Predator learning can resolve the paradox of local warning signal diversity

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Running title: Explaining local warning signal diversity

Keywords: aposematism, associative learning, classical conditioning, Müllerian mimicry, Pavlovian learning, positive frequency-dependent selection, predator-prey interaction

Type of article: letter

150 words in the abstract (max 150 words)

6775 words in the main text (max 5000 words)

112 references

3 figures and 1 table

Statement of authorship: CYK conceived the study, performed computer simulations, literature search and meta-analysis, and wrote the manuscript

Data accessibility statement: The dataset and R codes for the simulation and meta-analysis can be accessed at https://github.com/thekuolab/warning-signal-diversity

Novelty statement: This paper presents the first widely applicable and testable explanation for the stable coexistence of distinct warning signals within communities, which has long stood as a paradox as it defies the expectation of positive frequency-dependent selection acting on sympatric warning signals. Combining computer simulations and meta-analysis, this paper shows that local warning signal diversity is not paradoxical if prey elicit sufficient predator avoidance and, more importantly, if predators can retain enough learned avoidance within the focal prey's generation time. The meta-analysis also offers new insights into how causes of prey unprofitability, manner of predator-prey encounter, and type of warning signals can influence predator avoidance and the likelihood of local warning signal diversity, representing novel hypotheses to be further tested.

Abstract

Stable coexistence of multiple warning signals within communities has long been a paradox as selection is expected to preserve only the most common signal. This study presents the first generalizable and testable resolution to this paradox by showing that prey displaying rare warning signals can persist if they elicit sufficient predator avoidance and, more importantly, if predators can retain enough learned avoidance within the focal prey's generation time. I validated this hypothesis with empirical learning data that can be readily acquired from laboratory and field experiments. I also performed a meta-analysis examining the variation in predator avoidance. I found that predator avoidance and the likelihood of local warning signal diversity might be higher in communities with the following features – unprofitable prey are toxic instead of merely unpalatable, predators search widely for prey and/or prey aggregate, and when predators could differentiate between unprofitable and profitable prey using only color or pattern.

Introduction

Unprofitable prey often evolve conspicuous colorations to advertise their unsuitability (i.e., aposematism (Poulton 1890). These visual advertisements act as honest warning signals that predators can use to avoid these prey through associative learning. The convergence of warning signals among sympatric prey has inspired evolutionary ecologists to formulate hypotheses regarding the evolution and maintenance of mimicry (Müller 1879; Blakiston & Alexander 1883; Mallet 2001). Following Müller's pioneer theory, each predator has to attack a fixed number of prey to fully acquire learned avoidance. This results in a "safety-in-numbers" scenario in which bearers of rare warning signals are at a disadvantage due to there being fewer individuals to dilute the mortality cost of predator education, resulting in positive frequency-dependent selection (hereafter FDS) that will only preserve the most abundant warning signal in a community (Müller 1879). Müller's theory aptly explains the often-observed signal convergence among unprofitable prey (i.e., Müllerian mimicry) and predicts signal homogeneity at local scales. Yet, despite several well-established examples of Müllerian signal convergence, stable diversity in warning signals within communities does not appear to be a rare occurrence (Ruxton *et al.* 2018; Briolat *et al.* 2019). This stark contrast between theoretical expectations and reality has long stood as a paradox. Several ecological mechanisms have been proposed as potential resolutions to this paradox (reviewed in (Ruxton *et al.* 2018), but none is both broadly applicable and testable. It was hypothesized that species displaying distinct warning signals might segregate along certain microhabitat axes, and predators learn to avoid different signals in each microhabitat type (Gompert *et al.* 2011; Aubier *et al.* 2017). This possibility can be tested empirically but so far seems only able to explain local warning signal diversity in neotropical ithomiine butterflies, in which distinctively colored species fly at different height strata as a result of host plant distribution (Beccaloni 1997; Willmott *et al.* 2017). Notably, microhabitat segregation cannot explain the coexistence of distinct warning signals in two prominent systems of Müllerian mimicry: neotropical *Heliconius* butterflies and *Oophaga* poison frogs (Joron & Mallet 1998; Dugas *et al.* 2015).

Here I present a novel explanation for local warning signal diversity that directly relates to predator learning, and this explanation begins by re-examining the notion that number-dependent predator education will lead to positive FDS. Equating the former to the latter is based on an implicit assumption - the mortality cost of predator education is imposed on every prey generation, such that prey displaying rare signals repeatedly suffer from a disproportionally higher mortality rate (Mallet 2010). In other words, positive FDS results when predators do not retain enough learned avoidance within the focal prey's generation time, and when prey reproduction between generations is not enough to offset learning-based predation. The conditions for this assumption to hold have never been challenged and examined in detail from the perspective of predator learning. There have been studies that reported positive FDS based on the finding that unprofitable prey with novel colorations suffered higher predation rates in the field (e.g., (Chouteau *et al.* 2016). Yet, given the relatively short duration of the experiments (a few days) such results could very well be capturing the initial stage of predator learning, in which prey displaying novel warning signals were incurring the mortality cost of predator education for the very first time. Without information on forgetting rate, it cannot be ascertained whether such observations equate the presence of positive FDS. On the theoretical front, (Mallet & Joron 1999) used Müller's safety-in-numbers concept and found that if the mortality from predator education is low compared to population size (0.01 in their model), the fitness of an

allele encoding a novel warning signal would stay nearly identical over a wide range of allele frequency, forming a neutral basin of warning signal polymorphism (Figure 1A in (Mallet & Joron 1999). Another study by (Franks & Noble 2004) incorporated more detailed, albeit still restricted, predator learning rules to impose selection on multiple warning signals and found coexistence of multiple warning signals to be possible with a constant, low predator forgetting rate. While these studies each explored situations in which number-dependent predator education may not equate positive FDS, they did not broadly examine the conditions that would result in the persistence of prey displaying a rare signal resulting from a balance between learning-based predation and reproduction.

