



## Original Article

## Selection for multicomponent mimicry: equal feature salience and variation in preferred traits

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When should multiple traits on Batesian mimics be selected to resemble corresponding traits on model species? Here, we explore two possibilities. First, features of equal salience to predators may be used to categorize prey, selecting for multicomponent mimicry. Second, if different predators use single yet different traits to categorize prey, multicomponent mimicry may still be selected. We studied how blue tits categorized rewarding and unrewarding artificial prey items that are differentiated by a combination of two color dimensions. Many birds used both color dimensions to make decisions, and overall, the population selected for multicomponent mimicry. However, a subset of birds used one color or another to make decisions; among this subset, multicomponent mimicry was also favored. The cost of sampling did not affect selection. Our results suggest that multicomponent warning signals may be selected when traits are equally salient to individual predators, or when communities of predators focus on different traits to discriminate between prey.

**Key words:** complex signal, individual variation, learning, overshadowing.

## INTRODUCTION

Batesian mimicry is a phenomenon in ecology, evolution, and psychology (Bates 1862; Ruxton et al. 2004). In Batesian mimicry, undefended prey evolve to resemble defended prey because this resemblance deceives predators into believing that they are unprofitable. The signals that mimics must evolve are often complex, or multicomponent, that is, having multiple features (also called traits, components, or dimensions; Hebets and Papaj 2005; Balogh et al. 2010; Bradbury and Vehrencamp 2011). Consider for example the vibrant, multicolored hues of the venomous eastern coral snake and its harmless mimic, the scarlet kingsnake (Pfennig et al. 2001), or the variegated, polka-dotted wings of mimetic butterflies (Bates 1862). How and why multicomponent signals such as these arise is somewhat mysterious. The perceptual and cognitive biases of predators may play a critical role (Cuthill and Bennett 1993; Mallet 2001; Darst 2006; Chittka and Osorio 2007; Gamberale-Stille et al. 2012). In particular, predators' biases may explain why mimics resemble their models in some features but not others (Bain et al. 2007; Kikuchi and Pfennig 2010). Individual predators may use multiple features to identify prey, or different groups of predators may each have preferences for different ones (Carter 1948). Thus, selection for multicomponent mimicry may be mediated

by individual-level behavior and/or by communities of predators. Here, we explore these two possibilities.

It is becoming increasingly recognized that the relative salience of different features of prey appearance can affect which ones evolve to be mimetic (Kazemi et al. 2014, 2015; Sherratt et al. 2015). By salience, we mean how quickly a predator learns to associate a feature of prey appearance with prey defenses. Features that are more salient may "overshadow" other, less salient ones, preventing them from being associated with defenses (Mackintosh 1976). For example, color may overshadow pattern and shape to select for imperfect mimicry, so that only color is mimicked (Kazemi et al. 2014). By the same token, features of equal salience should be associated with prey defenses (Shettleworth 2010, p. 112), selecting for multicomponent mimicry (Kazemi et al. 2015). This phenomenon may help explain certain complex signals (Grether et al. 2004; Hebets and Papaj 2005) involved in mimicry. For example, butterflies must match multiple color patches of local noxious *Heliconius* butterflies to receive protection from predators (Kapan 2001; Merrill et al. 2012; Finkbeiner et al. 2014).

Equal stimulus salience cannot be the only mechanism for the evolution of multicomponent mimicry. Conjunctions of shape, patterns, or color are sometimes required for protection (Harper and Pfennig 2007; Penney et al. 2012; Skelhorn et al. 2015). These traits differ in salience to birds and humans (Kazemi et al. 2014; Sherratt et al. 2015), so it is not entirely obvious why multicomponent mimicry should evolve. One explanation is that selection

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for multicomponent mimicry could occur if different predators in a community vary in the traits that they use to make decisions. This might result from different traits appearing more salient to different predators, for example, if different predators had different prior biases in their senses or in their preferences for learning. It might also arise by chance associations formed while learning about mimics and models that lead to variation in the rules that predators use to discriminate prey. Such variation in prey preference can come about as a consequence of decisions made during the exploration phase of foraging. During this period, predators take risks to determine which prey are profitable. When costs of attacking defended prey are high, predators may be forced to take fewer risks in sampling prey that are potentially defended (DeWitt et al. 1998; Sherratt 2011). This should lead them to form more simplistic rules for categorizing prey than they would if costs were lower (Kikuchi and Sherratt 2015).

