

Discriminative predation: Simultaneous and sequential encounter experiments

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Abstract There are many situations in which the ability of animals to distinguish between two similar looking objects can have significant selective consequences. For example, the objects that require discrimination may be edible versus defended prey, predators versus non-predators, or mates of varying quality. Working from the premise that there are situations in which discrimination may be more or less successful, we hypothesized that individuals find it more difficult to distinguish between stimuli when they encounter them sequentially rather than simultaneously. Our study has wide biological and psychological implications from the perspective of signal perception, signal evolution, and discrimination, and could apply to any system where individuals are making relative judgments or choices between two or more stimuli or signals. While this is a general principle that might seem intuitive, it has not been experimentally tested in this context, and is often not considered in the design of models or experiments, or in the interpretation of a wide range of studies. Our study is different from previous studies in psychology in that a) the level of similarity of stimuli are gradually varied to obtain selection gradients, and b) we discuss the implications of our study for specific areas in ecology, such as the level of perfection of mimicry in predator-prey systems. Our experiments provide evidence that it is indeed more difficult to distinguish between stimuli – and to learn to distinguish between stimuli – when they are encountered sequentially rather than simultaneously, even if the intervening time interval is short [*Current Zoology* 58 (4): 649–657, 2012].

Keywords Receiver psychology, Stimulus selection, Discrimination, Imperfect mimicry, Predation

Discrimination is a key component of successful animal behaviors. Good discriminative ability is essential for any process whereby an animal needs to make a choice or distinguish between stimuli, which often represent cues or signals that convey important information. For example, many animals need to assess the relative quality of potential mates by distinguishing between the relative extent of their cues (such as tail length, body size, or vocal depth; Andersson, 1994); predators need to distinguish between edible prey and defended prey (e.g., Cott, 1940; Ruxton et al., 2004) and between masquerading prey and inanimate objects (Skelhorn et al., 2010); and prey need to distinguish between predators and non-predators (e.g., Ferrari and Chivers, 2006; Ferrari 2007, 2008).

Discrimination between stimuli can be extremely difficult for animals. In selection between potential mates, for example, discrimination of fitness cues can be challenging due to the need to tease apart small relative differences in intraspecific variation (e.g., Radwan, 2008).

Discrimination can be particularly difficult for predatory animals in distinguishing between prey, because many prey have evolved mimicry whereby they resemble other unprofitable prey (Bates, 1862, Ruxton et al., 2004). Mimicry can also make discrimination difficult for prey due to aggressive mimicry where predators have, for example, evolved to resemble harmless organisms or objects (Pietsch, 1978; Ruxton et al., 2004). Discriminative ability is expected to improve with experience as animals learn to focus on the most distinguishable characteristics of stimuli. In psychology the improvement of ability to perform perceptual tasks with experience is termed perceptual learning (Manfred and Poggio, 2002). In the case of discrimination this can simply be learning what parts of the stimuli to pay the most attention to. It has been shown, for example, that pigeons trained to differentiate between wasps and hoverflies learn to focus on antennal length as the most reliably distinguishable component (Bain et al., 2007; Dittrich et al., 1993).

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How predators distinguish between prey has important consequences for prey evolution and survival. It has been observed that mimetic accuracy (typically level of similarity) in nature is considerably variable, from mimics that very closely resemble their models (the species being mimicked), to those that only vaguely resemble a particular model (Sherratt, 2002, Gilbert, 2005). Models have been presented that suggest a role for counteracting selective pressures (Sherratt, 2002), kin selection (Johnstone, 2002), or physiological costs (Holen and Johnstone, 2004) as limits to more effective mimetic resemblance in some prey species. Another possibility is that predator discriminative ability under different conditions could be responsible for the observed differences in mimetic accuracy between species. Specifically, whether prey are encountered by the predator at the same time or in a sequence may influence a predator's ability to discriminate between mimic and model, and could therefore bring about differences in selection pressure for mimetic accuracy. Thus, a study of differences in predator discriminative ability under conditions of sequential and simultaneous encounters may be revealing.

