The Effect of Predator Population Dynamics on Batesian Mimicry Complexes

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Submitted December 11, 2020; Accepted September 29, 2021; Electronically published January 6, 2022

Online enhancements: appendixes.

ABSTRACT: Understanding Batesian mimicry is a classic problem in evolutionary biology. In Batesian mimicry, a defended species (the model) is mimicked by an undefended species (the mimic). Prior theories have emphasized the role of predator behavior and learning as well as evolution in model-mimic complexes but have not examined the role of population dynamics in potentially governing the relative abundances and even persistence of model-mimic systems. Here, we examined the effect of the population dynamics of predators and alternative prey on the prevalence of warning-signaling prey composed of models and mimics. Using optimal foraging theory and signal detection theory, we found that the inclusion of predator and alternative prey population dynamics could reverse traditional theoretical predictions: as alternative prey increase in numbers, mimics suffer because larger populations of predators are maintained, resulting in apparent competition. Under some circumstances, apparent competition affects model populations as well, although not as severely as it affects mimics. Our results bear on the intriguing puzzle that in nature warning signals are relatively scarce, yet experiments suggest that such signals can be highly advantageous. The availability of alternative prey and numerical responses by predators can overwhelm advantages observed in experiments to keep warning signals in model-mimic systems relatively scarce.

Keywords: warning signal, aposematism, apparent competition, signal detection theory, community ecology, dynamics.

Introduction

Prey have many strategies to avoid predation that can affect the connectivity of food webs. One is aposematism (Wallace 1867; Poulton 1890), wherein a defended prey species produces a signal that warns potential predators not to attack it. A related (and dependent) adaptation is Batesian mimicry, which occurs when an undefended prey species (the mimic) resembles an aposematic species (the model; Bates 1862; Ruxton et al. 2018), thereby co-opting protection from predators. Interestingly, although predators often limit prey populations (Hairston et al. 1960; Estes and Palmisano 1974; Paine 1974; Terborgh 2001), the effects of aposematism and mimicry on population dynamics and the potential reciprocal effects on the evolution of aposematism and mimicry have gone largely unexplored. Food web dynamics are guided in part by the flow of information, including honest and deceitful signaling (Dall et al. 2005; Vos et al. 2006; Holt 2007; Schmidt et al. 2010; Hein and Martin 2020). The question of how population dynamics are affected by predators' discrimination among prey thus lies at the interface of community ecology, sensory ecology, and cognitive ecology. There may be implications for conservation in some cases because the advantages conferred by Batesian mimicry may be critical to the persistence of certain threatened prey species (Valkonen and Mappes 2014; Umbers et al. 2020). Conversely, Batesian mimics at times may act as parasites that negatively affect vulnerable populations of their models (Charlesworth and Charlesworth 1975; Yamauchi 1993).

Some theory has examined the population dynamics of models and mimics in isolation (Yamauchi 1993; Kumazawa et al. 2006; Sekimura et al. 2017). However, populations of nonmimetic alternative prey in the community can influence these relationships. Alternative prey affect how predators make foraging decisions (Kokko et al. 2003;

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  https://doi.org/10.1086/718162

Lindström et al. 2004). Getty (1985) was the first to explore how alternative prey affect populations of models and mimics. His approach was novel in combining optimal foraging theory (Stephens and Charnov 1982) and the realistic assumption that predators may have imperfect prey discriminability (Sheppard and Duncan 1965; Oaten et al. 1975). This approach allowed him to determine the combination of models, mimics, and alternative prey that individual predators should attack to maximize nutritional rewards per unit time. Getty (1985) concluded that increasing the abundance of alternative prey released the mimicry complex from predation, allowing models and mimics to exist stably near their carrying capacities.

Getty's (1985) approach represented a major advance yet made the restrictive assumption that predator and alternative prey populations were fixed in size. In fact, one could interpret his study as featuring only a single predator individual with a saturating functional response to each prey in its diet (sensu Holling 1959). This accurately matches many laboratory experiments on mimicry (Lindström et al. 1997, 2004), where an individual predator feeds on an array of real or artificial prey. In such experiments, mimicry complexes are attacked less when the predator consumes alternative prey because such consumption dilutes predation on the models and mimics (a dilution effect; Lindström et al. 2004; Rowland et al. 2007; Kikuchi et al. 2019). Indeed, experiments often find an overwhelming advantage to warning signals versus cryptic prey (Gittleman et al. 1980; Roper and Redston 1987; Alatalo and Mappes 1996).

In contrast and somewhat puzzlingly, data from real communities indicate that both warning signals and mimicry are relatively rare (Mappes et al. 2014; Arbuckle and Speed 2015; Davis Rabosky et al. 2016; S. Strauss, personal communication). Elsewhere, we explore multiple potential reasons for this rarity, including constraints on the availability of defenses in the first place (Kikuchi et al. 2021*b*). Here, we examine the specific proposition that the dynamical feedbacks between populations of predators and their prey may help to resolve the discordance between laboratory studies showing that mimicry always wins and real communities where mimicry is rare. Our work fits within the larger realm of theory that incorporates foraging theory into community ecological interactions (Fryxell and Lundberg 1994; Křivan 1996; van Baalen et al. 2001; Holt and Kimbrell 2007; Kotler and Brown 2007; Valdovinos et al. 2013) and the even broader domain of behavioral theory that considers population dynamics (McNamara 2001; Kokko et al. 2006).

Our approach allows predator populations to vary dynamically as a function of individual foraging success. Individual predators still follow the adaptive foraging rules assumed by Getty (1985). However, when a predator population has the capacity to respond numerically to increases in its prey base, the dilution effect caused by alternative prey in Getty (1985) could be reversed because a larger predator population can be sustained on multiple prey species (i.e., apparent competition; Holt 1977; Holt and Kotler 1987; Holt and Bonsall 2017). Our study allows apparent competition to emerge in communities with a mixture of prey types, which collectively send a mixture of honest and dishonest signals to their predators. This allows us to identify when apparent competition decreases the abundances of warning-signaling prey and when it does not. We suggest examples of real communities that may fall into these two situations.