We designed an experiment to evaluate how blue tits (*Cyanistes caeruleus*) learn to discriminate between rewarding and unrewarding prey when they differ by two coloration traits. Some of the best known cases of mimicry have been experimentally shown to involve different color dimensions defined by the amount or presence/absence of discrete color patches. Indeed, in the laboratory, coloration traits have been shown to select for multicomponent mimicry when they are equal in salience (Kazemi et al. 2015). However, it is also possible that individual birds vary in the colors that they associate with rewards, which makes color appropriate for exploring how variation between individuals affects selection for mimicry.

During our experiment, we allowed individual birds to sample a variable number of prey of their choice, which permitted the development and expression of individual differences in discrimination strategies. We divided birds into two groups that featured different levels of sampling costs to encourage differences in behavior based on the balance of risks and rewards. Once we had collected data from 32 birds, we characterized selection for mimicry by all birds to see if two salient color dimensions would select for multicomponent mimicry. Then we evaluated the decision-making strategies of individual birds during their final trial and tested how those strategies were influenced by the number of prey they sampled in earlier trials. This allowed us to test whether differences in the costs of exploration affected their preferences. Finally, we evaluated selection for mimicry by a subset of predators that, individually, only used one dimension of color or the other (i.e., red–blue or yellow–green but not both) to make decisions, although as a group they comprised individuals with both preferences.

The design of this experiment has much in common with studies of animal cognition (Draulans 1985; Smith et al. 2004; Pearce et al. 2008; Zentall et al. 2014). This notwithstanding, our emphasis here is more on outcomes than cognitive mechanisms, with three novel features: first, the importance of equal stimulus salience in encouraging selection for multicomponent mimicry (see also Kazemi et al. 2015); second, the examination of costs of exploration as a predictor of category learning (this active learning process is particularly uncommon in studies of animal cognition); and third, the analysis of individual variation in behavior.

## METHODS

### Experimentation

We trained blue tits to participate in a novel world experiment where they foraged on artificial prey that are dissimilar from anything that they are likely to have encountered before (Alatalo and Mappes 1996). The novel prey were made from pieces of plywood

with wells drilled in them that we covered with colored targets (see below). Birds had to peck through targets to find pieces of sunflower seed. Unrewarding prey (models) had no sunflower seeds inside their wells, so birds paid a cost for attacking them. Targets varied in two dimensions (red vs. blue and yellow vs. green), producing four possible color combinations (RY, RG, BY, BG; Figure 1). The spectral reflectance curves of the colors that we used are available in Supplementary Figure 1.