Traditionally, predator learning is modeled with a Pavlovian process, which mathematically formulated Müller's original idea of number-dependent predator education (Turner 1984; Speed 1993, 2000, 2001; Turner & Speed 1996; Speed & Turner 2008; Turner *et al.* 2008), Supplementary Materials). In the Pavlovian framework, every interaction with an aposematic prey reduces a predator's future attack probability against that prey type towards an asymptotic value below 0.5, a value denoting neither preference nor avoidance. This final attack probability is determined in part by prey unprofitability; for highly unprofitable prey, the value could be nearly zero, whereas this value might be only slightly below 0.5 for prey that are barely harmful. It is worth noting that as long as predators' final attack probability towards a prey type is not exactly zero, there will always be a baseline predation even after learning is complete. In the absence of interaction with prey, learned avoidance will degrade (i.e., forgetting), modeled as a gradual increase of attack probability towards 0.5. A main criticism of Pavlovian learning and Müller's idea of number-dependent predator education is that they seem to contradict observations from laboratory and field studies, in which the number of unprofitable prey attacked in learning trials increase either proportionally or nearly so with prey abundance (Greenwood *et al.* 1989; Lindström *et al.* 2001b; Beatty *et al.* 2004; Rowland *et al.* 2010b; Chouteau *et al.* 2016). However, Pavlovian learning can lead to such observations when the final attack probability is not exactly zero, which is likely to be the case in these studies where prey were merely unpalatable. The observations that a proportionately smaller increase in the number of unprofitable prey with abundance (e.g., (Lindström *et al.* 2001b) can also be explained by a non-zero final attack probability coupled with predator satiation (i.e., Holling's type II functional response). Pavlovian learning also has a significant advantage over other alternatives (e.g., the Bayesian learning framework, (Sherratt 2011; Aubier & Sherratt 2015) in that the two key parameters - final attack probability and forgetting rate - can be directly measured with learning experiments (see Supplementary Materials).

I simulated predator-prey interactions and predator learning in a Pavlovian framework. With the simulations, I examined the conditions under which stable persistence of rare warning signals can be achieved as a balance between learning-related predation and reproduction. The predation rate towards prey displaying a particular warning signal is the product of encounter rate and attack probability, with the former determined by relative abundance and the latter by predator learning. The role of final attack probability is straightforward; it determines the lower bound of predation rate and the ever-present baseline mortality after learning is complete. The role of forgetting rate is twofold. First, forgetful predators may repeatedly impose mortality cost of predator education on each prey generation, leading to positive FDS. Moreover, when predators are quick to forget learned avoidance, their attack probabilities towards prey will often be higher than the final asymptotic value, making baseline predation mortality higher than it is expected to

be. These disadvantages are particularly severe for rare warning signals, as their low encounter rates lead to more opportunities for predator forgetting. The unforgetful predator hypothesis posits that when predators can retain learned avoidance for sufficiently long, the mortality cost for predator education can become trivial compared to the ever-present baseline predation. The long-term survival of prey is then predominantly an ecological balance between predation and reproduction. Whether and when the unforgetful predator hypothesis could explain local warning signal diversity hinges on final attack probability and forgetting rate of predators, as well as the reproductive capability of prey. In addition, I considered the effect of two important phenomena of predator learning - cognitive generalization and social learning. Cognitive generalization can occur when a novel warning signal resembles a learned signal. Social learning describes the phenomenon that avoidance learning can occur from observing the negative responses of other predators towards an aposematic prey. These two phenomena have been implemented in Pavlovian learning (Franks & Noble 2004; Thorogood *et al.* 2018), yet their facilitative effects on local warning signal diversity have never been explicitly tested.

In addition to testing the theoretical plausibility of the unforgetful predator hypothesis, the second goal of this study is to demonstrate how the hypothesis can be validated with empirical learning data. For this, I extracted the asymptotic attack probabilities and forgetting rates of selected predators from published studies and collected data on commonly observed prey intrinsic rates of increase. As final attack probability is a useful indicator of prey avoidance and an important determinant of baseline predation, the third goal of this study is to examine the causes of variation in predators' final attack probabilities. For this, I performed a meta-analysis of the avoidance learning literature, focusing on the roles of the following predictors: the reason for prey unprofitability, the manner in which predators encountered prey, and the features that distinguished profitable and unprofitable prey. Specifically, I tested the following hypotheses and predictions. First, the degree of prey unprofitability determined predator avoidance; predators would have lower attack probabilities towards more unprofitable prey, such as those that were highly bitter or toxic. Second, manner of prey encounter would affect the knowledge of prey distribution and availability. When predators encountered profitable and unprofitable prey simultaneously, predators would attack unprofitable prey less due to the knowledge that suitable prey were also present, resulting in lower attack probabilities. Third, the complexity of signals or cues differentiating prey types would affect their efficacy in predator education and therefore prey avoidance. Other things being equal, signals or cues that were more effective in educating predator would result in lower attack probabilities. One could argue that multi-component features might be more effective for predator education, as these offer more precise information to help predators differentiate between prey types. If this was true, more complex signals would result in lower final attack probabilities. Yet, this assumed that predator had the cognitive capacity to process and remember the information. If this was not true, more complex features would confuse the predators, resulting in lower educational efficacy and higher final attack probabilities.

Materials and Methods

All simulations and statistical analyses were performed in R (version 4.2.2, R Core Team).

Simulating predator-prey interactions and predator learning

The basic model

I constructed an individual-based model with discrete time steps and simulated interactions between Pavlovian predators and aposematic prey in one single habitat. The model did not consider any spatial segregation or habitat structuring for two reasons. First, the effect of heterogeneous habitat use on warning signal diversity has been examined in other studies, both independent from and in conjunction with predator learning (Joron & Iwasa 2005; Aubier & Sherratt 2015; Thorogood *et al.* 2018). More importantly, the intention here was to focus on explaining local warning diversity with predator learning alone without involving other mechanisms. The model also did not include a genetic component in which new mutant alleles arose within populations to produce novel warning signals. The reason for this choice was that in well studied Müllerian mimetic systems the coexistence of distinct warning signals is mostly the result of secondary contact between patterns that have evolved allo- or parapatrically, instead of resulting from sympatric originations of novel phenotypes (Mallet 1993; Posso-Terranova & Andrés 2016; Ebersbach *et al.* 2020). Under these scenarios, a genetic component describing the emergence of new warning signals within populations was not essential for capturing the dynamics of the predator-prey interactions and therefore not considered.

There were 20 predators and two prey types in the simulated community, one displaying a more abundant warning signal and the other displaying a rare warning signal. The more abundant warning signal was already familiar to the predators, and the rare signal was unfamiliar. Even though there could potentially be multiple species within each prey type, species identity was irrelevant as individuals within each group were treated as phenotypically indistinguishable. The local prey had an initial abundance of 200, and the new prey had an initial abundance of 10, 20, and 40 in separate simulations. Each simulation was run for 50,000 time steps, and in each time step a predator was randomly selected to be the forager. The forager would encounter prey based on relative abundance and then decide whether to attack the prey based on the current attack probability towards that prey type. Throughout the simulation, predators continued to modify their attack probabilities towards the two prey types following the Pavlovian learning rules (Speed 1993). The attack probability towards the familiar prey was set at its final asymptotic value at the beginning of the simulation, reflecting the fact that predators have completed learning. The attack probability towards the unfamiliar prey was set at 0.5 at the onset of the simulation, signifying predator naivete. There was no predator mortality in the model; nor was there competition between predators or between prey. Prey mortality was due solely to predation, jointly determined by encounter rate and attack probability that changed dynamically between time steps.