Theoretical Approach

We developed a theoretical framework based on Getty (1985),[1] following his assumptions about the rules governing adaptive foraging by individual predators and logistic population growth in both the model and mimic species. However, we additionally used equations that let the predator respond numerically to its prey and let the alternative prey vary dynamically too (so predator populations would not grow unbounded; see details below and in app. A; apps. A, B are available online).

We assumed that predators (of density P) attacked alternative prey (density n), mimics (density c, for copy), and models (density m) adaptively—that is, they altered their attacks in a way that tended to increase their rate of energy intake per unit time (Holling 1965; Getty 1985; Stephens et al. 2007). The predator benefits from consuming mimics and ignoring models. When models and mimics each vary continuously in appearance yet some mimics look more like models than others (in other words, their appearances have partially overlapping distributions), mimicry is imperfect: the predator cannot reliably distinguish the two. Getty (1985) had the insight that if mimicry were imperfect, members of the mimicry complex could be added to the predator's diet in a probabilistic way according to signal detection theory. The predator could adaptively alter its diet by becoming more or less selective in attacking a prey item that could turn out to be either a model or a mimic, constrained by its ability to distinguish the two. Less selective behavior resulted in more frequent attacks on mimics that the predators encountered, but also on many models. More

1. Terminological note: we use "model" to refer to a defended species in a Batesian mimicry complex; in lieu of the usage of "model" for systems of equations (and attendant assumptions), we use alternative locutions, such as "system" and "theory."

selective behavior resulted in attacks on only prey that look least like the typical model. Selective behavior reduced a predator's attack rate on both models and mimics, yet the ratio of mimics to models in its diet increased. Therefore, by becoming more selective, a predator increased the average value of prey consumed per attack but at the opportunity cost of passing up many mimics it could have captured. This approach assumes that predators are fully informed about the distribution of prey phenotypes, which is unlikely for real predators in nature, especially in systems where predators encounter few warning-colored prey during their lifetimes. Despite this assumption, however, signal detection theory has been highly successful in predicting predator behavior in laboratory experiments with artificial prey (Sheppard and Duncan 1965; McGuire et al. 2006; Kikuchi et al. 2015) and in real empirical systems (Harper and Pfennig 2007; Iserbyt et al. 2011; Penney et al. 2012).

Determining how selective the predator should be is a problem of maximizing the value of the prey it consumes per unit time. In the terminology of signal detection theory, a predator that correctly attacks a mimic has made a "hit," while incorrectly attacking a model is termed a "false alarm" (Swets et al. 1961; Egan 1975). The probability of a hit is p_c (the probability of attack given that a mimic is encountered), while the probability of a false alarm is p_m (the probability of attack given that a model is encountered). In our equations, following Getty (1985), the function that describes the relationship between these probabilities is $p_c = p_m^k$ with $k \in [0, 1]$. When $k = 0$, there is no mimicry (predators are able to distinguish all mimics from models), so the mimic should always be attacked and the model always rejected (assuming that the mimic is profitable to include in the diet and the model is not). If $k = 1$, mimicry is perfect: the predator should treat all mimics and models alike, attacking or rejecting the entire mimicry complex in an all-or-nothing manner ($p_c = p_m = 0$ or 1), given that it cannot tell models and mimics apart. However, for $0 < k < 1$, mimicry is imperfect and the inequality $p_c > p_m$ holds. Over this range, as k increases from 0 to 1, the predator has increasingly more difficulty discriminating a mimic from a model. Getty's predator often selects a value of p_c (and hence p_m) that leads to attacks on only some individuals of the mimic and model species. Higher p_c results in attacking more mimics overall, while lower p_c results in a higher ratio of mimics to models attacked (i.e., p_c/p_m is higher). The optimum p_c is usually an intermediate value, found by maximizing the prey value obtained from foraging per unit time,

$$\frac{S(xnV_n + cp_cV_c + (1-\sigma)mp_mV_m)}{1 + S[xnH_n + cp_cH_c + mp_m(\sigma H_{ms} + (1-\sigma)H_{me})]}, \tag{1}$$

which corresponds to equation (1) in Getty (1985) when there is a single alternative prey species in addition to models and mimics. Expression (1) generalizes the familiar disk equation (Holling 1959). Here, S is the predator's search rate, n is the density of alternative prey, and V_n and H_n are the value and handling time for alternative prey, respectively, while V_c and H_c are the value and handling time for a mimic, respectively, and V_m is the value of a model. Unlike Getty (1985), we allowed models to sometimes survive an attack by the predator, with the probability of survival given by σ, with separate handling times if the model survives (H_{ms}) or is eaten (H_{me}). Even if the predator rejects a prey item, it will nonetheless have invested some time in chasing it, but if it consumes that prey, additional time may be needed. When solving our differential equations numerically, predators maximized the function in expression (1) on the basis of prey densities at each time step by inclusion or exclusion of the alternative prey (here represented by the binary indicator variable $x \in \{0, 1\}$) and by selecting p_c (which determines p_m). For comparison with other signal detection models, see Holen and Sherratt (2021).