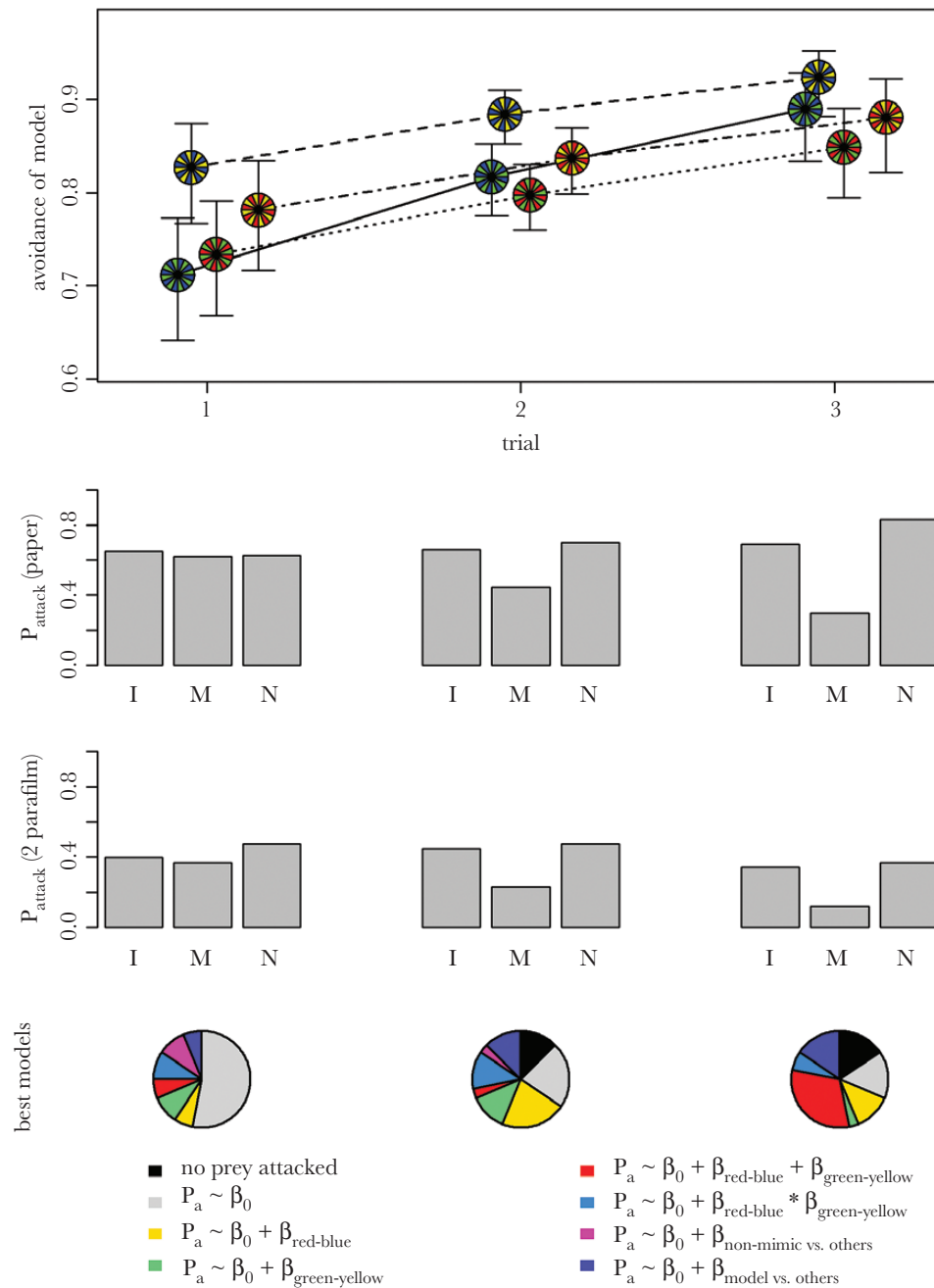
The study was conducted at the Konnevesi Research Station in central Finland during March 2015. Wild-caught birds were kept in individual cages on a diet of mixed seeds and water provided ad libitum unless they were being used in an experiment. We trained 32 birds to peck through grayscale targets before they participated in the experiment. We assigned 16 birds to a low-cost treatment with targets made only of printer paper, and 16 birds to a high-cost treatment with targets made of printer paper plus two layers of parafilm, making them harder to penetrate. These two levels of cost were used to induce variability in birds' willingness to sample prey. Birds took much longer to penetrate the parafilm (seconds vs. minutes in the early stages of learning) and also appeared to expend considerable energy in doing so. Our confidence in the high cost of the task also stems from the rejection of the prey by some of our subjects (see Results) and from the escape attempts and cries made by birds after attacking parafilm-covered targets without rewards. Birds were trained on the same level of cost that they experienced in the experiment. Birds' training took place in their home cages until their final round of training, which was conducted individually for each bird in one of the identical 13.5 m<sup>2</sup> rooms in which the experiment took place.

During the experiment, we made one of the four target types a model (without a reward) and placed rewards inside the other three. Thus, each model had two imperfect mimics that each shared one color in common with it, and a nonmimic that shared no colors in common with it. We rotated the target that served as a model so that within each level of cost, each combination of colors was used as a model for four different birds.

