate than surrounding flowers, possibly due to pollinator's preference for larger flowers (O'Hanlon et al. 2014).

Cognitive biases during learning also play a role in signal evolution. "Cue competition" describes a psychological phenomenon, whereby animals do not learn about all aspects of a compound stimulus (Pavlov 1927). For example, color may outcompete size during learning, resulting in animals only discriminating color, although size could also be a relevant factor (Sherratt et al. 2015). Cues may outcompete each other when more intense (or more salient) stimuli overshadow less intense (or less salient) stimuli or when pretraining on one component blocks learning about a second component (Mackintosh 1971; Oberling et al. 2000). In the context of imperfect mimicry, cue competition can also occur. Receivers may preferentially weigh some components of mimetic phenotypes over others. Consequently, lower-ranked components are under reduced selection, resulting in lower accuracy (Terhune 1977; Kazemi et al. 2014; Kikuchi et al. 2015; Sherratt et al. 2015). Conversely, when components are equal in salience, imperfect mimicry is not expected to result (Garcia and Koelling 1966; Kazemi et al. 2015; Kikuchi et al. 2016).

It is also possible that receivers respond to configurations of multiple components in a nonlinear way, i.e., they do not interpret them additively (Howse and Allen 1994; Thein et al. 2008; Shettleworth 2010). For example, the satyric mimicry hypothesis (Howse and Allen 1994) postulates that imperfect mimics can slow down predator responses because they present a combination of components that generate an ambiguous signal (Figure 1F).

The mechanisms described in this section have been labeled as nonadaptive since they result in nonoptimal discrimination by receivers. However, it is possible that the mechanisms are adaptive when interpreted from a wider perspective. For example, sensory and cognitive traits are metabolically costly (Laughlin et al. 1998), so the overall cost of improved discrimination may be greater than the benefit. Similarly, perceptual biases may lead to improved mate choices (Ryan and Cummings 2013), so they can be beneficial to receivers. Furthermore, it is also possible that these receiver behaviors are mediated by information limitation (sensu Sherratt and Peet-Paré 2017). If this were the case, then we might expect an important effect due to factors such as the costs of gathering information (Sherratt 2011; Kikuchi and Sherratt 2015), the relative abundance of models to mimics (Kikuchi and Sherratt 2015; Sherratt and Peet-Paré 2017), the number of traits the receiver evaluates (Sherratt and Peet-Paré 2017), and the complexity of the ecological community (Beatty et al. 2004; Ihalainen et al. 2012; Sherratt and Peet-Paré 2017; Kikuchi et al. 2019). And if these factors were shown to promote receiver biases, then those biases would be more appropriately listed under adaptive hypotheses for receiver behavior. On the other hand, phenomena such as developmental constraints or evolutionary lag may underlie these receiver behaviors, meaning they are nonadaptive. To the best of our knowledge, however, ultimate explanations for these mechanisms are yet to be elucidated.

MIMETIC BREAKDOWN

Mimetic breakdown can occur when the protection afforded by mimicry breaks down due to loss of predation (Bates 1862), loss of models (Pfennig et al. 2001), or changes in relative abundance of mimics and models (Brower 1960). Imperfect mimicry may persist if the remaining mimetic resemblance is selectively neutral, or the resemblance is maintained by gene flow from regions where mimicry is active (Harper and Pfennig 2008). This hypothesis overlaps with the "not a mimic" nonhypothesis, but differs in that the organisms were mimics in the past or still are elsewhere; their existence poses a much more interesting problem. Mimetic breakdown can be demonstrated by showing that the appropriate ecological conditions apply (i.e., loss of predation, loss of models, or changes in relative abundance of mimics and models), although such conditions alone are not sufficient to explain a reduction in mimetic accuracy. Mimetic breakdown will result in high levels of phenotypic variation, since selection for mimicry has been relaxed (Holloway et al. 2002). The evidence for this idea is mixed, with support from coral snake mimics (Harper and Pfennig 2008), but a lack of support in hoverflies (Holloway et al. 2002).

MEASURING ACCURACY

As previously mentioned, accuracy of mimicry can be measured by objectively quantifying the physical differences between mimics and their models or by testing the responses of a signal receiver. The two approaches are not interchangeable-rather they quantify different concepts, and may be used to test different predictions. Receiver responses have been measured by recording the behavioral responses of signal receivers to mimics or by electrophysiological investigation (Stökl et al. 2011). The studied receiver may be the signal receiver from the same mimicry complex as the mimic (Nelson et al. 2006; Brodmann et al. 2009; Nelson 2012; Harvey et al. 2018) or some kind of representative receiver (Dittrich et al. 1993). Representative receivers have included humans (Penney et al. 2012), pigeons (Dittrich et al. 1993; Green et al. 1999), and even neural network algorithms (Bain et al. 2007). Additionally, receiver response measurements could potentially be modeled using receiver-specific models, such as color measurements that incorporate receiver perception (e.g., Maxwell triangle; Kemp et al. 2015).

Trait measurements include morphometrics to quantify and compare body shapes (Reiskind 1970; Iserbyt et al. 2011; Penney et al. 2012), model-independent measurements of color (e.g., segment analysis; Kemp et al. 2015) and/or pattern (Vorobyev et al. 1998; Endler and Mielke 2005; Taylor et al. 2013, 2016), image analysis (Dittrich et al. 1993), chemical analysis of chemical mimics (Brodmann et al. 2009; Stökl et al. 2011), and quantitative behavioral analysis of models and mimics (Ceccarelli 2008; Pekár and Jarab 2011b; Shamble et al. 2017; Skowron Volponi et al. 2018).