We used expression (1) as the predator's birth rate (which assumes that prey value is measured in units of predator births). The predator also had an intrinsic death rate of μ_P. To allow us to capture density dependence among predators, we included the term $-fP$ in the per capita predator growth rate (although in most of our simulations we set $f = 0$). With these assumptions, the predator population dynamics were governed by

$$\frac{dP}{dt} = P\left(\frac{S(xnV_n + cp_cV_c + (1-\sigma)mp_mV_m)}{1 + S[xnH_n + cp_cH_c + mp_m(\sigma H_{ms} + (1-\sigma)H_{me})]} - \mu_P - fP\right). \tag{2}$$

We assumed that mimic and model population dynamics were similar to those in Getty (1985). Mimics and models had intrinsic growth rates r_c and r_m, with carrying capacities K_c and K_m, respectively. They also suffered mortality from predators proportional to their representation in the predator's diet, given by cp_c and mp_m. When we assumed competition between models and mimics, we used a Lotka-Volterra type expression, with parameters α_{cm} and α_{mc}, respectively, for the model's effect on the mimic and vice versa. The population dynamic equations for mimics and models were then, respectively,

$$\frac{dc}{dt} = r_c c\left(\frac{K_c - c - \alpha_{cm}m}{K_c}\right) - \frac{SPcp_c}{1 + S[xnH_n + cp_cH_c + mp_m(\sigma H_{ms} + (1-\sigma)H_{me})]}, \tag{3}$$

$$\frac{dm}{dt} = r_m m\left(\frac{K_m - m - \alpha_{mc}c}{K_m}\right) - \frac{(1-\sigma)SPmp_m}{1 + S[xnH_n + cp_cH_c + mp_m(\sigma H_{ms} + (1-\sigma)H_{me})]}. \quad (4)$$

We note that Getty (1985) did not include the denominators in the predation terms of equations (3)and (4), which are needed if one assumes that predators do not search while handling prey. The above expressions follow the form of familiar predator-prey equations (e.g., Rosenzweig and MacArthur 1963).

Getty (1985) assumed that multiple alternative prey species are present; for simplicity, we have just one alternative prey. Getty (1985) further assumed that alternative prey had fixed abundances. However, when the predator population is dynamic (with $f = 0$) and alternative prey are fixed and abundant, the predator population can grow in an unlimited fashion. A realistic system requires alternative prey numbers be reduced because of predation. In the main text we use a chemostat model for alternative prey, which can be depleted by predation but not eliminated. Our interest is in the model and mimic, not the conditions for coexistence of a suite of alternative prey (Holt 1977). In appendix A we examine different assumptions about prey recruitment (e.g., all prey species might have logistic growth). Qualitatively, the patterns we report below are sustained across these scenarios.

In particular, alternative prey entered the system at a constant rate D from a reservoir of density n_0 and also left the system at rate D. Such chemostat dynamics could also describe a system in which undefended cryptic insects emerge and die continuously throughout the year or baitfish swim into a coral reef (which host many mimicry rings; Cheney 2010; Winters et al. 2017). Although at first glance this may appear unrealistic, in even the simplest real systems alternative prey comprise many species with alternative modes of resource acquisition, competitive relationships, and spatiotemporal niche partitioning. Thus, chemostat dynamics in which the rate of alternative prey input is—at least on some scales—independent of alternative prey density and of predation may be a reasonable starting point. The chemostat assumption has the practical advantage that the alternative prey cannot become extinct. Also, constant recruitment tends to be stabilizing (Holt 1993), and it requires only one additional parameter (D). In our system, alternative prey suffered mortality from predators (assuming they were attacked) in proportion to the predator and alternative prey densities and the search rate, reduced by the fraction of time that predators spend handling prey. The dynamics of the alternative prey population were thus

$$\frac{dn}{dt} = D(n_0 - n) - \frac{SPxn}{1 + S[xnH_n + cp_cH_c + mp_m(\sigma H_{ms} + (1-\sigma)H_{me})]}. \quad (5)$$

A complete list of the variables and parameters used in this study is in table 1.

We numerically investigated equations (2)–(5) using a fixed-step-size second-order Runge-Kutta algorithm. We assumed that the predator could continuously adjust its behavior (p_c and x). Therefore, we used a small step size (0.02 time units) and chose p_c and x by maximizing expression (1) each time the right sides of equations (2)–(5) were evaluated (twice per time step). To maximize the function, we evaluated it at 10,001 equally spaced values of p_c between 0 and 1, both with and without the alternative prey, and chose p_c and x giving the largest value. We ran the simulations for 500 time units (usually starting with $n = n_0$, $m = 10$, and $c = 1$, as in Getty 1985), which allowed populations either to reach constant (equilibrium) densities or to become periodic. For results given below, constant final densities were reached unless otherwise indicated.

We began by analyzing the system with parameter values from Getty (1985) to explore how incorporating predator population dynamics might alter his results. Then we examined parameter values that correspond to a range of biologically relevant scenarios. Therefore, to begin, alternative prey had a value $V_n = 0.7$ and a handling time $H_n = 0.84$, and their input density was $n_0 = 20$ (close to the combination of the three most valuable prey examined in Getty 1985). Mimics were assumed more valuable than alternative prey ($V_c = 1$, $H_c = 1$), and models gave no fitness benefit (or cost) while conferring a small handling time penalty ($V_m = 0$, $H_{me} = 0.2$; models were not allowed to survive attacks in Getty 1985, so $\sigma = 0$, and H_{ms} was irrelevant). Predators that incorporated mimics into their diets incurred an opportunity cost for doing so because they sometimes attacked time-wasting models (Getty 1985). For the system of equations (2)–(5) with $f = 0$, a prey item was present in the predator's diet at equilibrium if and only if $V_i/H_i > \mu_P$ (see, e.g., Holt 1983). We used $\mu_P = 0.75$ so that the alternative prey were always included in the predator's diet at equilibrium (because $V_n/H_n = 0.833$) and all mimics would be included if there were no models ($V_c/H_c = 1$). The encounter rate with all types of prey was $S = 1$, and we set $f = 0$ so predators were not self-regulating. Also, as in Getty (1985), growth rates and carrying capacities for mimic and model populations were assumed equal: $r_c = r_m = 2$, $K_c = K_m = 10$. Differences in prey abundance thus entirely reflect different realized attack rates. We used $k = 0.5$ so