In the work presented here, we make the general and intuitive hypothesis that individuals find it more difficult to distinguish between stimuli when they encounter them sequentially rather than simultaneously. Regarding predator-prey interactions, we further hypothesize that when individuals observe model and mimic simultaneously, discriminative ability is high and a close resemblance is beneficial to mimetic prey; likewise, when individuals observe model and mimic sequentially, discriminative ability is lower and less accurate mimicry is sufficient to confuse a would-be predator.

To test these ideas we employed simulation experiments presenting computer-generated prey to human subjects. The use of human subject experiments has proven to be a fruitful approach in visual perception studies in both psychology (e.g., Blough, 1985; Honig and Stewart, 1988; Bruce et al., 2003) and behavioral ecology (e.g. Beatty et al., 2005; Stevens et al., 2008, Webster et al., 2009) to examine the phenomena of discrimination, categorization, and association. However, research in psychology and behavioural ecology has not examined the effect of simultaneous versus sequential presentations on levels of discriminative ability. We tasked human subjects with discriminating between two stimuli. We specifically examined discrimination of stimuli of varying levels of (dis)similarity under two

conditions: when stimuli were presented simultaneously, and when stimuli were presented sequentially. Our study is different from studies in psychology in that: a) the level of similarity of stimuli are gradually varied to obtain selection gradients, b) we discuss the implications of our study for specific areas in ecology, such as the level of perfection of mimicry in predator-prey systems.

1 Materials and Methods

The human subjects (94 student volunteers) used in these experiments had no knowledge of the experimental aims. No volunteer participated more than once in the study. Each participant was presented with clear instructions before undergoing an Ishihara simplified red/green colourblind test. Participants who did not pass the colourblind test were not informed (6 individuals), and the experiment continued as normal. The data from these participants, however, were excluded from our subsequent analysis.

The computer interactive took subjects sequentially through 30 screens. We used butterfly drawings that have a reasonable level of pattern complexity so that differences are not immediately obvious to participants (Fig. 1; supplementary material, ESM, Fig.s1). While we chose to use butterfly drawings for our stimuli, our selection is arbitrary and could have been any other appropriate stimuli, as our study was designed to test generally for differences in the ability to discern stimuli. Butterflies are however appropriate for our discussions of mimicry, which occurs in many species of butterfly. The images were created using Adobe Photoshop. The images are not examples of actual butterfly species but were designed to meet the criteria of our experiment. Our focus in designing the butterfly images used was to create stimuli consisting of multiple components so that the subject needs to learn which components to pay attention to when attempting to discriminate between forms. By creating these images we were able to gradually and systematically manipulate the level of similarity in a particular component of the stimulus.



Fig. 1 Example of two stimuli presented

There is a small difference in appearance due to a different colour intensity in a segment. The two stimuli presented here represent the maximum difference between the forms presented in the study

Two stimuli were presented and the question posed “Are they different?” The question was phrased this way because we are concentrating solely on the ability of subjects to discriminate stimuli. All of the butterfly images presented were similar to some degree, but we were interested in the ability to which subjects were able to tell them apart. Participants then had the option to select ‘yes’ or ‘no’ by clicking a respectively labeled button on the screen using the mouse. When a button was clicked the interactive moved on to the next screen. On clicking ‘yes’, a reward of +1 point was given if the stimuli were not identical, and a deduction of -1 point was incurred if they were identical. These points were given solely to provide motivation for participants to discriminate. We intentionally did not give points for clicking ‘no’ as it is analogous to turning down an opportunity to consume a prey item. In this case the subject either avoids a defended prey item (by correctly indicating that the individuals were not different, and so there was no mimic present), or suffers an opportunity cost in bypassing the prey (avoiding a mimic that might have been consumed). This matches natural conditions where predators do not receive an immediate punishment for not attacking prey; instead there is a long-term cost of a missed opportunity if the prey is edible. Due to these opportunity costs, the optimal response to the experiment was not to consistently select ‘no’ as a response to each presentation. Doing so would result in zero points, resulting in a missed opportunity cost of -15 points.