Difficulties in quantifying the accuracy of a mimic are caused by the need to identify: the model (Pekár et al. 2017a; Sherratt and Peet-Paré 2017), which need not be a single species (Gilbert 2005; Pekár et al. 2017b); the receiver, which also need not be a single species (Pekár et al. 2011); and the traits that can be observed by, and are salient to, the receiver or receivers (Kunze and Gumbert 2001; Kazemi et al. 2014; Skelhorn et al. 2016; Wang et al. 2017). Assessment of accuracy may be further complicated by unknown interactions between multiple components of mimicry such as appearance and behavior (Wang et al. 2017).

The differences between results generated by different measurements of accuracy may reveal valuable insights into the evolution and maintenance of imperfect mimicry (Dittrich et al. 1993), and classes of hypotheses predict some of these differences. Developmental constraints (Maynard Smith et al. 1985), evolutionary lag (Pekár 2014), and tradeoff hypotheses (Holen and Johnstone 2004) all predict that mimics will be assessed as imperfect by both trait measurements and receiver responses. Within the tradeoff hypotheses, the multiple predators hypothesis predicts that different predators will assess mimetic accuracy similarly, but some predators attack models while others avoid them (Pekár et al. 2011). According to the multiple models hypothesis, trait measurements should reveal that imperfect mimics are phenotypically intermediate between two or more models (Penney et al. 2012). The relaxed selection hypotheses predict that signal receivers will not respond differently to perfect and imperfect mimics; however, trait assessment will reveal imperfect mimicry (Sherratt 2002). Eye-of-the-beholder hypotheses predict that different assessment methods will yield different results. Perceptual bias exploitation predicts that signal receivers will rate accuracy inversely to trait assessment up to some limit (O'Hanlon et al. 2014). Stimulus salience predicts that signal receiver assessments will match trait assessments of some traits but not others, and different receivers may assess accuracy using different traits (Kazemi et al. 2014). The information limitation hypothesis predicts that naïve receivers will rate poor mimics as accurate, and become better able to discriminate poor from accurate mimics after sampling of mimics (Sherratt and Peet-Paré 2017).

Simultaneously Testing Multiple Hypotheses: Considerations For Experimental Design and Selecting Appropriate Study Systems

A powerful approach to objectively evaluate the proposed hypotheses is through direct comparison. Since results from tests on a single mimicry complex cannot always be generalized, hypotheses can best be compared by testing them within a single complex (Kikuchi and Pfennig 2013). Simultaneous hypothesis tests should be designed bearing in mind that many hypotheses are not mutually exclusive, and may apply to different systems. In general, however, mimetic systems suitable for testing multiple hypotheses should possess a number of characteristics. First, mimetic accuracy must be quantifiable. Second, the study system should contain variation in mimetic accuracy, ideally ranging from variation between individuals through to variation between species and higher taxonomic levels (Kikuchi and Pfennig 2013). Third, mimics and models should be abundant, hence making it easy to locate specimens, and more likely to quantify the desired variation. Finally, if models and mimics are well known and studied, errors such as misidentification of models (Sherratt and Peet-Paré 2017) are less likely to occur.

Rarely considered are effects that the number of mimic and/or model species within a mimicry complex, or the complexity of the broader ecological community and environment, may have on imperfect mimicry and its study. More species-rich complexes may provide a greater likelihood of manifestation and/or detection of rare or unusual phenomena. Furthermore, frequency-dependent selection may have different outcomes on imperfect mimicry in species-rich than species-poor systems. For example, evidence supporting the evolutionary lag hypothesis is most likely to be encountered in a mimicrich system such as ant-mimicking spiders (Cushing 1997). Conversely, mimetic breakdown may only occur in mimicry complexes with relatively few model species, such as the coral snake mimics (Harper and Pfennig 2008), since a model lost from such a system cannot easily be replaced by an alternative model species. Finally, as mentioned above, community structure may also affect how much information receivers use to decide which prey to eat (Beatty et al. 2004; Ihalainen et al. 2012; Kikuchi et al. 2019). Therefore, community context should be taken into account when selecting systems to test multiple hypotheses.

PAST SUBJECTS OF MIMICRY STUDIES

To assess which study systems are currently being used in mimicry studies, and what source of variation these systems embody, we conducted a literature analysis. We queried the Web of Science (http://apps.webof knowledge.com) for articles published after 1987 with the topic "Batesian mimicry," which returned 642 records (on 28 April 2018). Duplicates were removed, the records were shuffled into random order, and then we analyzed the first 65 relevant articles. Articles such as reviews or opinion pieces, or on unrelated topics, were excluded from the analysis. For each relevant article, mimic and model taxa and type of signal receiver were recorded (Supplemental Table 2, available at http:// www.journals.uchicago.edu/loi/qrb).

Our nonexhaustive literature analysis revealed that mimicry is mostly studied in insects (Figure 2; Supplemental Table 2), the most-studied order being Lepidoptera, including *Heliconius* butterflies (Bates 1862). Lepidoptera are both diverse and well studied, comprising around 10% of all described living organisms (see the Lepidoptera Taxome Project, available at http://www.ucl .ac.uk/taxome/), and documented in large abundance datasets (see the North American Butterfly Association Butterfly Counts, available at http://www.naba.org/pubs /countpub.html). The proximate mechanisms that underlie mimetic resemblance in lepidopterans are relatively well understood. For example, the multiple forms of polymorphic Batesian mimicry in Papilio dardanus and *P. memnon* are thought to be controlled by a single "supergene" (Joron et al. 2011; Merrill et al. 2015), which is a set of genes that are inherited together due to close linkage (Joron et al. 2006). Mimicry studies of Lepidoptera generally investigate systems in which both mimics and models are Lepidoptera (Figure 2). Variation in butterfly mimicry covers several levels, including between individuals, between sexes (sexual dimorphism; Kunte 2009), between different forms of a species (polymorphic mimicry; Kunte 2009), between populations (Bates 1862), and between species (Bates 1862). Predators of Lepidoptera are generally assumed to be birds (Molleman et al. 2010).