Table 1: Variables and parameters used in this study

Term	Type	Description
P	Variable	Predator density
μ_P	Parameter	Fixed predator death rate
S	Parameter	Predator search rate
n	Variable	Alternative prey density
n_0	Parameter	Density of alternative prey entering the system
D	Parameter	Rate of alternative prey influx and efflux
x	Variable	Indicator variable: 1 if alternative prey is in the diet, 0 if not
V_n	Parameter	Fitness value of consuming one alternative prey
H_n	Parameter	Time to handle one alternative prey
c	Variable	Mimic density
p_c	Variable	p(hit) = probability a mimic is eaten after encounter
r_c	Parameter	Intrinsic mimic growth rate
K_c	Parameter	Mimic carrying capacity
V_c	Parameter	Fitness value of consuming a mimic
H_c	Parameter	Time to handle a mimic
k	Parameter	Mimic-model resemblance [0, 1]
m	Variable	Model density
p_m	Variable	p(false alarm) = p_c^k = probability a model is attacked after encounter
r_m	Parameter	Intrinsic model growth rate
K_m	Parameter	Model carrying capacity
V_m	Parameter	Fitness value of consuming a model
σ	Parameter	Fraction of models that survive attacks
H_{me}	Parameter	Handling time of models that are eaten
H_{ms}	Parameter	Handling time of models that survive
α_{mc}	Parameter	Competitive effect of mimics on models
α_{cm}	Parameter	Competitive effect of models on mimics
f	Parameter	Density-dependent term for predator population change

that mimicry was fairly good but mimics could still be discriminated from models with reasonable accuracy (below, we consider higher values of k as well as differences between r_c and r_m). To assess the effect of apparent competition on the abundance of the model and mimic, we steadily increased the rate at which alternative prey entered the system (D).

Once we had explored this basic set of parameter values that matched the assumptions of Getty (1985), we perturbed them in ecologically relevant directions (table 2). First, we decreased the benefit of attacking models so that it was strongly negative ($V_m = -1$), implying a cost to predators beyond wasting time. For example, coral snakes have venom that subdues their prey (Roze 1996) but is also dangerous enough to seriously injure or kill their own predators (Brugger 1989). Some predators have even evolved innate aversions to coral snakes (Smith 1975, 1977), suggesting that coral snakes have a negative fitness value for them. Second, we set $\sigma = 0.5$ so models could sometimes survive attack and assumed separate handling times for surviving ($H_{ms} = 0.2$) versus eaten ($H_{me} = 1$) models. This scenario was inspired by Guilford (1994), who suggested that warning signals alert predators that they should "go slow" when attacking so that they will have time to assess prey defenses before committing fully. Go-slow behavior could depress the abundance of Batesian mimics, since models survive attacks while mimics do not (Svennungsen and Holen 2007; Halpin and Rowe 2010). Third, we increased the handling time of models to equal that of mimics—in other words, predators had to pay up front to learn about prey profitability. Fourth, we examined the potential influence of interspecific competition between models and mimics. Fifth, we allowed predators to exhibit direct density-dependent self-regulation by increasing f. In addition, we explored the sensitivity of our results to different values of alternative and mimetic prey as well as to changes in mimetic precision.

Effects of Alternative Prey and Other Ecologically Relevant Parameters

With the basic set of parameter values from Getty (1985), increasing the influx of alternative prey into the system amounted to providing an energy supplement to predator populations, boosting predator numbers (fig. 1*A*). At low influx rates model populations suffered as the influx rate

Table 2: Ecologically relevant parameter values of our equations, with their effects on apparent competition with alternative prey

Parameter change	Predator selectivity (p_c)	Net effect of apparent competition on		Ecological context(s)	Reference(s)
		Models	Mimics		
$.0 < D < .6$	Increases with D	Increases with D	Increases with D	Early-season temperate lepidopteran assemblages	Mappes et al. 2014
$.6 < D$	Increases with D	Decreases as D increases	Increases with D	Many tropical lepidopteran assemblages where local morphs of aposematic butterflies are well defended and Batesian mimics are rare	Benson 1972; Mallet and Barton 1989; Kapan 2001; Merrill 2012; Arias 2016; Finkbeiner et al. 2017, 2018
$V_m \downarrow$	Increases	Increases	Increases	Highly defended butterflies, beetles, or venomous snakes	Brower and Moffit 1974; Brugger 1989; Rowell-Rahier et al. 1995
$H_{me} \uparrow$	Increases	Increases	Increases	Mimicry of gelatinous zooplankton by nutritious fish larvae	Greer et al. 2016
$\sigma \uparrow$	Increases	Increases	Increases	Widespread but best studied in Neotropical Lepidoptera and with a higher value among predators that frequently sample butterflies	Chai 1986; Pinheiro 1996, 2003; Langham 2004; Pinheiro and Campos 2019
α_{cm}, $\alpha_{mc} \uparrow$	Increases	Decreases	Increases	Undocumented but postulated in butterflies and snakes	Pfennig and Kikuchi 2012; Kumazawa et al. 2006
$f \uparrow$	Decreases	Decreases	Decreases	Territorial avian predators	Terborgh et al. 1990; Thiollay 1994; Robinson et al. 2000; Kattan et al. 2013

Note: Arrows indicate direction of parameter change that we explored relative to the initial parameters based on Getty (1985).

increased, but at higher influx rates they benefited (fig. 1*A*; table 2). Mimics experienced consistently negative effects from increases in influx rate (fig. 1*A*; table 2).