We designed our experiments to exclude associative learning in not defining any of the stimuli as profitable or unprofitable. Instead participants were simply asked to discriminate between two stimuli. Because it was impossible for the subjects to associate an appearance with profitability, associative learning (i.e., a link between appearance and level of defense) cannot possibly occur but discriminative learning can. This allowed us to isolate the mechanism of discrimination acuity under our test conditions, and also made our study more general.

On each screen, one of the stimuli was fixed, such that it was identical across all screens. The other stimulus in each pair was varied experimentally. Of the 30 screens encountered, 15 presented pairs where the stimuli were identical; in the other 15 pairs, the second stimulus had a phenotype that differed in similarity to the fixed one. Different levels of resemblance in these second stimuli were achieved by systematically increasing the intensity of green in the RGB value of a central

component of the stimuli’s pattern by 10 units for each imperfect appearance. Thus, imperfect-appearance-1 was the most accurate with a green value only 10 points higher than the fixed appearance, while imperfect-appearance-15 was the least accurate with a green value of 150 points higher than the fixed appearance (giving a distinctive fluorescent green coloration to that component of the butterfly image). This gave us a gradual range of similarities between stimuli from those that were virtually identical to those that were notably different. Although we used colour to vary the level of similarity/dissimilarity between stimuli, we could have used any number of continuously varying differences. In the natural world, for example, we find differences in length (e.g., tails in peacocks, antennae in wasps), density of speckles (e.g., on eggs or wing-patterns), similarity in movement, etc.

All participants within a treatment were presented with the same set of 30 screens, in a different random order for each participant. Varying the appearance of only one of the stimuli allows us to systematically examine differences in discrimination across different levels of dissimilarity/similarity (if we had varied both forms there would have been a bias towards presenting pairs of stimuli with more similar appearances). The position (left or right) of the fixed stimuli was also randomized for each screen, and the vertical position of each stimulus was randomly displaced by between +/- 1 and +/- 30 pixels to avoid predictable alignment.

We conducted the experiment with two treatments. In Treatment 1 we presented the stimuli simultaneously on each screen for four seconds before they disappeared. In Treatment 2 we presented the two stimuli sequentially on each screen, for four seconds each, with a second between presentations (during which no stimuli was present), such that the participant never saw both at the same time. Thus, exposure to the sequential stimuli is in sum twice that of the simultaneous stimuli. This makes the test conservative with respect to our hypothesis.

2 Results

Receiver behavior was examined over the full length of each replicate for all 30 screens, the first 15 screens of each replicate (selected to represent the uneducated phase) and the final 15 screens of each replicate (selected to represent more educated discrimination). For all of our experiments we analyze the results in terms of ‘yes’ and ‘no’ clicks when the stimuli in which appearance was varied was identical to the fixed stimulus and when it was not identical to the fixed stimulus. Analyz-

ing the overall dataset over all 30 screens we found that fewer non-identical stimuli were identified as different when stimuli were presented sequentially rather than simultaneously (Fig. 2; Mann-Whitney rank U -test: $U = 584.5$, $n_1 = 49$, $n_2 = 45$, $Z = -3.972$, $P < 0.0001$). This difference is due to different efficiencies in learning what part of the stimuli to use in discrimination. This is demonstrated by there being no attacks on the identical stimuli in either treatment in the late stage, but a significant difference in the early stage ($U = 1375$, $n_1 = 49$, $n_2 = 45$, $Z = -2.06$, $P = 0.0197$, Bonferroni correction significance level of 0.025). Educated subjects showed the same levels of discrimination in both treatments, as measured over the last 15 screens: a period after which subjects had learned to discriminate prey in both presentation formats. Conversely, we found that in the overall dataset, identical stimuli were more frequently misidentified as being different when stimuli were presented sequentially rather than simultaneously (Fig. 3; Mann-Whitney U -test: $U = 1375$, $n_1 = 49$, $n_2 = 45$, $Z = -2.06$, $P = 0.0197$). These results suggest that subjects found it more difficult to learn to discriminate when stimuli were presented sequentially.