Wasps, bees, and ants (Hymenoptera) were the second most frequently studied order within our study sample (Figure 2; Supplemental Table 1). Hymenopterans were most commonly serving as models rather than mimics, although some studies covered Müllerian mimics with hymenopteran co-mimics (Wilson et al. 2015). There were two groups within the hymenopteran systems: bee or wasp mimics, and flightless ant mimics. The majority of studied mimics of bees or wasps are hoverflies (Syrphidae). Syrphids are widespread, abundant, and well studied (Owen and Gilbert 1989; Thompson and Vockeroth 1989). Among hoverflies that mimic stinging hymenopterans, mimetic accuracy varies from poor to good (Penney et al. 2012), some exhibit polymorphic mimicry (Howarth et al. 2000) and, unlike the lepidopteran mimics, they mimic diverse model taxa (i.e., bees and wasps). Hoverflies are generally considered to be Batesian mimics, with insectivorous birds and insects as predators (Howarth et al. 2000).

Ant mimics are unique within our sample studies as the only system addressed by multiple studies in which mimics and models belong to different taxonomic classes (Figure 2). Most ant mimics are considered to be Batesian mimics (McIver and Stonedahl



Figure 2. Mimics and Their Models in 65 Randomly Selected Studies of Mimicry Covering the 30 Years From 1988 to 2018

Each link is an arrow that points from the taxon of a mimic to that of its model. Mimics and models may belong to the same taxon (e.g., amphibians). The width of the link represents the number of studies covering that relationship. Mimicry systems are categorized on taxonomic class, except for insects, which are broken down into orders. If multiple mimicry systems were described in a single article, it was split into two (or more) data points. Diagram plotted in R using the circlize package (Gu et al. 2014). Data used to create the figure are available in Supplemental Table 2. See the online edition for a color version of this figure.

1993), with some aggressive mimics (Allan et al. 2002). Although there are many known nonarachnid ant mimics, particularly bugs and beetles (McIver and Stonedahl 1993), all ant mimics in our nonrepresentative sample of studies were spiders, with the exception of a putative case of ant mimicry by

flowers. Ant mimics are extremely abundant, widespread, and diverse, with more than 2000 species in 200 genera and 54 families (McIver and Stonedahl 1993). They exhibit variation from within-individual variation (i.e., transformational mimicry; Booth 1990) through to differences between animal lineages at many taxonomic ranks (McIver and Stonedahl 1993) and possibly even across different kingdoms (Lev-Yadun 2009). Ant mimics vary from poor to very good in accuracy of resemblance to their models (Pekár and Jarab 2011b). Ant mimicry exists across a range of sensory modalities, including visual, behavioral, and chemical, and they are prey to a wide range of different predators (McIver and Stonedahl 1993). This extreme diversity and variation renders them suitable for comparative studies, allowing a wide range of hypotheses to be tested within a single mimetic system. Additionally, the substantial "taxonomic distance" between ant mimics and their models, as well as between different ant mimics, may generate results that are more generally applicable and less taxonspecific. However, only five of the 18 hypotheses have been tested and supported by empirical evidence in studies of ant mimics while three hypotheses have been tested but not supported. The remainder of the hypotheses have not been tested in ant mimics. Difficulties in studies of ant mimicry may include the fact that many ant mimics (and, indeed, ants) are yet to be described (Ceccarelli and Crozier 2007; Ward 2007) and, in many cases, the identity of the organisms that act as the signal receivers for ant mimics are not well established (Huang et al. 2011; Ramesh et al. 2016).

Angiosperms were the only group of mimics or models studied that were not animals. Most mimics of angiosperms are themselves flowers, although there are some notable exceptions. The orchid mantis visually mimics flowers, thereby attracting pollinators that it preys on (O'Hanlon et al. 2014) and some coniferophagous (conifer-feeding) beetles appear to mimic the warning chemicals emitted by nonedible trees. The beetles may do this to protect their host tree from attack by additional coniferophagous insects (Huber et al. 1999). There are approximately 8000 species of angiosperms that lack floral rewards, and the majority are orchids pollinated by animals that are deceived into expecting food or other rewards (Jersáková et al. 2006, 2009). The mimetic accuracy of deceptive flowers covers a spectrum from a highly accurate resemblance to a specific

model species (Anderson et al. 2005) through to a vague resemblance to a generalized model (Gumbert and Kunze 2001). The latter case is considered to be "generalized food deception" rather than mimicry since the system is lacking an identifiable model (Cropper and Calder 1990; Jersáková et al. 2009; Ruxton and Schaefer 2011). Nonetheless, there may be an adaptive cost to the inaccurate resemblance, since pollinators are able to learn to discriminate between nonrewarding and rewarding flowers, so generalized food deceptive flowers often rely on naïve pollinators that have not yet learned to discriminate (Jersáková et al. 2009).

A number of mimicry systems were addressed by single studies in our literature sample (Figure 2). The focus of these studies generally appears to be the documentation of a novel and interesting form of putative mimicry rather than an attempt to identify universal principles. These studies included morphological and behavioral mimicry of hairy, brightly colored, and toxic caterpillars by bird nestlings (with modified feathers that resemble the hairs of the caterpillar and slow "caterpillar-like" movements; Londoño et al. 2015), auditory mimicry of rattlesnake warning signals by birds (Straneck 1999), and chemical mimicry of trees by beetles (Huber et al. 1999).