To understand why models and mimics experienced different effects from higher influx rates, it is helpful to examine impacts on p_c (fig. 1*B*). The probability of an individual predator attacking a mimic on encounter (p_c) actually decreased with the availability of alternative prey—why take risks when you do not have to? But because there were so many more predators, the overall consumption rate of mimics (proportional to Pp_c) nevertheless increased. In other words, when alternative prey were more abundant, each individual predator became more discriminating, attacking only increasingly poor mimics. Yet mimics suffered greater total predation because the abundance of these discriminating predators was so high. Models

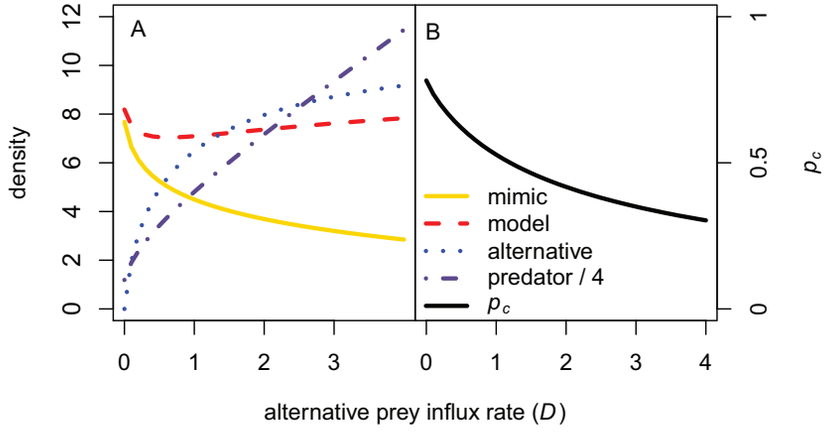

Figure 1: Abundance (density) of all four species (*A*) and probability that an encountered mimic was attacked (p_c; *B*) plotted against the alternative prey influx rate.

experienced a smaller penalty because a decrease in p_c results in a much greater decrease in p_m (because $p_m = p_c^{1/k}$). Note that mimics always benefitted from resembling models; although mimics suffered as alternative prey increased, this increase in predation was less than it would have been were the mimic not part of a mimicry complex.

The relationship between equilibrium model (and mimic) density and influx rate D was thus governed by the balance between two different processes. When the relationship was negative, apparent competition dominated (Holt 1977). Alternative prey supplemented the diet of the predator so that the latter increased in population size. When the relationship was positive, apparent competition was still present, but its effect was smaller than the behavioral effect of the predators becoming more selective as the influx of alternative prey increased. For mimics, apparent competition was always the predominant phenomenon—increasing the influx of alternative prey consistently decreased mimic populations. This result is striking because it produces a prediction contrary to previous work on how alternative prey affect model-mimic dynamics (Getty 1985; Lindström et al. 2004). Rather than benefitting Batesian mimics, alternative prey can increase attack rates because the effect of apparent competition is stronger than the combined impacts of dilution and increases in individual predator selectivity.

Shifting the value, survival probability, or handling time of models (V_m, σ, or H_{me}, respectively) each had very similar effects (fig. 2; table 2). Mimics continued to suffer from apparent competition with alternative prey, although mimic populations were higher than for the basic Getty (1985) parameter values (fig. 2*A*). Model populations were also consistently higher, although they also consistently suffered—although to a lesser degree than mimics—from apparent competition (fig. 2*B*). Predators' optimal probability of attack on mimics (p_c) was lower (fig. 2*C*). This occurred because models provided a greater umbrella of protection around the mimicry complex.

Competition between mimics and models (positive α_{cm}, α_{mc}) caused models to benefit from increasing the abundance of alternative prey over the entire range of influx rates that we explored (i.e., dilution outweighed apparent competition). The mimics, by contrast, suffered to a greater degree from apparent competition with alternative prey (fig. B1; figs. A1, A2, B1–B4 are available online). Introducing predator density dependence (positive f) reduced the effects of apparent competition on both models and mimics (fig. B1), as expected from general theory (Holt 1977). We also examined sensitivity to V_n/H_n and V_c/H_c, which respectively determine the suitability of alternative prey and mimics for the predator's diet. Alternative prey are excluded from the diet at equilibrium if $V_n/H_n < \mu_P$ (predator death rate). As V_n/H_n increases above μ_P, the effects of apparent competition become more severe for the mimic because although the predators become more discriminating, the predator population is boosted in numbers (fig. B2). At the same time, models switch from experiencing apparent competition to the benefits of the dilution effect (fig. B2). As with alternative prey, the mimicry complex is excluded from the predator's diet if $V_c/M_c < \mu_P$, but if V_c/M_c is even slightly greater than μ_P, the mimicry complex is adopted into the diet and mimics begin to experience apparent competition (fig. B3). More details are given in appendix B.

The alternative prey influx rate impacted community structure: as the influx rate of alternative prey increased, warning-signaling prey (models + mimics) became a smaller proportion of all prey (fig. B1). This held true when models and mimics competed with each other and when predators were self-limiting.

Improvements to Mimetic Precision (Higher k)

Imperfect mimicry is a pervasive feature of natural prey phenotypes (Holling 1965; Edmunds 2000; Kikuchi and Pfennig 2013; Sherratt and Peet-Paré 2017; Ruxton et al. 2018; McLean et al. 2019). The value of $k = 0.5$ that we used above is a reasonable starting point for new theory on many natural mimicry systems. The precision to which mimicry evolves may be limited by selective trade-offs (Holen and Johnstone 2004; Pfennig and Kikuchi 2012) or by developmental constraints (Kikuchi and Pfennig 2013). In the absence of such factors constraining the evolution of mimicry, however, natural selection on mimics should result in their continual improvement as long as better resemblance to models reduces predation (Nur 1970; Holmgren and Enquist 1999; Sherratt 2002; Franks et al. 2009). For example, highly precise, near-perfect mimicry is found in some lepidopteran systems (Deshmukh et al. 2017). In other cases, imperfect mimics probably persist because the relevant predators are unable to distinguish them from models, so they are effectively perfect (e.g., Dittrich et al. 1993; Kikuchi and Pfennig 2010; Pekár and Jarab 2011; Penney et al. 2012; Pekár et al. 2017). These observations led us to consider higher values of k and the consequences that they have for the dynamics of mimicry complexes.