We examined the level of similarity between stimuli

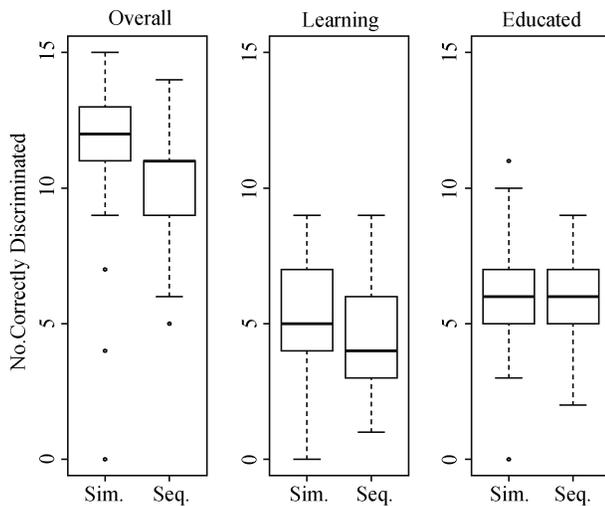


Fig. 2 Summary statistics for correct discriminations ('yes' clicks where the stimuli were different) for the simultaneous and sequential treatments

The first box ("overall") is for the full length of each replicate (all 30 screens), the second box ("learning") is for the first 15 screens of each replicate, and the third box ("educated") is for the final 15 screens of each replicate. Fewer stimuli were generally correctly discriminated ('yes' clicks) overall when they were presented sequentially, although educated subjects behaved the same in both cases. There is an extreme outlier (included in the plot) for the simultaneous treatment who failed to discriminate anything. Shown are the sample minimum, lower quartile, median, upper quartile, and sample maximum.

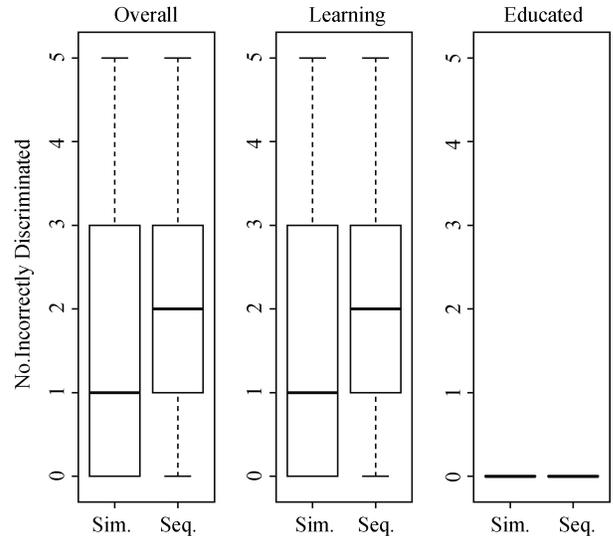


Fig. 3 Summary statistics for incorrect discriminations ('yes' clicks where the stimuli were not different) for the simultaneous and sequential treatments

For explanations of the categories see the legend of figure 1. A higher number of identical pairs of stimuli were incorrectly identified as different overall when prey were presented sequentially, although educated subjects behaved the same in both cases. Shown are the sample minimum, lower quartile, median, upper quartile, and sample maximum.

necessary in each treatment for them to be confused by subjects. To do this we recorded the minimum level of resemblance correctly discriminated for each subject. This was measured as the non-identical stimuli most similar to the fixed stimuli that could still be discerned by subjects, where 1 is virtually identical, and 15 is notably different. Once subjects were educated, the minimum level of resemblance correctly discriminated was lower for simultaneous treatment than for the sequential treatment (Fig. 4; $U = 1533$, $n_1 = 49$, $n_2 = 45$, $Z = -3.25$, $P = 0.0006$). Thus subjects could discriminate more effectively between highly similar stimuli when encounters were simultaneous than when they were sequential. There was however no significant difference when subjects were learning what part of the stimuli to use in their discrimination (first 15 screens, $U = 1254$, $n_1 = 49$, $n_2 = 45$, $Z = -1.15$, $P = 0.125$). This difference between the naïve and educated phases is likely to be due to subjects not knowing which component of the stimuli to focus on when discriminating the stimuli in the early stages. However, once they had learned what to pay attention to they were limited only by their visual discriminative ability in each case, where sequential presentations made visual discrimination of colour intensity much more difficult. We found a significant difference in the median levels of similarity discriminated