CONCLUSION

Mimicry, despite being a topic of interest and study for well over 150 years, is still not fully understood. Finding general principles governing the widespread existence and persistence of imperfect mimicry is a particular challenge that will require broad comparative studies coupled with a clear understanding of the relationships between the hypotheses and the subjects and types of phenomena they describe. To provide results that are applicable beyond a single taxon, studies should encompass variation in mimetic accuracy at multiple levels (e.g., between individuals, between populations, and between species), multiple types of mimicry across multiple sensory modalities, broad taxonomic range, and a wide variety of models.

The phenomenon of imperfect mimicry is an ideal model system for understanding how the phenotype is shaped by adaptive and neutral processes and constraints. Imperfect mimics, regardless of taxon, present us with the rare opportunity of knowing the "optimal" mimetic phenotype: perfect mimicry. Comparing "optimal" and actual phenotypes allows us to identify the processes that result in the observed evolutionary pathways. Our hope is that this review sparks more focused and systematic testing of imperfect mimicry hypotheses and aids the redevelopment of mimicry theory, leading to a deeper understanding of the principles of evolutionary biology.

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REFERENCES

- Abbott K. R., Sherratt T. N. 2013. Optimal sampling and signal detection: unifying models of attention and speed–accuracy trade-offs. *Behavioral Ecology* 24:605–616.
- Akcali C. K., Pfennig D. W. 2014. Rapid evolution of mimicry following local model extinction. *Biology Letters* 10:20140304.
- 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.
- Allan R. A., Capon R. J., Brown W. V., Elgar M. A. 2002. Mimicry of host cuticular hydrocarbons by salticid spider *Cosmophasis bitaeniata* that preys on larvae of tree ants *Oecophylla smaragdina*. *Journal of Chemical Ecology* 28:835–848.
- Anderson B., Johnson S. D., Carbutt C. 2005. Exploitation of a specialized mutualism by a deceptive orchid. *American Journal of Botany* 92:1342–1349.
- Arnold S. J. 2003. Performance surfaces and adaptive landscapes. *Integrative and Comparative Biology* 43: 367–375.
- Bain R. S., Rashed A., Cowper V. J., Gilbert F. S., Sherratt T. N. 2007. The key mimetic features of hoverflies through avian eyes. *Proceedings of the Royal Society B: Biological Sciences* 274:1949–1954.
- Bates H. W. 1862. XXXII. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidæ. *Transactions of the Linnean Society of London* 23:495–566.
- Beatty C. D., Beirinckx K., Sherratt T. N. 2004. The evolution of Müllerian mimicry in multispecies communities. *Nature* 431:63–66.
- Booth C. L. 1990. Evolutionary significance of ontogenetic colour change in animals. *Biological Journal of the Linnean Society* 40:125–163.
- Boppré M., Vane-Wright R. I., Wickler W. 2017. A hypothesis to explain accuracy of wasp resemblances. *Ecology and Evolution* 7:73–81.

- Brodmann J., Twele R., Francke W., Yi-bo L., Xi-qiang S., Ayasse M. 2009. Orchid mimics honey bee alarm pheromone in order to attract hornets for pollination. *Current Biology* 19:1368–1372.
- Brower J. V. Z. 1960. Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *American Naturalist* 94: 271–282.
- Buss D. M., Haselton M. G., Shackelford T. K., Bleske A. L., Wakefield J. C. 1998. Adaptations, exaptations, and spandrels. *American Psychologist* 53:533– 548.
- Bybee S. M., Yuan F., Ramstetter M. D., Llorente-Bousquets J., Reed R. D., Osorio D., Briscoe A. D. 2012. UV photoreceptors and UV-yellow wing pigments in *Heliconius* butterflies allow a color signal to serve both mimicry and intraspecific communication. *American Naturalist* 179:38–51.
- Carter G. S. 1948. Colour and colour vision in animals. Nature 162:600–601.
- Ceccarelli F. S. 2008. Behavioral mimicry in *Myrmarachne* species (Araneae, Salticidae) from North Queensland, Australia. *Journal of Arachnology* 36:344–351.
- Ceccarelli F. S., Crozier R. H. 2007. Dynamics of the evolution of Batesian mimicry: molecular phylogenetic analysis of ant-mimicking *Myrmarachne* (Araneae: Salticidae) species and their ant models. *Journal of Evolutionary Biology* 20:286–295.
- Cheney K. L., Marshall N. J. 2009. Mimicry in coral reef fish: how accurate is this deception in terms of color and luminance? *Behavioral Ecology* 20:459–468.
- Chittka L., Osorio D. 2007. Cognitive dimensions of predator responses to imperfect mimicry. *PLOS Biology* 5:e339.
- Chittka L., Skorupski P., Raine N. E. 2009. Speed–accuracy tradeoffs in animal decision making. *Trends* in Ecology and Evolution 24:400–407.
- Cropper S. C., Calder D. M. 1990. The floral biology of *Thelymitra epipactoides* (Orchidaceae), and the

implications of pollination by deceit on the survival of this rare orchid. *Plant Systematics and Evolution* 170:11–27.