As mimicry became more perfect, predator responses to them became more stepwise. When mimicry was merely good ($k = 0.7$) with other parameters as in Getty (1985), the system interestingly developed unstable dynamics at intermediate influx rates before recovering stability at high influx rates (fig. 3). When $k = 1$, predators incorporate the mimicry complex into their diets in an all-or-nothing fashion. At equilibrium, a predator should

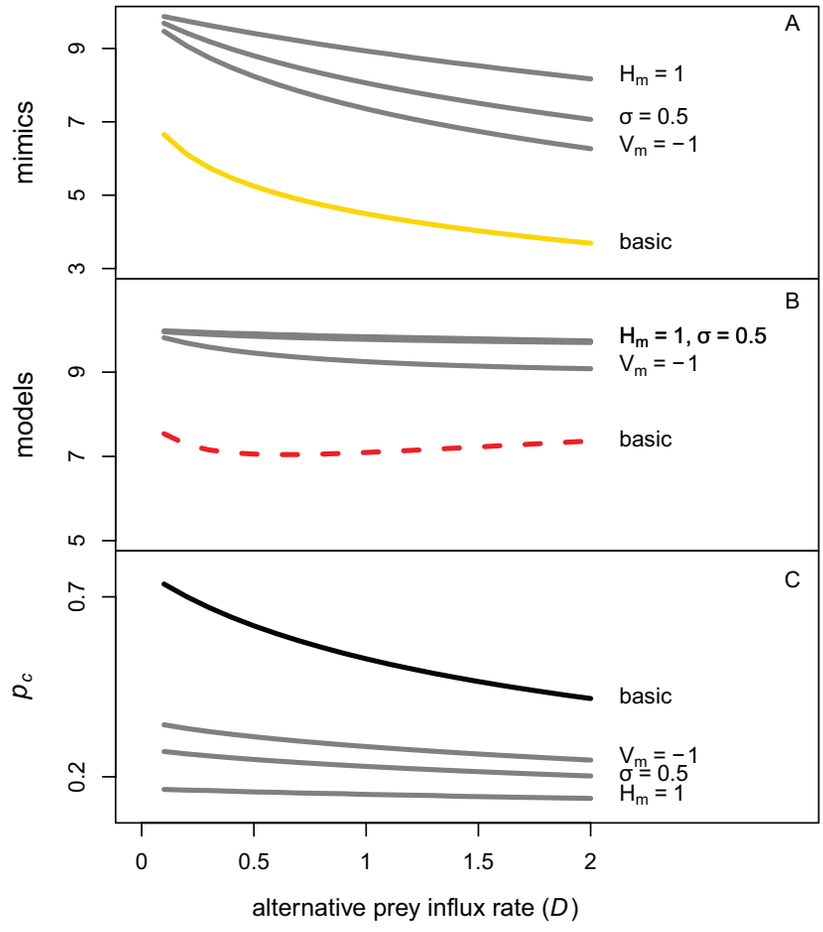

Figure 2: Effects on mimic abundance (*A*), model abundance (*B*), and p_c (*C*) of increasing model handling time ($H_m = 1$), conferring negative benefits on models ($V_m = -1$ and H_m at the baseline value of 0.2) and allowing models to survive attacks 50% of the time ($\sigma = 0.5$, $H_{me} = 1$, $H_{ms} = 0.2$).

include them in its diet if their average value over handling time is greater than the predator death rate:

$$\frac{mV_m + cV_c}{mH_m + cH_c} > \mu_P. \tag{6}$$

If the model and mimic have the same r and K and are attacked at the same rate, then they will have the same density, and inequality (6) reduces to

$$\frac{V_m + V_c}{H_m + H_c} > \mu_P. \tag{7}$$

Given the parameter values from Getty (1985), the left-hand side of inequality (7) equals 0.83, which means the mimicry complex was always included in the diet at equilibrium (because we assumed $\mu_P = 0.75$ in all our simulations). With no alternative prey, predators could not drive models and mimics extinct even if they are always attacked because predator densities were limited by model and mimic availability (left side of the upper right panel of fig. 3). However, models and mimics can be driven extinct when predators include the mimicry complex in their diets if predator populations are supplemented by alternative prey (right side of the upper right panel of fig. 3). Although this is the first theory, to our knowledge, to show this when predators are sustained by apparent competition, the conclusion that precise mimicry can lead to the entire mimicry complex collapsing is by now a standard theoretical result (expressions conceptually similar to ineq. [6] have been found multiple times; Oaten et al. 1975; Getty 1985; Johnstone 2002). Note that this does not mean the mimicry complex will become extinct—it might not, such as when the complex is completely ignored or sometimes when mechanisms exist to allow models to survive attack (e.g., predators might show go-slow behavior; Guilford 1994).

To better characterize conditions in which mimicry complexes persist, we varied the intrinsic per capita rate

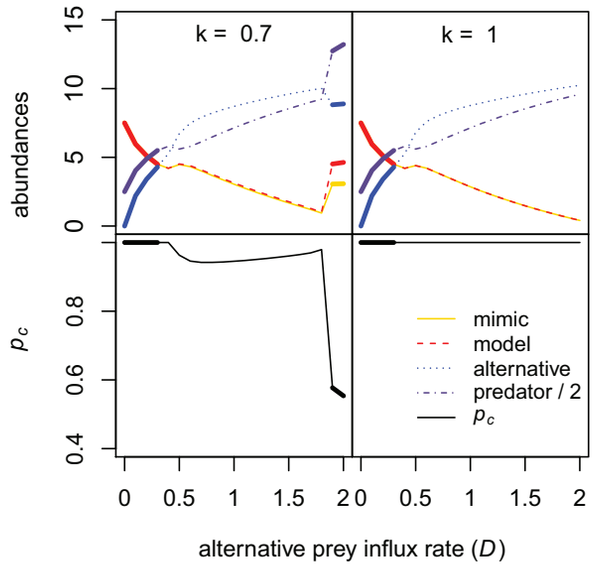

Figure 3: When $k = 0.7$ (good mimicry) and influx rates are low, $p_c = 1$, so all mimics and models were attacked. This region coincided with stable population dynamics (thick lines; colors the same as in fig. 1). At higher D, stable dynamics broke down (thin lines represent the mean of cyclic oscillations) before recovering at very high D. When $k = 1$ (perfect mimicry; colors and styles the same as in fig. 1), models and mimics were always attacked, yet cyclic dynamics still ensued for $D > 0.3$, with model and mimic average densities decreasing with increasing D.