Before each experimental trial, birds were deprived of food for 2 h. Each trial featured 10 prey of each target type for a total of 40 prey. Birds were allowed to forage until one of the following conditions was met: 1) they sampled 27 total prey (a more natural break might have been 30, but birds could get confused trying to find a few remaining palatable targets), 2) 90 min elapsed, or 3) more than 30 min passed between sampling. Each bird was given three experimental trials (thus encountering a total of 120 prey). Our rationale was that birds should be allowed to choose which prey and how many prey they sampled. On their first trial, birds were allowed to remain in the aviary until they began sampling prey, but on the second and third trials they were stopped after 1 h if they did not sample any prey. We recorded the identity of prey sampled by each bird during every trial.

### Analysis

To ensure that there was no significant bias associated with how quickly birds learned to avoid different combinations of colors (and hence, that colors were approximately equal in their salience), we calculated how quickly birds learned to avoid RY, RG, BY, and BG targets. We employed logistic regression with the number of attacks on rewarding prey out of all prey attacked as the response variable. Our predictors were trial (continuous), color combination of the model (factor), and their interaction as fixed effects. We included bird identity as a random intercept.

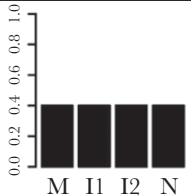
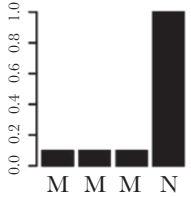
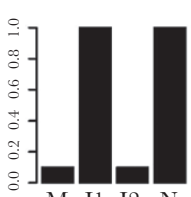
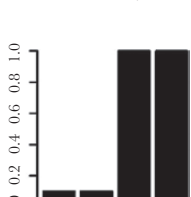
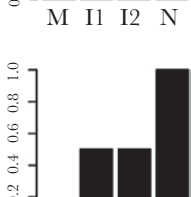
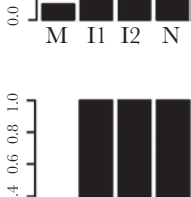
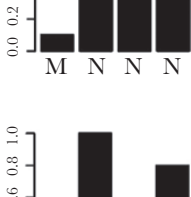
**Figure 1**

Top row: proportion of prey attacked that were not models during each trial. Symbols on the graph are the actual model targets (costs combined). Birds learned to avoid all types of models at statistically indistinguishable rates. Second row: Proportion of prey of each phenotype (I, imperfect mimic; M, model; N, nonmimic) attacked during each trial when birds had to peck through paper (low cost). Third row: Proportion of prey of each phenotype attacked during each trial when birds had to peck through 2 layers of parafilm (high cost). Bottom row: Pie charts displaying the proportion of birds whose attack behavior was best fit by each of the statistical models we considered in Table 1.

It is easier to interpret results when thinking in terms of models, imperfect mimics, and nonmimics rather than specific color combinations. Therefore, we performed an additional logistic regression where the number of prey attacked out of total number available of each phenotype was an additive function of phenotype (whether the prey was a model, imperfect mimic, or nonmimic), the trial number, and the level of cost in the experiment. Because our data were tabulated differently for this analysis, we included individual as a random intercept.

Predators in this experiment did not learn as a population, but as individuals. Variability in individual behavior may have arisen from both pre-existing variation in birds' preferences and stochasticity in the prey that they sampled as the experiment progressed. It was important to know how variable individuals were in attacking prey; this let us assess whether selection on prey was a deterministic outcome of invariant cognitive processes that take place in all individuals, or whether selection was the product of different predator attack behaviors simultaneously acting on the prey population. We

**Table 1**  
**Statistical models fit to the attack probability of individual birds**

Rank	Model formula	Description of bird's behavior	Attack probability
–	$P_a \sim \beta_0$	Appearance of prey is not related to probability of attack	
1	$P_a \sim \beta_0 + \beta_{\text{nonmimic vs. all others}}$	Attacks mainly nonmimic	
2	$P_a \sim \beta_0 + \beta_{\text{red-blue}}$	Uses red-blue to make decision; attack nonmimic and 1 imperfect mimic	
2	$P_a \sim \beta_0 + \beta_{\text{green-yellow}}$	Uses yellow-green to make decision; attack nonmimic and the other imperfect mimic	
3	$P_a \sim \beta_0 + \beta_{\text{red-blue}} + \beta_{\text{green-yellow}}$	Uses red-blue plus yellow-green to make decision—the 2 color dimensions additively determine attack probability	
4	$P_a \sim \beta_0 + \beta_{\text{model vs. all others}}$	Attacks everything but the model	
–	$P_a \sim \beta_0 + \beta_{\text{red-blue}} + \beta_{\text{green-yellow}}$	Attacks each prey phenotype with a unique probability. No rank assigned because this category is a catch-all for strategies we have not explicitly considered	