- Cushing P. E. 1997. Myrmecomorphy and myrmecophily in spiders: a review. *Florida Entomologist* 80:165– 193.
- Cushing P. E. 2012. Spider-ant associations: an updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. *Psyche* 2012:151989.
- Dalziell A. H., Welbergen J. A. 2016. Mimicry for all modalities. *Ecology Letters* 19:609–619.
- Darst C. R., Cummings M. E. 2006. Predator learning favours mimicry of a less-toxic model in poison frogs. *Nature* 440:208–211.
- Dawkins R. 1982. The Extended Phenotype: The Gene as the Unit of Selection. Oxford (United Kingdom): W. H. Freeman and Company.
- de Froment A. J., Rubenstein D. I., Levin S. A. 2014. An extra dimension to decision-making in animals: the three-way trade-off between speed, effort perunit-time and accuracy. *PLOS Computational Biology* 10:e1003937.
- de L. Brooke M., Davies N. B. 1988. Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature* 335:630–632.
- Dittrich W., Gilbert F., Green P., McGregor P., Grewcock D. 1993. Imperfect mimicry: a pigeon's perspective. *Proceedings of the Royal Society B: Biological Sciences* 251:195–200.
- Duncan C. J., Sheppard P. M. 1963. Continuous and quantal theories of sensory discrimination. *Proceed*ings of the Royal Society B: Biological Sciences 158:343– 363.
- Duncan C. J., Sheppard P. M. 1965. Sensory discrimination and its role in the evolution of Batesian mimicry. *Behaviour* 24:269–282.
- Edmunds M. 2000. Why are there good and poor mimics? Biological Journal of the Linnean Society 70:459–466.
- Endler J. A., Basolo A. L. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution* 13:415–420.
- Endler J. A., Mielke P. W., Jr. 2005. Comparing entire colour patterns as birds see them. *Biological Journal* of the Linnean Society 86:405–431.
- Estrada C., Jiggins C. D. 2008. Interspecific sexual attraction because of convergence in warning colouration: is there a conflict between natural and sexual selection in mimetic species? *Journal of Evolutionary Biology* 21:749–760.
- Fisher R. A. 1930. *The Genetical Theory of Natural Selection.* Oxford (United Kingdom): Clarendon Press.
- Ford E. B. 1953. The genetics of polymorphism in the Lepidoptera. *Advances in Genetics* 5:43–87.
- Fuller R. C. 2009. A test of the critical assumption of the sensory bias model for the evolution of female mating preference using neural networks. *Evolution* 63:1697–1711.

- Fuller R. C., Houle D., Travis J. 2005. Sensory bias as an explanation for the evolution of mate preferences. *American Naturalist* 166:437–446.
- Garcia J., Koelling R. A. 1966. Relation of cue to consequence in avoidance learning. *Psychonomic Science* 4:123–124.
- 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.
- Gehlbach F. R. 1972. Coral snake mimicry reconsidered: the strategy of self-mimicry. *Forma et Functio* 5:311–320.
- Getty T. 1985. Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. *American Naturalist* 125:239–256.
- Gilbert F. 2005. The evolution of imperfect mimicry. Pages 231–288 in *Insect Evolutionary Ecology: Proceedings of the Royal Entomological Society's 22nd Symposium*, edited by M. D. E. Fellowes, G. J. Holloway, and J. Rolff. Wallingford (United Kingdom): CABI Publishing.
- Gould S. J., Lewontin R. C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proceedings of the Royal Society B: Biological Sciences* 205:581–598.
- Green P. R., Gentle L., Peake T. M., Scudamore R. E., McGregor P. K., Gilbert F., Dittrich W. H. 1999. Conditioning pigeons to discriminate naturally lit insect specimens. *Behavioural Processes* 46:97–102.
- 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.
- Gu Z., Gu L., Eils R., Schlesner M., Brors B. 2014. circlize implements and enhances circular visualization in R. Bioinformatics 30:2811–2812.
- Guilford T., Dawkins M. S. 1991. Receiver psychology and the evolution of animal signals. *Animal Behav*iour 42:1–14.
- Gumbert A., Kunze J. 2001. Colour similarity to rewarding model plants affects pollination in a food deceptive orchid, Orchis boryi. Biological Journal of the Linnean Society 72:419–433.
- 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 B: Biological Sciences* 274: 1955–1961.
- Harper G. R., Jr., Pfennig D. W. 2008. Selection overrides gene flow to break down maladaptive mimicry. *Nature* 451:1103–1106.
- Harvey J. A., Visser B., Lammers M., Marien J., Gershenzon J., Ode P. J., Heinen R., Gols R., Ellers J.

2018. Ant-like traits in wingless parasitoids repel attack from wolf spiders. *Journal of Chemical Ecology* 44:894–904.

- Hebets E. A., Papaj D. R. 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* 57:197–214.
- Hetz M., Slobodchikoff C. N. 1988. Predation pressure on an imperfect Batesian mimicry complex in the presence of alternative prey. *Oecologia* 76:570–573.
- Holen Ø. H., Johnstone R. A. 2004. The evolution of mimicry under constraints. *American Naturalist* 164: 598–613.
- Holloway G., Gilbert F., Brandt A. 2002. The relationship between mimetic imperfection and phenotypic variation in insect colour patterns. *Proceedings of the Royal Society B: Biological Sciences* 269:411–416.
- Howarth B., Clee C., Edmunds M. 2000. The mimicry between British Syrphidae (Diptera) and aculeate Hymenoptera. *British Journal of Entomology and Natural History* 13:1–39.
- Howse P. E. 2013. Lepidopteran wing patterns and the evolution of satyric mimicry. *Biological Journal of the Linnean Society* 109:203–214.
- Howse P. E., Allen J. A. 1994. Satyric mimicry: the evolution of apparent imperfection. *Proceedings of the Royal Society B: Biological Sciences* 257:111–114.
- Huang J.-N., Cheng R.-C., Li D., Tso I.-M. 2011. Salticid predation as one potential driving force of ant mimicry in jumping spiders. *Proceedings of the Royal Society B: Biological Sciences* 278:1356–1364.
- Huber D. P. W., Gries R., Borden J. H., Pierce H. D., Jr. 1999. Two pheromones of coniferophagous bark beetles found in the bark of nonhost angiosperms. *Journal of Chemical Ecology* 25:805–816.
- Ihalainen E., Lindström L., Mappes J. 2007. Investigating Müllerian mimicry: predator learning and variation in prey defences. *Journal of Evolutionary Biology* 20:780–791.
- Ihalainen E., Rowland H. M., Speed M. P., Ruxton G. D., Mappes J. 2012. Prey community structure affects how predators select for Müllerian mimicry. *Proceedings of the Royal Society B: Biological Sciences* 279:2099– 2105.
- Iserbyt A., Bots J., Van Dongen S., Ting J. J., Van Gossum H., Sherratt T. N. 2011. Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proceedings of the Royal Society B: Biological Sciences* 278:3116–3122.
- Jamie G. A. 2017. Signals, cues and the nature of mimicry. Proceedings of the Royal Society B: Biological Sciences 284:20162080.
- Jersáková J., Johnson S. D., Kindlmann P. 2006. Mechanisms and evolution of deceptive pollination in orchids. *Biological Reviews* 81:219–235.
- Jersáková J., Johnson S. D., Jürgens A. 2009. Deceptive behavior in plants. II. Food deception by plants: from generalized systems to specialized floral mim-