Reproduction occurred every 100 time steps in all simulations, and prey were perennial with overlapping generations. No predation occurred during reproduction and both prey types replenished their populations following a logistic growth function:

$$\Delta N_i = rN_i\left(1 - \frac{N_i}{K_i}\right) \tag{4}$$

For prey type i, ΔN was the increase in population size, N was the population size at the end of the previous time step, r was the intrinsic rate of increase, which was set to be the same for both prey types, and K was the carrying capacity. For both prey types, I set K as equal to their initial

abundance. This constrained the relative abundance of the rare warning signal to be close to the initial condition throughout the simulation (i.e., a relative abundance of 0.2, 0.1, or 0.05). Separate K values for each prey group also reflected the fact that individuals bearing different signals often use different resources (Posso-Terranova & Andrés 2016; Jiggins 2017).

For each simulation, the parameter space of the simulations was a 10 by 10 grid defined by the final attack probability λ and forgetting rate β, both of which ranged from 0 to 0.5. I considered values of λ between 0 and 0.5 as these values represented unprofitable prey that were avoided. For β, the value of 0 denoted no forgetting, whereas the value of 0.5 represented the most forgetful predators, which would forget all the learned avoidance towards even the most unprofitable prey (λ = 0) within one single time step without reinforcement. I ran 20 replicate simulations for each combination of λ and β. Abundance of the both prey types were recorded at the end of each simulation. There were three possible simulation outcomes: the extinction of both prey types, the extinction of prey with the rare warning signal, and the persistence of both prey types. The outcome also depended on the intrinsic rate of prey increase (r), which in theory could take any positive value. To select reasonable r values, I used the range of r commonly observed in insects and some mammals (Schmitz & Lavigne 1984; Hickling & Pekelharling 1989; Puche & Funderburk 1992; Jahn *et al.* 2005; Emmert *et al.* 2008; Damos 2013; Papanikolaou *et al.* 2014).

Generalization between prey types

The above procedure described the basic scenario, in which avoidance learning for the local and the new prey occurred independently – predator learning with one prey type did not alter their attack probabilities towards the other prey type. Each predator also learned independently. To model the effect of generalization, I introduced a parameter *G* to account for the fact that change in the attack probability towards prey type *i* would have a carry-over effect on the attack probability towards prey type *j*, such that:

$$\Delta P_{L,j,t} = G \times \Delta P_{L,i,t} \tag{5}$$

In addition,

$$P_{new,t=0} = 0.5 - (0.5 - \lambda) \times G \tag{6}$$

The equation above reflected the fact that the initial attack probability towards the new prey was affected by its similarity to the local prey. Overall, a non-zero G meant that predators' initial attack probability towards the new prey would be reduced based on its similarity to the local prey and that change in attack probability from attacking one prey type would simultaneously reduce the attack probability towards the other prey type. When G equaled one, the attack probability towards the new prey would already be identical to the final attack probability at the onset of the simulation, and learning was completely transferable between prey types. A G equaled zero was equivalent to the basic scenario described above. In simulations with generalization, G was set to be 0.5.

Social learning

In separate sets of simulations, I incorporated social learning in the Pavlovian learning framework following the formulation in (Thorogood *et al.* 2018) by introducing two parameters. The first parameter b determined the percentage of non-forager individuals that were able to observe the prey interaction of the forager. Larger b values meant that more predators would benefit from social learning. The other parameter q described the efficacy of social learning. Similar to how the parameter G functioned, q was a percentage denoting a "discount" in learning effect relative to first-hand experience, such that

$$\Delta P_{L,m,i,t} = q \times \Delta P_{L,n,i,t} \tag{7}$$

At time step t, predators m observed the foraging outcome between the forager n and prey type i. If q equaled one, social learning would cause the same decrease in attack probability for observers as it would from direct learning. If q equaled zero, witnessing a foraging outcome would have no effect on the observers. In simulations with social learning, both b and q were set to be 0.5.

Model validation with empirical learning data

Extracting final attack probabilities and forgetting rates from published studies

I performed literature search using keyword combinations (topic = *aposemat** or defen* or *avoid** + topic = learning) in the Web of Science database, yielding a total of 387 articles. I then screened for studies that quantified attack probability in the context of avoidance foraging with focal animals under normal conditions (e.g., not injured, not sick, not under high stress, not surgically or genetically modified). This resulted in 112 articles from which I extracted attack probabilities. These studies all followed a standard experimental design, in which animals were presented with prey in a series of learning trials. I calculated predators' attack probabilities towards the unprofitable prey from the last trial as the final attack probability. In the majority of the study, each animal was presented with both control and unprofitable prey that differed consistently in at least one sensory modality, most commonly visual appearance. The trial ended when an animal attacked a predetermined number of prey. For these studies, I calculated final attack probability towards the unprofitable prey as the number of unprofitable prey attacked divided by the number of control prey attacked in the last trial, with the assumption that the final attack probability towards the profitable control prey was one (see Supplemental Methods). A small number of studies presented the focal animals with only one type of unprofitable prey. Final attack probability towards unprofitable prey in these studies was calculated as the number of such prey attacked divided by the number of prey presented in the last trial. Calculating attack probabilities also allowed for the estimations of forgetting rate, the magnitude of generalization and social learning efficacy. When applicable, forgetting rate was calculated as the difference in attack probabilities between trials immediately before and after the forgetting period, divided by the duration of that period. These forgetting rates were then scaled, when necessary, to be percent changes per day (see the section below). I also extracted the strength of generalization and social learning from studies that quantified these effects (Supplementary Methods).

Mapping empirical learning data onto model parameter space

For predators whose final attack probabilities and forgetting rates towards unprofitable prey are quantified, their data can be mapped onto the parameter space of the model to evaluate their potential for permitting local warning signal diversity. Empirically measured final attack probability was immediately appropriate for the parameter space in the simulations. Mapping empirical forgetting rates onto the parameter space required one extra step. In the model, each time step equaled 0.01 prey generation time. Using a prey generation time of 30 days, each time step in the model was then equivalent to 0.3 days. An empirical forgetting rate of 0.1 per day would thus equal to a value of 0.03 in the model. In general, any empirically measured forgetting rate could be scaled to unit per day and converted to values appropriate for the parameter space by multiplying the per day value with 0.01 focal prey generation time.