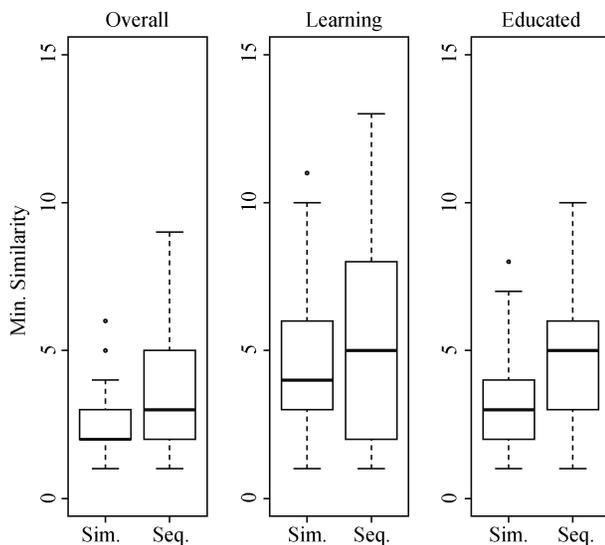


Fig. 4 Summary statistics for the minimum level of similarity of correctly discriminated stimuli for the simultaneous and sequential treatments

For explanations of the categories see the legend of figure 1. The most accurate level of imperfect similarity is 1 while the least accurate level is 15. Throughout the interactive the minimum level of similarity correctly discriminated (correct 'yes' clicks) is lower (stimuli of closer resemblance were still discriminated) for the simultaneous treatment. Shown are the sample minimum, lower quartile, median, upper quartile, and sample maximum.

between the treatments ($U = 611.5$, $n_1 = 49$, $n_2 = 45$, $Z = -3.6$, $P < 0.0001$).

3 Discussion

We provide evidence that it is more difficult to distinguish between stimuli, and to learn what component of the stimuli to use to best distinguish between stimuli, when they are encountered sequentially rather than simultaneously. This is a general principle that might be considered intuitive, yet discriminative abilities when levels of similarity are systematically varied under these different conditions has not to our knowledge been experimentally tested, and is often not considered in the design of models, or in the interpretation of a wide range of studies that focus on discriminative abilities. Several authors (Hetz and Slobodchikoff, 1988; Lindström et al., 1997; Lindström et al., 2004) have suggested that simultaneous or sequential presentations in experimental designs in receiver psychology and stimulus selection experiments might affect the results; we provide some of the first quantitative evidence to support this. These results have broad biological and psychological implications from the perspective of signal perception, signal evolution, and discrimination, and could potentially apply to any system where individuals are making relative judgments or choices between two

or more stimuli or signals.

While we used humans in our experiments, these results could apply to a wide range of systems relating to animal behaviour. Ditttrich et al. (1993), for example, showed that pigeons and humans demonstrate a general agreement in categorizing the extent of mimicry when discriminating a range of hoverflies from their wasp models. Additionally, a large number of other studies have been published in the psychology literature showing similarities between pigeons and humans in stimulus identification (e.g., Zuzne, 1970; Blough, 1985). The general agreement between pigeons and humans is evidence that we can use humans effectively as discriminators when studying general concepts, such as the one we studied here (see also Summers and Clough, 2001). Beatty et al. (2005) also demonstrated that humans behave remarkably similarly to great tits *Parus major* in a foraging task involving both associative and discriminative learning. Our finding that individuals learn to pay attention to the most distinguishable part of the stimuli relates to the finding that pigeons trained to differentiate between wasps and hoverflies learn to focus on antennal length as the most reliably distinguishable component (Bain et al., 2007; Ditttrich et al., 1993). However, we show that this task of learning what aspect to pay attention to is more difficult when encounters are sequential. Discrimination is also shown to be more difficult when encounters are sequential, even when the subjects know which parts of the stimuli to pay attention to. These findings are even more noteworthy considering the short interval between encounters in our sequential presentations.