icry. Pages 223–246 in *Plant-Environment Interactions*, edited by F. Baluška. Berlin (Germany): Springer.

- Johnstone R. A. 2002. The evolution of inaccurate mimics. *Nature* 418:524–526.
- Joron M., Papa R., Beltrán M., Chamberlain N., Mavárez J., Baxter S., Abanto M., Bermingham E., Humphray S. J., Rogers J., Beasley H., Barlow K., ffrench-Constant R. H., Mallet J., McMillan W. O., Jiggins C. D. 2006. A conserved supergene locus controls colour pattern diversity in *Heliconius* butterflies. *PLOS Biology* 4:e303.
- Joron M., Frezal L., Jones R. T., et al. 2011. Chromosomal rearrangements maintain a polymorphic supergene controlling butterfly mimicry. *Nature* 477: 203–206.
- Kazemi B., Gamberale-Stille G., Tullberg B. S., Leimar O. 2014. Stimulus salience as an explanation for imperfect mimicry. *Current Biology* 24:965–969.
- Kazemi B., Gamberale-Stille G., Leimar O. 2015. Multitrait mimicry and the relative salience of individual traits. *Proceedings of the Royal Society B: Biological Sciences* 282:20152127.
- Kemp D. J., Herberstein M. E., Fleishman L. J., Endler J. A., Bennett A. T. D., Dyer A. G., Hart N. S., Marshall J., Whiting M. J. 2015. An integrative framework for the appraisal of coloration in nature. *American Naturalist* 185:705–724.
- Kikuchi D. W., Dornhaus A. 2018. How cognitive biases select for imperfect mimicry: a study of asymmetry in learning with bumblebees. *Animal Behaviour* 144: 125–134.
- Kikuchi D. W., Pfennig D. W. 2010a. Predator cognition permits imperfect coral snake mimicry. *Ameri*can Naturalist 176:830–834.
- Kikuchi D. W., Pfennig D. W. 2010b. High-model abundance may permit the gradual evolution of Batesian mimicry: an experimental test. *Proceedings of the Royal Society B: Biological Sciences* 277:1041–1048.
- Kikuchi D. W., Pfennig D. W. 2013. Imperfect mimicry and the limits of natural selection. *Quarterly Review* of Biology 88:297–315.
- Kikuchi D. W., Sherratt T. N. 2015. Costs of learning and the evolution of mimetic signals. *American Naturalist* 186:321–332.
- Kikuchi D. W., Malick G., Webster R. J., Whissell E., Sherratt T. N. 2015. An empirical test of 2-dimensional signal detection theory applied to Batesian mimicry. *Behavioral Ecology* 26:1226–1235.
- Kikuchi D. W., Mappes J., Sherratt T. N., Valkonen J. K. 2016. Selection for multicomponent mimicry: equal feature salience and variation in preferred traits. *Behavioral Ecology* 27:1515–1521.
- Kikuchi D. W., Dornhaus A., Gopeechund V., Sherratt T. N. 2019. Signal categorization by foraging animals depends on ecological diversity. *eLife* 8:e43965.
- Kunte K. 2009. Female-limited mimetic polymorphism: a review of theories and a critique of sexual

selection as balancing selection. *Animal Behaviour* 78:1029–1036.

- Kunze J., Gumbert A. 2001. The combined effect of color and odor on flower choice behavior of bumble bees in flower mimicry systems. *Behavioral Ecol*ogy 12:447–456.
- Laughlin S. B., de Ruyter van Steveninck R. R., Anderson J. C. 1998. The metabolic cost of neural information. *Nature Neuroscience* 1:36–41.
- Lev-Yadun S. 2009. Ant mimicry by Passiflora flowers? Israel Journal of Entomology 39:159–163.
- Londoño G. A., García D. A., Martínez M. A. S. 2015. Morphological and behavioral evidence of Batesian mimicry in nestlings of a lowland Amazonian bird. *American Naturalist* 185:135–141.
- Mackintosh N. J. 1971. An analysis of overshadowing and blocking. Quarterly Journal of Experimental Psychology 23:118–125.
- Mappes J., Alatalo R. V. 1997. Batesian mimicry and signal accuracy. *Evolution* 51:2050–2053.
- Maynard Smith J., Burian R., Kauffman S., Alberch P., Campbell J., Goodwin B., Lande R., Raup D., Wolpert L. 1985. Developmental constraints and evolution: a perspective from the Mountain Lake Conference on development and evolution. *Quarterly Review of Biology* 60:265–287.
- McGuire L., Van Gossum H., Beirinckx K., Sherratt T. N. 2006. An empirical test of signal detection theory as it applies to Batesian mimicry. *Behavioural Pro*cesses 73:299–307.
- McIver J. D., Stonedahl G. 1993. Myrmecomorphy: morphological and behavioral mimicry of ants. *Annual Review of Entomology* 38:351–377.
- Merrill R. M., Dasmahapatra K. K., Davey J. W., Dell'Aglio D. D., Hanly J. J., Huber B., Jiggins C. D., Joron M., Kozak K. M., Llaurens V., Martin S. H., Montgomery S. H., Morris J., Nadeau N. J., Pinharanda A. L., Rosser N., Thompson M. J., Vanjari S., Wallbank R. W. R., Yu Q. 2015. The diversification of *Heliconius* butterflies: what have we learned in 150 years? *Journal of Evolutionary Biology* 28:1417–1438.
- Molleman F., Whitaker M. R., Carey J. R. 2010. Rating palatability of butterflies by measuring ant feeding behavior. *Entomologische Berichten* 70:52–62.
- Nelson X. J. 2012. A predator's perspective of the accuracy of ant mimicry in spiders. *Psyche* 2012: 168549.
- Nelson X. J., Jackson R. R., Li D., Barrion A. T., Edwards G. B. 2006. Innate aversion to ants (Hymenoptera: Formicidae) and ant mimics: experimental findings from mantises (Mantodea). *Biological Journal of the Linnean Society* 88:23–32.
- Nesse R. M. 2005. Maladaptation and natural selection. Quarterly Review of Biology 80:62–70.
- Nilsson L. A. 1992. Orchid pollination biology. Trends in Ecology and Evolution 7:255–259.