Meta-analysis of the variation in final attack probability

Since final attack probability was an important determinant for the likelihood of local warning signal diversity, I performed a meta-analysis to examine the roles of three factors in determining predators' final attack probabilities towards prey: the reason for prey unprofitability, the manner in which predator encountered prey, and the feature that differentiated profitable prey from unprofitable ones. To obtain a sufficiently balanced dataset, I focused on 39 of the 112 studies for the meta-analysis, with a total of 134 final attack probability measurements (Supplementary Data). These studies shared enough similarities in experimental design while varying in crucial aspects, allowing for meaningful analyses. The focal predators were either the great tit (*Parus major*), the blue tit (*Cyanistes caeruleus*), the European starling (*Sturnus vulgaris*), or the domestic chicken (*Gallus gallus domesticus*). In addition, animals were presented with both control and unprofitable artificial prey within each learning trial, either simultaneously or sequentially. The reason for prey unprofitability was either bitterness (using harmless, bitter chemicals) or toxicity (using toxic prey extracts), and the feature that consistently differentiated the two prey types was either color alone, pattern alone (i.e., the distribution of colors or the use of different geometric symbols), both color and pattern, or color and size or odor.

To perform statistical analyses, I used individual measurements of final attack probability as the response variable, with species and the aforementioned three factors as predictors. Individual study was originally included as a random-effect factor to account for potential nonindependence of data points within studies. However, doing so resulted in model overfitting, and I excluded study from the statistical model. I also did not consider the phylogenetic relationship between species since the number of species was small. To additionally test whether the effective concentration of the bitter chemical was associated with variation in final attack probabilities, I focused on 35 of the 39 studies that used bitter experimental prey. The majority of the studies used quinine derivatives, whereas four studies used denatonium benzoate (Supplementary Data). (Skelhorn & Rowe 2005) reported that 2% quinine sulfate and 0.1% denatonium benzoate (weight percentages) elicited comparable aversion in domestic chicks, signifying a 20-fold difference in effective concentration between the two. I therefore converted the concentrations of denatonium benzoate to equivalent concentrations of quinine derivatives by multiplying them by 20. To test whether an increase in the concentration of bitter compounds caused lower attack probabilities, I performed a gamma regression with manner of prey encounter, the standardized concentration of bitter compounds, and the interaction between the two as fixed-effect predictors.

More details on model validation are described in the Supplementary Methods. When reporting results, I followed (Muff *et al.* 2021) and used the language of evidence instead of significance dichotomy.

Results

Unforgetful predators can allow for local warning signal diversity, especially with generalization and social learning

The persistence of the rare signal depended on its relative abundance, its intrinsic rate of increase (r), predators' final attack probability, and predator forgetting rate (Figure 1). Across the range of r, predators with lower final attack probabilities and lower forgetting rates were more conducive to the persistence of the rare signal, with forgetting rate being a more limiting factor (Figure 1). Given the r values in the simulations, the rare signal was unlikely to persist when its relative abundance was below 0.05 under the basic scenario (Figure 1), indicating a threshold of relative abundance for warning signal diversity if there was no generalization and social learning. For prey with higher r values, the condition for signal diversity would be more forgiving regarding predator learning. Both generalization and social learning increased the likelihood of warning signal diversity (Figure 2). When the new prey was on the brink of ecological elimination, however, the existence of generalization appeared inconsequential, while the facilitative effect of social learning was the most striking (bottom graphs in Figure 2). Nine pairs of final attack probabilities and forgetting rates from six species (one spider, one fish, one lizard, two birds, and one mammal) were mapped onto the parameter space to evaluate their potential for facilitating local warning signal diversity (Table S2 and Figure 2). The focus here was not the species identity *per se*, but the combination of their final attack probabilities and forgetting rates. There were only nine data points because forgetting rates were rarely quantified in avoidance learning studies. Even with limited number of cases, the combination of avoidance level and forgetting rate from most of the predators were at the lower left corner of the parameter space, suggesting that it might not be a rare occurrence that natural predators could facilitate local warning signal diversity.

The strengths of generalization and social learning

I quantified 32 magnitudes of generalization from 11 studies using birds (eight studies), fish (one study), lizards (one study) and spiders (two studies) (Table S1). Values ranged from zero to one, with an average of 0.34 with a standard deviation of 0.43. Notably, there were 17 instances in which the researchers found no evidence for generalization, most of which occurred in avian predators (Table S1). The average magnitude for non-zero generalization effect was 0.73 with a standard deviation of 0.29. Two studies in particular offered some comparative insights. (Paez *et al.* 2021) demonstrated that the blue tit were better able to generalize between visually similar evasive prey than between those that were equally similar visually but were chemically defended instead, suggesting that reason for unprofitability might affect magnitudes of generalization. (Aronsson & Gamberale-Stille 2008), on the other hand, showed that domestic chicks could generalize between similar colors during avoidance learning but were unable to generalize between similar patterns.

Regarding the efficacy of social learning, the six social efficacy estimates had a mean of 0.44 and a standard deviation of 0.15 (Table S1). Studies by (Hämäläinen *et al.* 2019, 2020) found that the great tits avoided bitter almonds more when they acquired the information from social learning as opposed to when they learned the association between taste and appearance from first-hand experience. The study by (Salva *et al.* 2009) found that domestic chicks could learn to avoid distasteful objects socially, but the avoidance learned in this manner was not as strong compared to direct learning, with an efficacy of 0.30 (Table S1).

Causes of variation in final attack probabilities

Compared with bitter prey, there was very strong evidence that toxic prey led to a higher probability of complete avoidance (i.e., an attack probability of zero), but being toxic did not reduce non-zero attack probabilities (Table 1 and Figure 3A). There was also no evidence that increasing bitterness led to lower attack probabilities ($z = -0.23$, $P = 0.82$, Figure 3B). There was very strong evidence that predators avoided unprofitable prey more when profitable prey were also present (Table 1 and Figure 3C). Finally, there was no evidence that predators avoided unprofitable prey differently when the feature differentiating prey types involved only color, only pattern, or color plus size or odor (Table 1 and Figure 3D). However, when the signals or cues differed in both color and pattern, there was very strong evidence that predators avoided unprofitable prey less, suggesting that signals with complex color patterns might be less effective for predator education, at least for the four avian species examined (Table 1 and Figure 3D).