Chittka and Osorio (2007) presented a verbal argument to explain the evolution of imperfect mimicry from the perspective of cognitive predator responses to mimicry. One of their suggestions was that imperfect mimics confuse predators enough to survive: that in the time it takes for predators to discriminate them and make a decision as to whether or not to attack, the prey will have opportunity to escape. This suggests that the slower the discriminative ability of the predator, the less perfect the mimicry needs to be. Although their idea involves discrimination learning, its mechanics are reliant on predator speed-accuracy trade-offs. We suggest a novel explanation for the evolution of imperfect mimicry, based purely on predator discriminative ability under two different simple scenarios (with equal speed-accuracy tradeoffs). We show that discriminative predation is more difficult when prey are encountered

sequentially than when they are encountered simultaneously. This is because discrimination is easier when a direct comparison can be made between two prey individuals, rather than a comparison between a current prey individual and a memory (even if extremely recent). From the perspective of Chittka and Osario (2007), discrimination accuracy is the product of time spent by the predator in assessing prey and the cognitive ability of the predator to discriminate. Thus there is a direct relationship between time spent assessing prey and discrimination accuracy. In our experiments, however, we keep time spent assessing prey constant and only vary the presentation between simultaneous and sequential encounters.

Recently, Skelhorn and Ruxton (2010) performed experiments with domestic chicks and masquerading prey (in this case twig-mimicking caterpillars). Chicks were first exposed to the model (twigs) and allowed to experience them. Later, they were presented caterpillars under conditions when their models were present nearby or absent; in the latter case, two caterpillars were presented rather than a caterpillar and twig. They found the intriguing result of reduced benefit from masquerade when the model was present. Here, we more directly tested differences in presentation context over a range of systematic fine adjustments to the level of mimetic resemblance (i.e. level of similarity between stimuli) and examined how different levels of similarity are perceived in simultaneous versus sequential presentations. We found that the level of potential benefit of mimicry, such as being mistaken for a similar defended prey item, is closely related not only to the level of mimetic accuracy, but also the conditions under which mimic and model are encountered.

A related study in psychology is also revealing. Symonds and Hall (1995) tasked rats with discriminating between stimuli (*A* and *B*). There were three treatments related to pre-exposure to the stimuli. In the first, there was no pre-exposure, in the second rats were pre-exposed to the stimuli in alternating order (*A*, *B*, *A*, *B*, etc) in the third pre-exposure was 'blocked' so that all pre-exposures of stimuli *A* were presented before all pre-exposures of stimuli *B* were presented. The rats that experienced the alternating pre-exposure were able to readily discriminate between the stimuli, whereas those that experienced the blocked pre-exposure were unable to discriminate between them. This has also been demonstrated in chicks (Honey et al. 1994) and humans (Mundy et al 2006; 2007).

When considering the implications of our experi-

ments to the evolution of mimicry, our results suggest stronger selection for accurate Batesian mimicry when prey are encountered simultaneously than when they are encountered sequentially. Predators are also shown to generalize more widely when prey are presented sequentially. The corollary is that we should expect imperfect mimicry to be more common where profitable and unprofitable species are encountered sequentially. Because of wider generalization, we should also expect mimicry in general to be more common with sequential encounters (Franks and Sherratt, 2007; Ruxton et al., 2008). In considering Müllerian mimicry, in which groups of *defended* species share a common phenotype (Müller, 1879), our experiments have different implications. When preys are encountered sequentially, predators make more errors by incorrectly identifying identical individuals as being different. In Müllerian mimicry this would have the consequence of predators mistakenly attacking defended prey because they have incorrectly identified it as being distinct from its co-model, even when it is in fact identical. However, predators generalize more widely when prey are encountered sequentially, meaning there is less selection on Müllerian mimics to resemble each other perfectly.