- Nonacs P. 1985. Foraging in a dynamic mimicry complex. American Naturalist 126:165–180.
- 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.
- Oberling P., Bristol A. S., Matute H., Miller R. R. 2000. Biological significance attenuates overshadowing, relative validity, and degraded contingency effects. *Animal Learning & Behavior* 28:172–186.
- O'Hanlon J. C., Holwell G. I., Herberstein M. E. 2014. Pollinator deception in the orchid mantis. *American Naturalist* 183:126–132.
- Owen J., Gilbert F. S. 1989. On the abundance of hoverflies (Syrphidae). *Oikos* 55:183–193.
- Pasteur G. 1982. A classificatory review of mimicry systems. Annual Review of Ecology and Systematics 13:169– 199.
- Pavlov I. P. 1927. Conditioned Reflexes: An Investigation of the Physiological Activity of the Cerebral Cortex. London (United Kingdom): Oxford University Press.
- Pekár S. 2014. Is inaccurate mimicry ancestral to accurate in myrmecomorphic spiders (Araneae)? Biological Journal of the Linnean Society 113:97–111.
- Pekár S., Jarab M. 2011a. Life-history constraints in inaccurate Batesian myrmecomorphic spiders (Araneae: Corinnidae, Gnaphosidae). *European Journal* of Entomology 108:255–260.
- Pekár S., Jarab M. 2011b. Assessment of color and behavioral resemblance to models by inaccurate myrmecomorphic spiders (Araneae). *Invertebrate Biology* 130:83–90.
- Pekár S., Jarab M., Fromhage L., Herberstein M. E. 2011. Is the evolution of inaccurate mimicry a result of selection by a suite of predators? A case study using myrmecomorphic spiders. *American Naturalist* 178:124–134.
- Pekár S., Petráková L., Corcobado G., Whyte R. 2017a. Revision of eastern Australian ant-mimicking spiders of the genus *Myrmarachne* (Araneae, Salticidae) reveals a complex of species and forms. *Zoological Journal of the Linnean Society* 179:642–676.
- Pekár S., Petráková L., Bulbert M. W., Whiting M. J., Herberstein M. E. 2017b. The golden mimicry complex uses a wide spectrum of defence to deter a community of predators. *eLife* 6:e22089.
- Penney H. D., Hassall C., Skevington J. H., Abbott K. R., Sherratt T. N. 2012. A comparative analysis of the evolution of imperfect mimicry. *Nature* 483:461– 464.
- Penney H. D., Hassall C., Skevington J. H., Lamborn B., Sherratt T. N. 2014. The relationship between morphological and behavioral mimicry in hover flies (Diptera: Syrphidae). *American Naturalist* 183: 281–289.

- Pfennig D. W., Kikuchi D. W. 2012. Competition and the evolution of imperfect mimicry. *Current Zoology* 58:608–619.
- Pfennig D. W., Harcombe W. R., Pfennig K. S. 2001. Frequency-dependent Batesian mimicry. *Nature* 410: 323.
- Quicke D. L. J. 2017. *Mimicry, Crypsis, Masquerade and Other Adaptive Resemblances.* Hoboken (New Jersey): John Wiley and Sons.
- Ramesh A., Vijayan S., Sreedharan S., Somanathan H., Uma D. 2016. Similar yet different: differential response of a praying mantis to ant-mimicking spiders. *Biological Journal of the Linnean Society* 119: 158–165.
- Reiskind J. 1970. Multiple mimetic forms in an antmimicking clubionid spider. *Science* 169:587–588.
- Reiskind J. 1977. Ant-mimicry in Panamanian clubionid and salticid spiders (Araneae: Clubionidae, Salticidae). *Biotropica* 9:1–8.
- Rodd F. H., Hughes K. A., Grether G. F., Baril C. T. 2002. A possible non-sexual origin of mate preference: are male guppies mimicking fruit? *Proceedings* of the Royal Society B: Biological Sciences 269:475–481.
- Rothschild M. 1984. Aide mémoire mimicry. *Ecological Entomology* 9:311–319.
- Ruxton G. D., Schaefer H. M. 2011. Alternative explanations for apparent mimicry. *Journal of Ecology* 99: 899–904.
- Ruxton G. D., Sherratt T. N., Speed M. P. 2004. Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals, and Mimicry. Oxford (United Kingdom): Oxford University Press.
- Ruxton G. D., Allen W. L., Sherratt T. N., Speed M. P. 2018. Avoiding Attack: The Evolutionary Ecology of Crypsis, Aposematism, and Mimicry. Second Edition. Oxford (United Kingdom): Oxford University Press.
- Ryan M. J., Cummings M. E. 2013. Perceptual biases and mate choice. Annual Review of Ecology, Evolution, and Systematics 44:437–459.
- Ryan M. J., Fox J. H., Wilczynski W., Rand A. S. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature* 343:66–67.
- Shamble P. S., Hoy R. R., Cohen I., Beatus T. 2017. Walking like an ant: a quantitative and experimental approach to understanding locomotor mimicry in the jumping spider *Myrmarachne formicaria*. Proceedings of the Royal Society B: Biological Sciences 284: 20170308.
- Sheppard P. M. 1959. Natural Selection and Heredity. New York: Philosophical Library.
- Sherratt T. N. 2002. The evolution of imperfect mimicry. *Behavioral Ecology* 13:821–826.
- Sherratt T. N. 2003. State-dependent risk-taking by predators in systems with defended prey. *Oikos* 103:93– 100.
- Sherratt T. N. 2011. The optimal sampling strategy for unfamiliar prey. *Evolution* 65:2014–2025.