Discussions

Local warning signal diversity is not paradoxical

When predators can retain learned avoidance for long enough, the persistence of rare signals in communities can be achieved through balanced predation and reproduction and is entirely nonparadoxical. Empirical learning data also suggest that natural predators from a range of major taxa may have sufficiently low forgetting rates to allow for local warning signal diversity. However, local warning signal diversity was unlikely to occur if the novel signal is less than 5% in relative abundance, at least under commonly observed intrinsic rates of increase and without generalization or social learning. Clearly, this value depends on the prey intrinsic rate of increase and should not be taken as a hard threshold. Even though the relative abundance of stably coexisting warning signals has only been quantified for a small number of systems, it appears to be generally true that the rare signals often constitute at least ~ 5% of the population (Myers *et al.* 1995; Chouteau *et al.* 2016; Thurman *et al.* 2019). The result may also help further explain the observation that warning signal diversity is often the result of secondary contact following dispersal (Mallet 1993; Posso-Terranova & Andrés 2016; Ebersbach *et al.* 2020), in which neither signal is likely to be astronomically dominant in number.

The diversity and convergence of warning signals at the regional and local scales has been thought to reflect a shifting balance involving local drift (phase I), local selection (phase II), and the spread of competing, locally adaptive peaks from regional to local scales (phase III)(Mallet & Joron 1999; Mallet 2010). Results in this study offer further ecological insights into the shifting balance process. First, generalization and especially social learning can further flatten

the “adaptive trough” for rare warning signals (Figure 1 in (Mallet & Joron 1999). This can facilitate the establishment of new waring phenotypes locally through processes such as kin founding, especially if individuals with the new warning signals have a fitness advantage, for example, from being more unprofitable or more conspicuous. When all prey are equally unprofitable, the facilitative effects of generalization and social learning are only apparent when the prey intrinsic rate of increase is sufficiently high. The fact that number-dependent predator education does not necessarily lead to positive FDS also points to an alternative outcome during phase III of the shifting balance, in which two adaptive peaks meet without one replacing the other. Interestingly, if the number of immigrants with novel warning signals are large enough, aside from a higher likelihood of local warning signal diversity it also enhances the opportunities for the local aposematic prey to survive when predators are more forgetful and/or when the prey themselves are not severely unprofitable (the size and distribution of red areas in the rightmost column of Figure 1).

Aside from predator forgetting, positive FDS can result when predator turnover rate is comparable to prey generation time, such that every prey generation faces naïve predators. Even though the simulations did not directly model predator turnover, the erosion of learned avoidance over time can be viewed as a consequence of predator turnover in a community that is similar to forgetting of individual predators. For example, if each predator in the model is treated as a group that contains multiple individuals, the same process in which attack probabilities increase towards 0.5 over time can represent the replacement of experienced predator individuals with naïve ones in each predator group. The only modification required for simulating predator turnover in the model is that the erosion of learned avoidance will occur at each time step regardless of whether predators attack the focal prey. In contrast with predator forgetting, predator turnover is guaranteed to take place at each time step and can therefore have a stronger limiting effect on the likelihood of local warning signal diversity. Since most Müllerian prey are insects and frogs, a substantial turnover of predators within one prey generation may be unlikely (e.g., one month for butterflies and one year for poison frogs, (Duellman & Trueb 1986; Jiggins 2017). For Müllerian prey with longer generation time, such as the putative mimicry rings between some mustelid, viverrid, and herpestid mammals (Caro 2005), significant predator turnover could occur between prey generations and thus might play a more pivotal role.

Testing the unforgetful predator hypothesis in natural communities

All key parameters of the unforgetful predator hypothesis - final attack probability, forgetting rate, strength of generalization, and the efficacy of social learning - can be measured with learning experiments. Usually, these parameters are measured in a laboratory setting, which allows data collection from individual predators. Laboratory experiments are particularly useful in assessing the variation in learning parameters within and among individuals. In communities where individual predators can be identified and their learning parameters estimated, the model can be easily modified such that predators differ in their Pavlovian learning parameters in ways that faithfully reflecting the observed heterogeneity in predator behavior and cognition. Even though data are still limited, it appears that predators with simpler or less derived nervous systems (e.g., spiders) can have forgetting rates comparable to those of birds and mammals. This suggests that predator possessing low enough forgetting rate for allowing local warning signal diversity might be more common than we might expect. When collecting learning data from

individual predators are not feasible, field learning experiments represent a suitable alternative. The design of field learning experiments is similar to laboratory experiments, except that prey are presented to all potential predators in the community instead of targeting specific predator individuals (e.g., (Noonan & Comeault 2009; Stevens *et al.* 2009; Chouteau & Angers 2011; Casas Cardona *et al.* 2018; Fukuda & Konuma 2019; Hernández-Agüero *et al.* 2020; Yamazaki *et al.* 2020; Postema 2021). Final attack probabilities, forgetting rates, and the strength of generalization can be derived from proportions of different prey being attacked in the same way as in laboratory experiments. The key difference is that data obtained this way represent values averaged over all potential predators. Field learning experiments can be very useful in testing how likely warning signal diversity is being maintained by predator learning in complex communities with highly heterogeneous predators that belong to multiple species, which is the norm in nature. The efficacy of social learning can also be estimated in field learning experiments, in which video playbacks of predator-prey interactions are presented to predators before measuring their attack probability. The result can then be compared to data obtained from direct learning conducted in a separate site of the same community to estimate the efficacy of social learning. So far, no field learning experiment has attempted to quantify forgetting rate, nor has one quantified the efficacy of social learning. In fact, the vast majority of the avoidance learning studies has focused on final attack probability as an indicator for overall level of avoidance, and the lack of data on forgetting rate, the strength of generalization, and social learning efficacy are major knowledge gaps, as well as fruitful future directions. Filling this knowledge gap is crucial for more broadly understanding the role of predator learning in the maintenance of waring signal diversity in natural communities.