All models were logistic regressions. We ranked them by how conservative the sampling strategy they are associated with is. More conservative strategies reflect more risk-averse sampling behavior. Although our descriptions apply strictly to responses with certain signs of parameter, we have listed the most likely interpretation. M, model; I1/I2, imperfect mimics, N, nonmimic.

compiled a list of models that we considered realistic decision-making strategies and fit all of them to each bird for each trial. All were logistic regressions with whether or not prey were attacked as a function of different predictor variables that describe appearance. The models ranged from conservative (attack only the nonmimic) to liberal (attack everything except for the model), as well as a null model (random guessing) that could represent attacking or rejecting at random. Each strategy required a different investment in information. If birds were wary, a negative experience with the model prey could lead them to avoid everything that has something in common with it. If colors (red–blue and yellow–green) were unequal in salience or if birds had positive experiences with one of them, then they would be more likely to choose a model where they sampled prey based on the presence or absence of just a single color. Finally, if birds cared little about errors, they could sample prey randomly until they realized the model’s phenotype was the only one that did not provide a reward, and then avoid only it. All the strategies that we considered are summarized in Table 1. For each bird for each trial, we selected the best model using the Akaike Information Criterion (Akaike 1974).

To see if attacks by a population of birds that used just one dimension of coloration could nonetheless select for multicomponent mimicry, we performed an additional test. Among the subset of five birds whose behavior was best described by using a single color dimension, we analyzed attacks in the third trial as a function of phenotype using a logistic regression with individual included as a random intercept. Independent contrasts were used to compare the relative attack rates on models versus imperfect mimics and nonmimics, and nonmimics versus imperfect mimics.

If birds’ decision rules were a product of experiences with sampling prey rather than prior biases, then more conservative sampling strategies should be associated with attacking fewer prey. It would have taken far fewer experiences to decide to attack only nonmimics than it would to attack all prey phenotypes except for the model. Therefore, we tested for an association between the number of prey sampled across the first and second trials and the conservatism of the strategy that best described each bird’s behavior on its third (last) trial. This reflected our assumption that birds learned little on their last trial. To perform this test, we fitted a linear regression between the rank order of how conservative strategies used in the last trial were (Table 1) and the number of prey sampled in the first two trials.

RESULTS

We found that although birds exhibit a trend toward avoiding BY prey during all trials (Wald  $z$ -test,  $z = 1.77$ ,  $P = 0.077$ ), there was no interaction between trial number and model color combination

on avoidance behavior (likelihood ratio test,  $\chi^2_3$ ,  $1.552=0.67$ ). Therefore, although birds appeared to avoid BY models at a higher rate than others, the rate at which they subsequently learned to improve their avoidance did not depend on model phenotype, supporting our assumption that all colors were of equal salience (to the population as a whole, at least, which was also true of birds in the experiments of Kazemi et al. 2014, 2015).

The effect of predator learning on the attack rates of models, imperfect mimics, and nonmimics can be seen in the middle two rows of Figure 1—the model is increasingly well protected with each subsequent trial. Imperfect mimics gain little benefit from sharing a single color in common with the model. These patterns are constant across levels of cost; although in our logistic regression with phenotype of prey expressed in terms of mimicry rather than color combinations, cost was a significant predictor of how likely prey were to be attacked overall. This occurred because birds simply attacked fewer prey in the high-cost treatment (paper + two parafilm; Table 2). Indeed, cost and phenotype both had large effects on the probability that prey would be attacked, although the color combination of the model and the trial number were also significant predictors (Table 2).

By the final trial, models were attacked much less frequently than other phenotypes of prey. A conjunction of two colors were needed for protection despite the fact that in the final trial, only 5 out of 32 birds’ behavior was best represented by the strategy of only avoiding the model prey. Other birds’ behavior was best described by strategies using additive combinations of the two color dimensions or only red–blue or yellow–green to make decisions, or even random guessing (bottom row of Figure 1). There was considerable uncertainty in the best-fit models for many birds’ behavior (Supplementary Table 1).