- Sherratt T. N., Peet-Paré C. A. 2017. The perfection of mimicry: an information approach. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372:20160340.
- Sherratt T. N., Whissell E., Webster R., Kikuchi D. W. 2015. Hierarchical overshadowing of stimuli and its role in mimicry evolution. *Animal Behaviour* 108:73– 79.
- Shettleworth S. J. 2010. Cognition, Evolution, and Behavior. Oxford (United Kingdom): Oxford University Press.
- Skelhorn J., Holmes G. G., Hossie T. J., Sherratt T. N. 2016. Multicomponent deceptive signals reduce the speed at which predators learn that prey are profitable. *Behavioral Ecology* 27:141–147.
- Skowron Volponi M. A., McLean D. J., Volponi P., Dudley R. 2018. Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of Southeast Asian rainforests. *Biology Letters* 14: 20180152.
- Smith S. M. 1975. Innate recognition of coral snake pattern by a possible avian predator. *Science* 187:759–760.
- Smith S. M. 1977. Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* 265:535–536.
- 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 B: Biological Sciences* 278:3566–3573.
- Stökl J., Brodmann J., Dafni A., Ayasse M., Hansson B. S. 2011. Smells like aphids: orchid flowers mimic aphid alarm pheromones to attract hoverflies for pollination. *Proceedings of the Royal Society B: Biological Sciences* 278:1216–1222.
- Straneck R. 1999. Una vocalización del pijuí común de cola parda, Synallaxis albescens (Aves, Furnariidae), es similar al sonido mecánico de advertencia de la víbora de cascabel, Crotalus durissus terrificus (Serpentes, Crotalidae). Revista del Museo Argentino de Ciencias Naturales nueva serie 1:115–119.
- Taylor C. H., Gilbert F., Reader T. 2013. Distance transform: a tool for the study of animal colour patterns. *Methods in Ecology and Evolution* 4:771–781.
- Taylor C. H., Reader T., Gilbert F. 2016. Why many Batesian mimics are inaccurate: evidence from hoverfly colour patterns. *Proceedings of the Royal Society B: Biological Sciences* 283:20161585.
- Terhune E. C. 1977. Components of a visual stimulus used by scrub jays to discriminate a Batesian model. *American Naturalist* 111:435–451.
- Thein T., Westbrook R. F., Harris J. A. 2008. How the associative strengths of stimuli combine in compound: summation and overshadowing. *Journal of Experimental Psychology: Animal Behavior Processes* 34:155–166.
- Thompson F. C., Vockeroth J. 1989. Family Syrphidae. Pages 437–458 in *Catalog of the Diptera of Australasian* and Oceanian Regions, edited by N. L. Evenhuis. Honolulu (Hawaii): Bishop Museum Press.

- Turner J. R. G. 1987. The evolutionary dynamics of Batesian and Muellerian mimicry: similarities and differences. *Ecological Entomology* 12:81–95.
- Vane-Wright R. I. 1980. On the definition of mimicry. Biological Journal of the Linnean Society 13:1–6.
- Vereecken N. J., Schiestl F. P. 2008. The evolution of imperfect floral mimicry. *Proceedings of the National Academy of Sciences of the United States of America* 105: 7484–7488.
- Vorobyev M., Osorio D., Bennett A. T. D., Marshall N. J., Cuthill I. C. 1998. Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* 183:621–633.
- Wang M.-Y., Vasas V., Chittka L., Yen S.-H. 2017. Sheep in wolf's clothing: multicomponent traits enhance the success of mimicry in spider-mimicking moths. *Animal Behaviour* 127:219–224.
- Ward P. S. 2007. Phylogeny, classification, and specieslevel taxonomy of ants (Hymenoptera: Formicidae). *Zootaxa* 1668:549–563.

- Wickler W. 1965. Mimicry and the evolution of animal communication. *Nature* 208:519–521.
- Wilson J. S., Jahner J. P., Williams K. A., Forister M. L. 2013. Ecological and evolutionary processes drive the origin and maintenance of imperfect mimicry. *PLOS ONE* 8:e61610.
- Wilson J. S., Jahner J. P., Forister M. L., Sheehan E. S., Williams K. A., Pitts J. P. 2015. North American velvet ants form one of the world's largest known Müllerian mimicry complexes. *Current Biology* 25: R704–R706.
- Wright S. 1988. Surfaces of selected value revisited. American Naturalist 131:115–123.
- Zuk M., Bastiaans E., Langkilde T., Swanger E. 2014. The role of behaviour in the establishment of novel traits. *Animal Behaviour* 92:333–344.

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