Variation in final attack probabilities and the implications for local warning signal diversity

Even though data in the meta-analyses were conducted on a small number of birds under laboratory settings, findings from the meta-analysis are broadly informative as the experiments were all designed to capture the essence of predator learning. The analysis revealed that being toxic can be more effective than unpalatability for dissuading some predators, resulting in complete avoidance. However, for predators that would consume toxic prey, either because of a higher toxicity tolerance or more urgent energetic needs, toxicity does not appear to offer more protection than mere bitterness. Studies that presented toxic food to predators either used naturally toxic prey (D'Heursel & Haddad 1999; Cock & Matthysen 2001) or prepared artificial food items with extracted prey toxin (Chouteau *et al.* 2019). These prey have chemical defenses that dissuade rather than severely harm predators, which is how defense is expected to function in Müllerian systems. It is therefore reasonable to extrapolate this result to how predators might avoid Müllerian prey in general. In addition, increasing bitterness does not appear to be more effective in eliciting higher avoidance, at least within the range of bitterness in the analysis (weight percentage 0.002 – 0.1). It is possible that the 50-fold difference in the effective concentration of bitter chemicals does not result in corresponding changes in bitter perception in birds. Alternatively, this result could indicate that birds respond to prey bitterness in a uniform fashion, despite continuous bitter perception. Data on taste sensory physiology, coupled with controlled tests of taste response, would help differentiate these two hypotheses. All in all, results from the meta-analysis suggest that Müllerian systems with toxic prey could have higher potential for local warning signal diversity, but only if the toxins cause complete avoidance. On the other hand, local warning signal diversity is equally likely to occur in Müllerian systems with

highly distasteful species than in those whose prey are less obnoxious in taste. Evasiveness is another important cause of prey unprofitability but is not include in the meta-analysis because only one study has quantified attack probabilities towards evasive prey. Using the blue tit as predators, (Paez *et al.* 2021) showed that evasive prey with conspicuous colorations elicited a lower level of avoidance but a stronger generalization effect than colorful, chemically defended prey. Examining predator learning in other Müllerian systems with evasive prey (e.g., the Amazonian *Morpho* butterflies (Llaurens *et al.* 2021; Roy *et al.* 2021) and more predators will be important for further testing the effectiveness of being evasive in eliciting predator avoidance and to examine whether local warning signal diversity is more or less likely to occur in these systems.

Predators avoid unprofitable prey more when profitable alternatives are present in the environment. Even though this result comes from laboratory experiments, it has important implications for predator-prey interactions in natural communities. The simultaneous and sequential prey presentations in laboratory experiments represent two extremes of the prey-encounter continuum. In the field, the foraging habits of predators and the density and distribution of prey can both determine how predators encounter prey. Sit-and-wait predators are more likely to encounter prey in a sequential manner than widely ranging predators and therefore might avoid unprofitable prey to a lesser extent. Similarly, predators are more likely to encounter prey sequentially in habitats where prey density is low and/or where prey do not aggregate. Under these conditions, predators are also expected to exhibit lower avoidance towards unprofitable prey. Findings from the meta-analysis suggest that, all else being equal, local warning signal diversity is more likely to occur in communities when main predators actively search for prey and when prey are abundant and/or have a concentrated distribution. These predictions have never been tested. In addition to predator forgetting rate, a comparative analysis examining the relationship between the presence of local warning signal diversity, predators' foraging habits, and prey distribution would offer valuable insight.

The nature of the warning signal can affect predators' final attack probabilities; predators avoided unprofitable prey more when they differed from profitable prey in only color or pattern. Studies have also shown that different colors vary in their educational efficacy (Marples *et al.* 1998; Skelhorn & Rowe 2006a; Miller & Pawlik 2013; Nokelainen *et al.* 2014; Taylor *et al.* 2014, 2016). Based on this finding, local warning diversity might be more easily achieved in communities where profitable prey have simple visual appearance and could be differentiated from unprofitable prey based on color or pattern alone. This does not mean that unprofitable prey cannot possess visually complex warning signals, as long as predators can prioritize on color or pattern to select suitable prey. There is ample evidence indicating that predators do focus on certain features of prey appearance more than others during avoidance learning (unequal feature salience or overshadow effects; (Kikuchi & Pfennig 2010, 2013; Kazemi *et al.* 2014, 2015; Kikuchi & Sherratt 2015; Kikuchi *et al.* 2016). However, it is worth noting that this finding was based on results from a small number of species and might have limited generality. Particularly, we know next to nothing about avoidance learning abilities in tropical birds, which are the main predators of the most classic Müllerian prey (e.g., (Langham 2004, 2005; Pinheiro & Campos 2019). Quantifying learning and forgetting in tropical avian predators can be challenging but would provide crucial information on the maintenance of local warning signal diversity in some of the most remarkable Müllerian systems.

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Figure legends

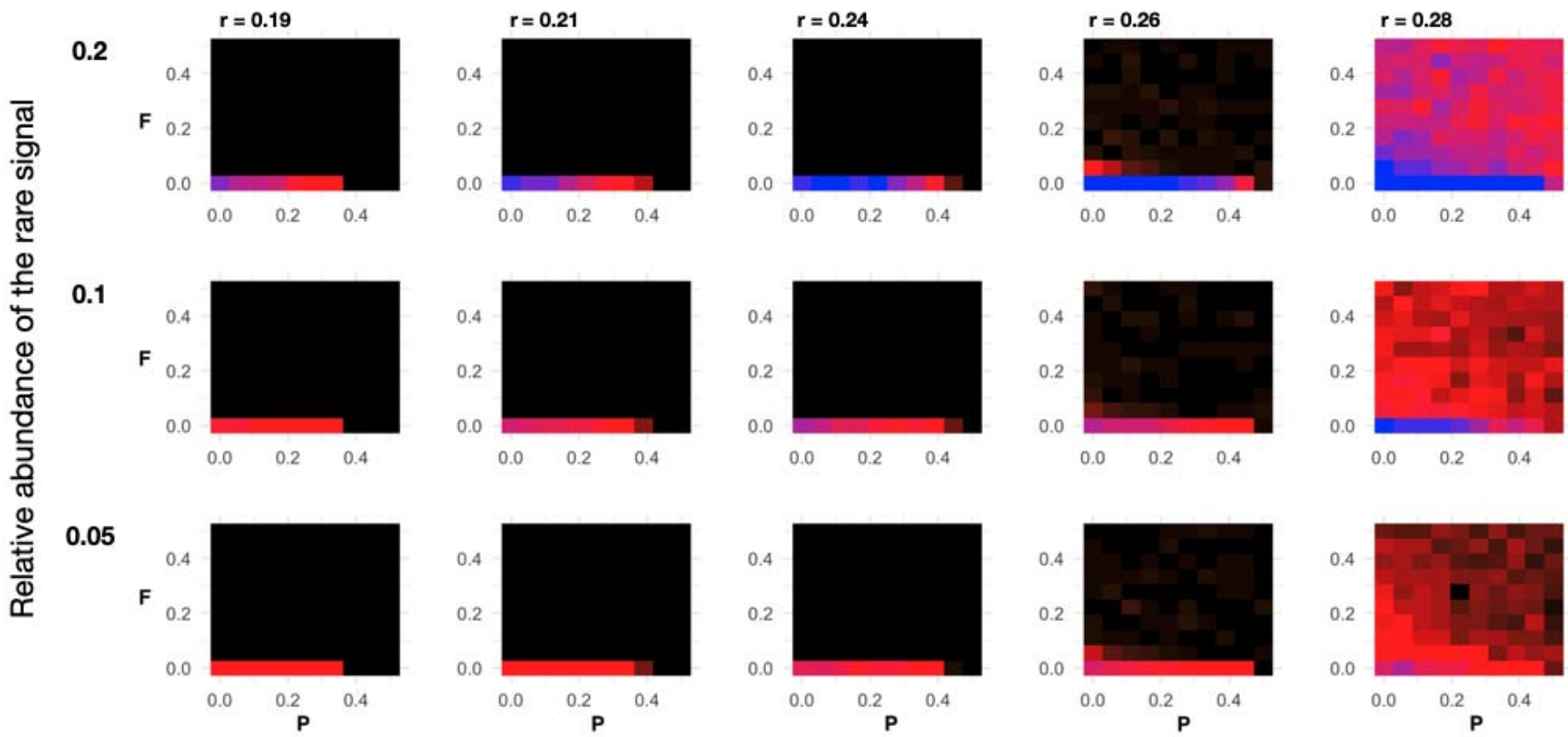
Figure 1. Outcomes of simulated predator-prey interactions after 50,000 time steps. In each graph, black cells denote the extinction of both signals, red cells denote the extinction of the rare signal, and blue cells denote the persistence of both signals. The vertical panels are simulations under five intrinsic rates of prey increase (*r*). The three horizontal panels are simulations under different relative abundances of the rare signal. The occurrence of local warning signal diversity (blue cells) is more likely under higher *r*, lower final attack probability (P), and lower forgetting rate (F).