When we examined the subset of five birds that tended to use one color dimension or the other to make attack decisions in the third trial (that there were also five different birds best fit by this model and five birds best fit by avoiding only the model prey is purely coincidental), we found that models were attacked significantly less often than imperfect mimics or nonmimics (Figure 2; Wald  $z$ -test,  $z = -4.62$ ,  $P < 10^{-5}$ ), and that nonmimics were attacked at a higher rate from imperfect mimics (Wald  $z$ -test,  $z = 3.05$ ,  $P = 0.002$ ). This recapitulated the pattern of attacks among the whole population of birds in both cost treatments (middle two rows of Figure 1, right side), although none of the birds in this group of five used a strategy that involved both color dimensions. This analysis ignores the cost treatment to which they were assigned. Within the low-cost treatment, one bird used yellow–green and two used red–blue (two birds in the high-cost treatment also used this decision rule).

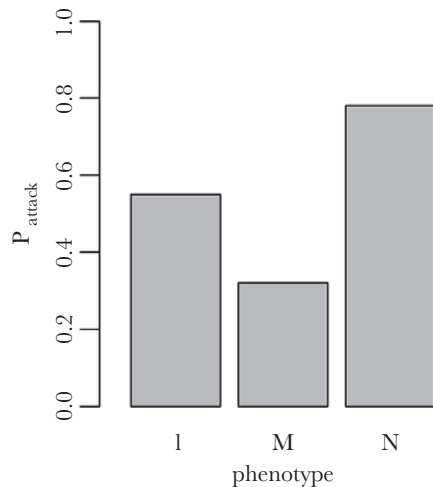
Table 2

Table of fixed effects in our generalized linear mixed model of attacks on prey out of total available (binomial errors) with phenotype (imperfect mimic, model, nonmimic—please note that this is different from the regression used to produce Figure 1), trial, and cost as fixed effects, with random intercepts fitted to each bird

Fixed factor levels	Estimate	SE	$z$	$P$
Intercept: imperfect mimic, cost = parafilm, trial 1	−0.32	0.27	−1.19	0.235
Model	−0.93	0.09	−10.28	<10 <sup>−15</sup>
Nonmimic	0.25	0.09	2.77	0.006
Trial number (continuous)	−0.16	0.04	−3.56	<10 <sup>−3</sup>
Cost = paper	1.37	0.36	3.83	<10 <sup>−4</sup>

The test statistics presented are Wald  $z$ -tests, the default test performed by the glmer function of the lme4 package. Estimates (and SEs) are logit-transformed and must be combined with the intercept before being back-transformed. Significance of values from Wald  $z$ -test agrees with analysis of deviance; we present only the former for clarity.





**Figure 2**

Attacks on imperfect mimics, models, and nonmimics by birds whose behavior was best represented by models using 1 color dimension or another in the third trial (light green and yellow in the third Pie chart of Figure 1). Models were attacked at a significantly lower rate than the other 2 phenotypes.

Although there was great variability among birds in the number of prey that they sampled, contrary to our prediction, we found no correlation between the number of prey sampled and the conservatism of the model that best described their behavior ( $r^2 = 0.04$ ,  $t_{18} = -0.83$ ,  $P = 0.42$ ).

## DISCUSSION

In a community where warning signals have multiple colors and predators are experienced, our data suggest that multicomponent mimicry would be selected because complete resemblance to the model is required for predator avoidance. Without examining individual-level decision-making strategies, this would be considered *prima facie* evidence that both dimensions of color variation that we used in this study are equally salient to birds in general. Indeed, the high proportion of birds that used an attack-everything-but-the-model strategy or an additive/interaction model of both color dimensions suggests that to many birds, both color dimensions were important. Furthermore, a recent study has shown that when populations of birds find features to be equally salient, multicomponent mimicry is indeed selected (Kazemi et al. 2015). Therefore, it seems reasonable to conclude that features of equal salience to individual predators could result in selection for multicomponent mimicry. However, in the present study, some birds only used one dimension or the other to make decisions, suggesting that the dimensions were not equally salient to those individuals. Four birds used red–blue while only one used yellow–green in the final trial, suggesting that the former was preferred by more birds than the latter. An additional explanation for the evolution of multicomponent mimicry is that differences in predator preferences result in multiple components coming under selection, even if they differ in salience.