of increase for mimics (r_c) over values greater than the intrinsic per capita rate of increase for models (r_m was always equal to 2). This would be reasonable if the mimic does not have to use resources to produce a defense or if it has a higher rate of increase on the margin of the model's range. Higher mimic growth rates reduce the effect of predation on their density, so predators can continue to attack them with a high probability—and therefore the probability of attacking models also remains high. We found in some cases that extinction occurs. See figure B4 for an example where mimics drive models extinct. In other cases (i.e., $\sigma = 0.5$, $V_m = -1$, and $H_{me} = 1$), models provided enough disincentive to predators that the entire mimicry complex was ignored and so excluded from the predator's diet. As a consequence, perfect mimicry allowed model and mimic populations to move to their carrying capacities.

The quantitative details of the above results and the patterns shown in the figures reflect the particular assumptions we made about prey recruitment—logistic growth for the model and mimic and chemostat-like recruitment for alternative prey. We explored versions of the equations in which all prey had chemostat-like recruitment on the one hand or logistic growth on the other. We report some representative findings in appendix A. Most qualitative patterns are retained except that the model only benefited slightly from increasing alternative prey. Our overall conclusions are thus robust to various assumptions about prey dynamics.

Discussion

There is a rich literature on how generalist predators influence the abundance and dynamics of alternative prey. But as a recent review by Holt and Bonsall (2017) notes, there has been little attempt to date to link this issue in community ecology with the evolutionary ecology of mimicry. This study is a step toward combining these two distinct bodies of literature. We have shown that an influx of alternative prey to prey-limited populations of generalist predators can cause mimics—and in some situations, models—to suffer from apparent competition. This result could describe how populations of warning-colored prey respond across a spatial or temporal gradient that governs the productivity or influx rate of alternative prey. In Finland, warning-colored lepidopteran larvae time their emergence so that it does not coincide with the emergence of cryptic lepidopteran larvae (Mappes et al. 2014). This suggests a kind of temporal character displacement in phenology to reduce apparent competition that may change the proportion of warning-signaling prey in the community (see fig. B1).

This study shows how incorporating the dynamics of predator and alternative prey populations into mimicry theory can produce more complex relationships between prey species than earlier theory that assumed a fixed number of predators (table 2). Our study provides new predictions on the relationship between so-called mimetic load and predator attack rates on Batesian mimicry complexes. Mimetic load refers to the ratio of mimics to models. High mimetic loads have long been considered a burden on model populations that might increase the attack rates they experience, a kind of parasitism (Fisher 1930; Nur 1970; Franks et al. 2009; Akcali et al. 2018). In our study, when mimetic loads are highest, p_c is also highest, so more mimics (and potentially models) are indeed attacked (figs. 1, 2). There is evidence to support higher attacks on mimics when mimetic loads are high in butterflies (Kristiansen et al. 2018) and in snakes (Pfennig et al. 2007). Interestingly, however, as models became better protected, p_c decreased *and* mimic abundance increased (fig. 2; model abundance also slightly increased). This occurred because the superior function of antipredator defenses in the models allowed more mimics to obtain protection (Brower and Brower 1962; Oaten et al. 1975; Sherratt 2002). Therefore, it is possible that mimetic load and the degree of protection afforded to members of a mimicry complex can both increase over a gradient of antipredator defenses—in other words,

having a high mimetic load may actually be a characteristic of exceptionally stable mimicry complexes (a potential example might be coral snake mimicry complexes in Costa Rica, where models are well protected despite the presence of several Batesian mimics; Brodie 1993; Hinman et al. 1997).

Our theory, we suggest, also implies something interesting about factors that limit the population sizes of Batesian mimics. Mimicry may often evolve to the point where it is, in effect, perfect (Cuthill and Bennett 1993; Penney et al. 2012; Kikuchi and Pfennig 2013; Sherratt and Peet-Paré 2017; McLean et al. 2019), sometimes making imperfect mimicry evolutionarily transient. Indeed, apparent competition could hasten the evolution of more precise mimicry because it elevates predation pressure on Batesian mimics and makes predators more discriminating. When predators can no longer distinguish models from mimics, our results predict that the whole mimicry complex will be either attacked or avoided. This will depend on the relative abundance of models and mimics and the relative costs and benefits of attacking each (see ineq. [6]). This result has been found many times (e.g., Oaten et al. 1975; Getty 1985; Johnstone 2002; Sherratt 2002). However, what has been less obvious is that if mimic populations are not as constrained—relative to the model population—by demographic rates (r or K), mimics can increase to the point where the predator will always attack the mimicry complex. This can even lead to the extinction of models and/or mimics, and the mimicry complex ceases to exist as such (although such an outcome might be less likely if models sometimes survive attacks). Perhaps more significantly, the theory presented here predicts that when mimicry is at least functionally perfect and leads to complete avoidance of both models and mimics, the type of predators we considered here cannot be the ecological agents that limit mimic populations. Instead, populations of perfect mimics must be held in check by other factors, such as food availability, intraspecific density dependence, or specialist predators. This idea was suggested by Nicholson (1927) on the basis of the natural history of Lepidoptera, and the present study lends theoretical support to his verbal argument. Of course, when mimicry does not function to deter attacks (i.e., $p_c = 1$, as in the right side of fig. 3), predators can limit mimics, but then it is not fair to call it a warning signal.