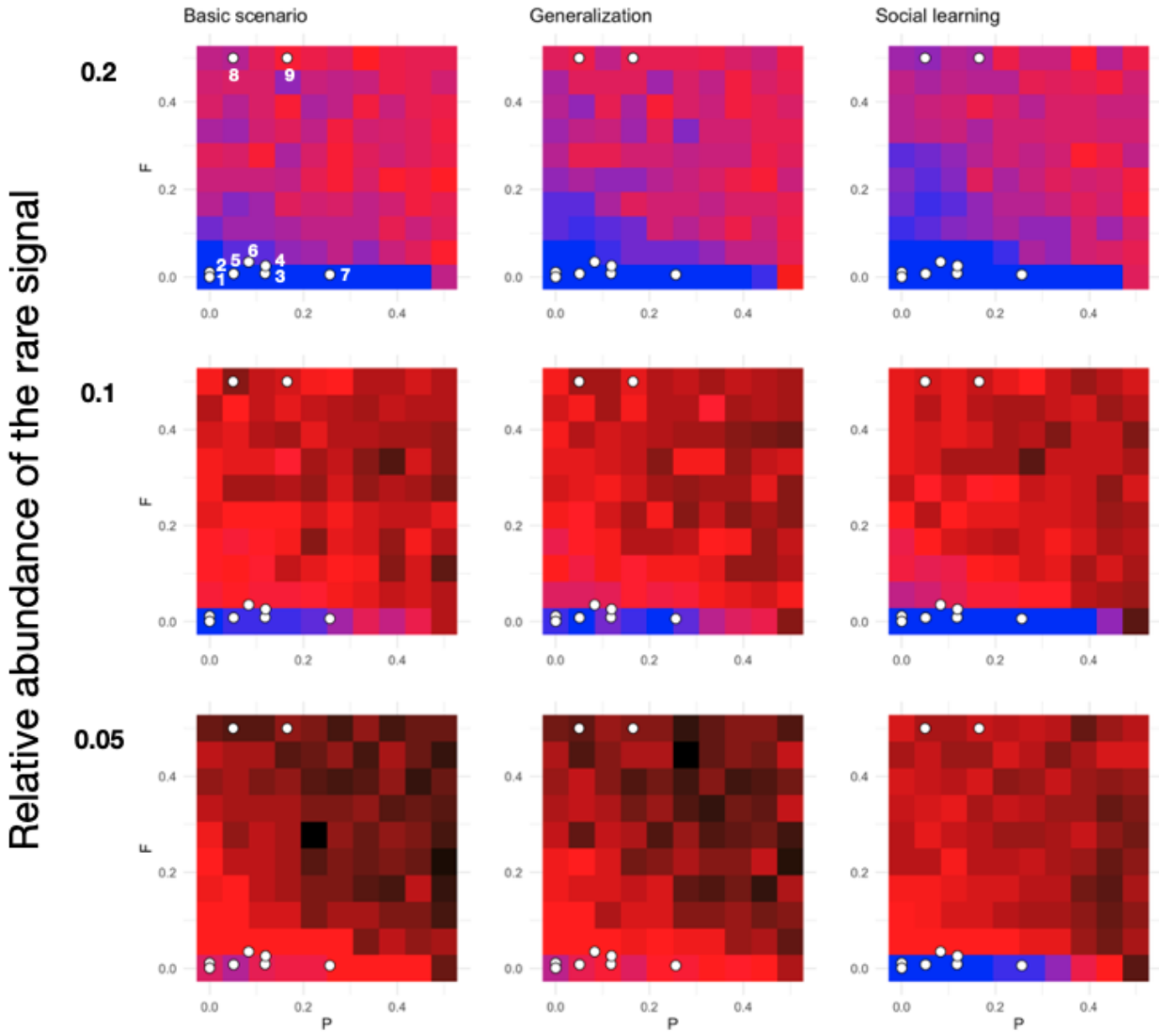
Figure 2. Simulation results illustrating the facilitative effect of generalization and social learning on the likelihood of local warning signal diversity, using $r = 0.28$. The coloring of the cells are the same as in Figure 1. The vertical panels represent results without generalization or social learning (left), with generalization (middle), and with social learning (right). The horizontal panels are results under different relative abundances of the rare prey. White dots are pairs of empirically measured final attack probability and forgetting rate from predators: 1. *Planigale maculata* (Webb *et al.* 2008), 2. *Habronattus pyrrithrix* (Taylor *et al.* 2016), 3-5. *Parus major* (Lindström *et al.* 2006), 6. *Chalcides sexlineatus* (Beneš & Veselý 2017), 7. *Gallus gallus domesticus* (Siddall & Marples 2008), 8-9. *Thalassoma bifasciatum* (Miller & Pawlik 2013)