The pattern of attacks that birds made during this experiment could have been produced by many mixtures of predator decision-making strategies, ranging from all predators using both color dimensions to one subgroup of predators using exclusively one dimension while another used the other. Individual variability in predators has the potential to influence the evolution of mimicry;

selection may differ from population to population depending on the mixture of innate biases and experiences in different predator populations. The hypothesis that predators that focus on different traits of prey selects for multicomponent mimicry was reported by Carter (1948), but evidence to support it has seldom been put forth. We found such a pattern among the birds using one color dimension or the other in our population (Figure 2). Our sample size is admittedly small, but even two birds, each with different preferences for traits used to make decisions, would have sufficed to demonstrate the principle in our laboratory setting. A far more challenging task would be finding evidence in the field, for such a study would not only have to demonstrate variability in predator preferences, but also that those predators sample mimics often enough to have a significant impact on their evolution. We are unaware of such a study, but feel it would be valuable.

Birds used a variety of strategies to make decisions about which prey to attack, but we did not find evidence to support our prediction that the rules they use would be tied to the number of prey that they have sampled. This is surprising, considering experimental evidence that birds show improved discrimination when they have more experience (Duncan and Sheppard 1965; Lindström et al. 2001; Rowland et al. 2010; Ihalainen et al. 2012; Kazemi et al. 2014). Some complications contribute to the results we observed. Five birds in the high-cost treatment refused to sample in the last trial. This is a very conservative strategy, but we cannot statistically distinguish birds that randomly sample few from those that randomly sample many because birds differ in their levels of motivation to complete the task. Therefore, we did not consider these individuals in our analysis. In addition, there was an initial bias among the birds toward assuming all prey were palatable because they received no negative reinforcement during training on grayscale targets. Thus, most sampled extensively during the first two trials, although more cautious individuals might have sampled more conservatively in the wild. This interpretation is consistent with birds using prior expectation to guide their behavior, which is a key component of recent categorization theory that uses Bayesian inference (Kikuchi and Sherratt 2015). A final issue may be with our way of imposing costs: Although the parafilm treatment increased the cost:benefit ratio for attacking models compared with rewarding prey, it also lowered the benefit for attacking rewarding prey in an absolute sense. The small benefit provided by the rewarding prey may have made birds agnostic about the costs of exploration, that is, they might have attacked high-cost models because non-models represented an undesirable food supply in the first place. In fact, many individuals in the high-cost treatment spent considerable time foraging in the various cracks and crannies around the experiment room and only attacked targets when they were very hungry. Overall, we did not find evidence that birds choose their decision-making strategies to economize their learning costs. Instead, in this experiment, differences between birds in the traits they used to make decisions may reflect prior biases.

Our data illustrate that individual variation in predator decision-making strategies can have important ramifications for selection on their prey. From the perspective of an evolutionary biologist studying mimicry, it might seem to matter little whether all predators use all traits on a prey item to assess whether or not they should attack it, or whether each predator fixates on a single trait according to chance experience and its prior preferences; in both cases, the population of prey will fall under selection for multicomponent mimicry. However, there may be important consequences to variation in how predators learn to attack prey. For example,

foraging information diffuses rapidly through wild populations of blue tits, and information acquired socially can have pervasive cultural effects (Aplin et al. 2015). If an individual passes on a preference for prey with one feature or another, it will affect the number of predators that use a particular feature to make decisions, and hence the strength of selection for multicomponent mimicry. In such a situation, assumptions about selection that do not take into account the variability between predators may not hold (Bolnick et al. 2011).

We have shown that although one particularly salient feature may overshadow others and lead to the evolution of imperfect mimicry, the natural corollary to this assertion is that features of equal salience may select for multicomponent mimicry. An alternative (but not mutually exclusive) pathway to the evolution of multicomponent mimicry is for predators to focus on different traits in the prey population to make their discriminations, leading to selection on many features in the population of mimics. These two processes help explain variation in the number of features that fall under selection in empirical studies of mimicry.

## SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>

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