In natural systems, to estimate the importance of apparent competition in regulating the numbers of models and mimics, particular data are key. First, we need to know whether warning signals actually function to deter predation in the wild: the model's phenotype must be compared with a cryptic alternative prey, an allopatric warning signal, or a novel warning signal (depending on the specifics of the system and question). Second, the relative protection of the local model versus a local Batesian mimic is needed to estimate predator discrimination (i.e., how p_m relates to p_c). To determine where this lies in the wild, a field experiment could be used, or if abundances of models and mimics are known, their frequencies could be replicated in the laboratory to measure predator behavior there. Then the hard part begins: is there a positive correlation between the abundance of alternative prey and the abundance of predators? For Finnish Lepidoptera larvae, this appears to be true in springtime (Mappes et al. 2014). If this is true, how does it affect predator behavior toward models and mimics, and is there a negative correlation between the alternative prey and Batesian mimics? In Finnish Lepidoptera, attack rates on warning-signaling prey rise with the influx of alternative prey and the proportion of warning-signaling prey drops, suggesting that apparent competition does indeed limit their prevalence (Mappes et al. 2014).

How likely is it that apparent competition plays an important role in the regulation of warning-signaling species across space, time, and phylogeny? Our lack of data—especially from nonlepidopteran systems—makes that a hard thing to estimate. Most natural communities have abundant alternative prey, which is the most important prerequisite. At the same time, however, density-dependent regulation of predators (and predation on them by organisms of higher trophic levels) also seems likely (table 2). In those cases, Getty's (1985) predictions might better characterize the system (see app. B for analysis). Getty's (1985) one-predator model and scenarios where predators have an unlimited numerical response (either through reproduction, as we explored here, or through movement and aggregation; Holt and Kotler 1987) are two limiting cases of a continuum of effects that alternative prey have on mimicry complexes. Direct density dependence in the predator weakens the predator numerical response and, hence, the strength of apparent competition, so predators with moderate density-dependent self-regulation fall somewhere in the middle of this continuum. Thus, the impact of alternative prey on mimicry complexes could depend on where in the food web the predators exerting selection on prey are found as well as on crucial details of predator natural history. In general, our theory with three prey and a predator forms a "module" of interactions in a community (sensu McPeek 2019) whose dynamics will be affected by populations of other species in the trophic network. In other words, the influence of apparent competition on warning signals could thus be "dialed" up or down depending on network connections.

There are ecological factors that are not included in this article that we need to understand to explain the population ecology of mimicry. We need information about the factors that limit populations of both models and mimics, which is a role that might be filled by specialist predators

(meaning those that are undeterred by model defenses; Endler and Mappes 2004). There is evidence that aposematic European adders are subjected to predation by specialist snake-eating buzzards (Valkonen et al. 2012), and these predators could also very well attack their mimics (Valkonen and Mappes 2014). Spiders that mimic ants can also easily fall victim to ant-specialist spiders (Pekár et al. 2011). However, whether these specialist predators cause population limitation is unclear. Nicholson (1927) gives anecdotal evidence for positive density-dependent predation on the larvae of warning-colored Lepidoptera, but the generality of this mechanism is unknown. In pine sawfly larvae at least, more larvae are killed in large aggregations (50 individuals) than in small ones (10 individuals; Lindstedt et al. 2011). Important additional factors that we have not considered include prey evolution, the effect of predator learning or search image formation, the conspicuousness of warning signals, and spatial effects. Predator learning could make apparent competition with alternative prey stronger for models, since larger predator populations might make more total mistakes. We also note that there are mimicry systems where predator aversions toward warning signals are innate and follow the predictions of signal detection theory (e.g., Smith 1975, 1977; Harper and Pfennig 2007).

Finally, we need to know more about patterns of variation in warning signals across communities (Kikuchi et al. 2021*b*). For the vast majority of taxa and regions, our only source of records comes from poring over field guides. There are at least three dimensions of warning signals of interest: their representation among species, their relative abundance as distributed among the individuals of those species, and their phenotypic distributions (e.g., how many mimicry complexes are there, how closely do their members resemble one another, and how easily are they confused with alternative prey?).

It is our hope that we have shown how the mimetic relationships can be influenced by population dynamics yet also how incorporating behavior into population theory can help explain community-wide patterns of phenotypic diversity.

Acknowledgments

We thank the Wissenschaftskolleg zu Berlin for inviting our focus group Integrating Mimicry into Community Ecology and for furnishing a supportive environment for collaboration. The University of Florida Foundation also provided support to M.B. and R.D.H. M.E.H. was supported by the Australian Research Council through DP190101028. J.M. was supported by the Academy of Finland (project 319124). D.W.K. was partially funded by the German Research Foundation (DFG) as part of the SFB TRR 212 (NC^3), project 316099922. M.E.H. acknowledges the Wallumattagal clan of the Dharug nation as the traditional custodians of the Macquarie University land.

Statement of Authorship

R.D.H., J.M., M.E.H., and D.W.K. conceived of the study. R.D.H. and M.B. designed the model and chose the theoretical approach. M.B. wrote and coded the model. D.W.K. visualized the model output and wrote the draft manuscript. R.D.H., M.B., J.M., and M.E.H. contributed to the writing. *Diversity and inclusion statement*: We strongly support equity, diversity, and inclusion in science. The authors come from different countries (Finland, Austria, and the United States) and represent different career stages (from postdoctoral to senior researchers). One or more of the authors self-identifies as a member of the LGBTQ+ community.

Data and Code Availability

No data were generated in this study. Original Fortran code for the model is available from Zenodo (https://doi.org/10.5281/zenodo.5644610; Kikuchi et al. 2021*a*).

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Associate Editor: Krushnamegh Kunte
Editor: Daniel I. Bolnick