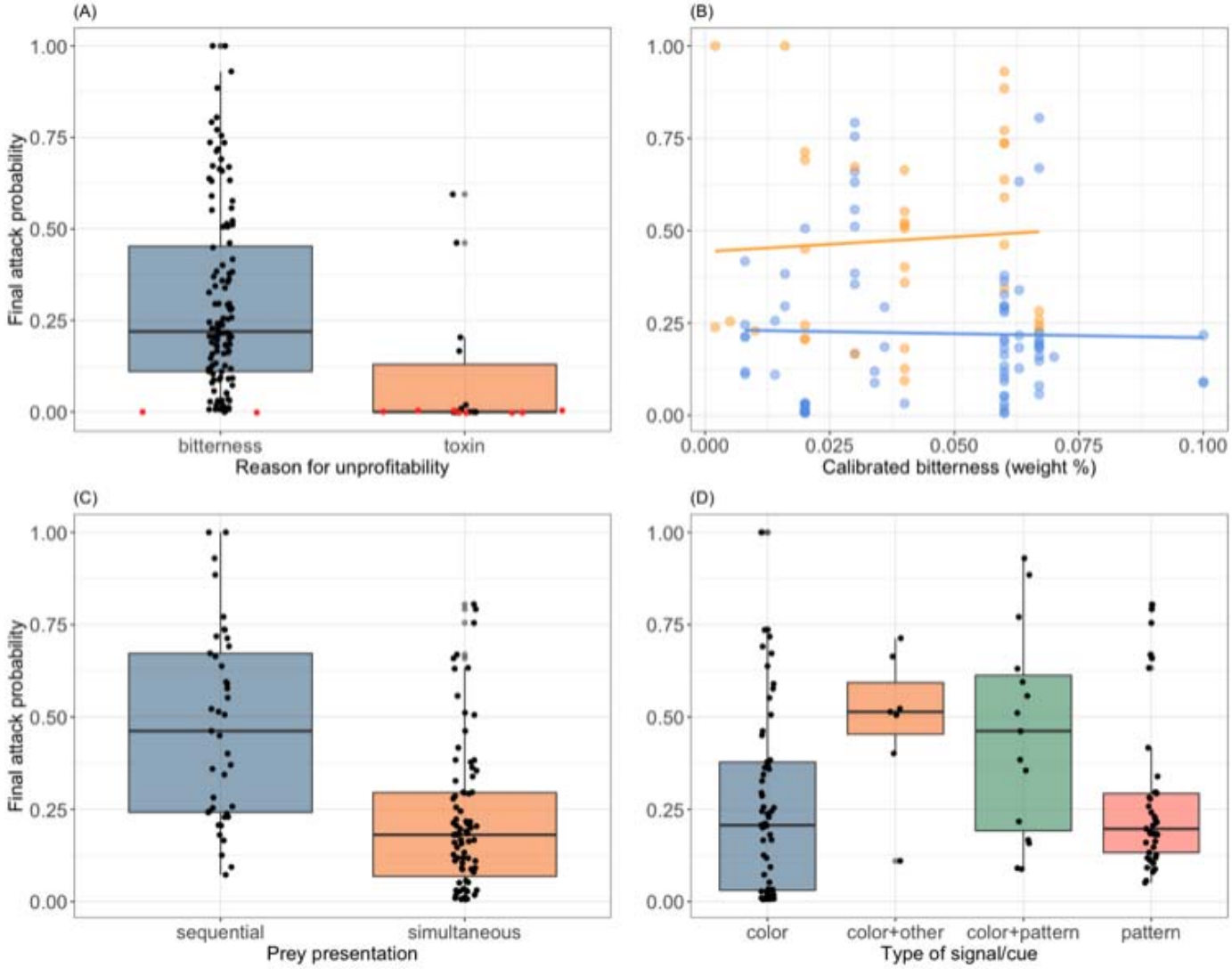
Figure 3. Factors that influenced predators' final attack probabilities towards unprofitable prey. (A) Reason for unprofitability, (B) level of bitterness, (C) manner of prey encounter, and (D) type of signal or cue. Red dots in (A) are attack probabilities that equal zero. Yellow dots and line in (B) are when predators encounter profitable and unprofitable prey sequentially, and blue dots and line are when predators encounter the two prey types simultaneously. Data were from (Gagliardo & Guilford 1993; Roper 1993; D'Heursel & Haddad 1999; Cock & Matthysen 2001; Lindström *et al.* 2001a, 2004, 2006; Skelhorn & Rowe 2005, 2006a, b, 2007, 2009, 2010; Barnett *et al.* 2007, 2012, 2014; Ihalainen *et al.* 2007; Aronsson & Gamberale-Stille 2008, 2009, 2012; Lindstedt *et al.* 2008; Siddall & Marples 2008; Salva *et al.* 2009; Rowland *et al.* 2010b, a; Skelhorn 2011; Halpin *et al.* 2013, 2014; Fabricant *et al.* 2014; Smith *et al.* 2014, 2016; Bosque *et al.* 2018; Rönkä *et al.* 2018; Chouteau *et al.* 2019; Hämäläinen *et al.* 2019, 2020; Paez *et al.* 2021; Pegram *et al.* 2021)

Table 1. Statistical results of the zero-inflated gamma regression examining the cause of variation in predators' final attack probabilities towards unprofitable prey.

Factor	**Coefficient**	**Standard error**	**z-value**	**P-value**
Conditional component				
Species				
Gallus gallus domesticus	0.52	0.28	1.86	0.063
Parus major	0.54	0.27	2.00	0.05
Sturnus vulgaris	0.70	0.37	1.91	0.06
Cause of unprofitability				
toxin	-0.29	0.31	-0.92	0.36
Type of signal/cue				
color + other	0.38	0.25	1.52	0.13
color + pattern	0.84	0.19	4.32	< 0.0001
pattern	0.40	0.25	1.60	0.11
Prey encounter				
simultaneous	-0.88	0.23	-3.80	0.0001
Zero-inflated component				
Cause of unprofitability				
toxin	4.37	0.89	4.88	< 0.0001


Relative abundance of the rare signal
0.2
0.1
0.05
r = 0.19
r = 0.21
r = 0.24
r = 0.26
r = 0.28
F
P
0.0
0.2
0.4


Basic scenario
Generalization
Social learning
Relative abundance of the rare signal
0.2
0.1
0.05
F
P
0.0
0.2
0.4
1
2
3
4
5
6
7
8
9


(A)
Final attack probability
1.00
0.75
0.50
0.25
0.00
bitterness
toxin
Reason for unprofitability
(B)
1.00
0.75
0.50
0.25
0.00
0.000
0.025
0.050
0.075
0.100
Calibrated bitterness (weight %)
(C)
Final attack probability
1.00
0.75
0.50
0.25
0.00
sequential
simultaneous
Prey presentation
(D)
1.00
0.75
0.50
0.25
0.00
color
color+other
color+pattern
pattern
Type of signal/cue