In the wild, where model and mimic are spatially well-mixed (in that they appear in the same locality) and both are fairly common or dense, we would expect more simultaneous encounters and consequently good mimicry. In environments where model and mimic are less well-mixed spatially (so there are more sequential encounters) we would expect imperfect mimicry. Predators will often encounter prey on an individual basis, such that they may need to take what they have learned on previous encounters and apply it to a prey item currently under consideration (Pinheiro, 2007). This is likely to happen as a predator moves through its environment. Likewise, some ecological conditions such as communal roosting can bring about large clusters of different potential prey species, such that the predator will have opportunity to compare directly between potential prey (DeVries, 1987; Pinheiro et al., 2008). One situation where we would expect simultaneous encounters to be standard is in brood parasitism, where egg mimicry is important (e.g., Lyon, 2003; Spottiswoode and Stevens, 2010). Because eggs are positioned next to each other in the nest, our results predict that the level of mimicry of the parasitic egg needs to be extremely high to succeed. This prediction is supported by large-sample studies of eggs showing that there are significant correlations between cuckoo and host eggs

within a clutch in volume, ground colour, and size and percentage coverage of the spots (Moksnes and Roskaft, 1995). Similarities are also seen amongst defended insects that feed on milkweed (genus *Asclepias*), the source of their chemical defense. These Müllerian mimics are members of a number of different insect orders (e.g. Lepidoptera, Hemiptera and Coleoptera), but share very similar phenotypes (Ruxton et al., 2004; Plate 2 and elsewhere).

In addition to the evolution of prey appearance, selection on prey behavior in terms of mixing strategy might evolve. In Batesian mimicry this strategy could be part of the 'advergence' arms race (Marshall, 2009) where the model uses spatial mixing as a way of distinguishing itself from the mimic. In response we might expect subsequent selection on the mimic to avoid spatial mixing (at the extreme by relocating). Profitable prey are known to be typically dispersed rather than aggregated (Nilsson and Forsman, 2003; Alatalo and Mappes, 1996; Beatty et al., 2005). There are many benefits of this (Sillén-Tullberg, 1988; Sillén-Tullberg and Leimar, 1988; Beatty et al., 2005) and our study suggests another in the case of Batesian mimics: it is difficult for models to spatially mix with them if they are disperse, and thus their level of mimicry is improved without modifications to their appearance. There is also evidence for temporal differences in daily activity of Batesian mimics and their models, such that mimics are active later in the day than their models (Pinheiro, 2007). These differences could also minimize the likelihood of predators encountering model and mimic simultaneously.

Further, there may be ecological implications of the observed differences in mimetic accuracy in types of prey. There are some fundamental differences in ecological constraints on Batesian and Müllerian mimics. For many Müllerian mimics, the defense they share may be derived from a common specialized source, such as a host plant or insect (Jaenike, 1990; Darst et al., 2005). This requires that these mimics spend considerable time where these food sources are available, and thus may have a more clustered distribution in space, increasing the probability that predators will encounter individuals simultaneously. Batesian mimics, not under such constraints, may be able to move more freely in their environment and thus minimize the amount of time they are seen with their models. These ecological differences may help to explain the large range in mimetic accuracy seen between some Batesian mimics.

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References

- Alatalo RV, Mappes J, 1996. Tracking the evolution of warning signals. *Nature* 383: 708–710.
- Andersson M, 1994. *Sexual Selection*. Princeton, NJ: Princeton University Press.
- Bain RS, Rashed A, Cowper VJ, Gilbert FS, Sherratt TN, 2007. The key mimetic features of hoverflies through avian eyes. *Proc. Roy. Soc. B*. 274: 1949–1954.
- Bates HW, 1862. Contributions to an insect fauna of the Amazon valley. *Lepidopetra: Heliconidae*. *Tran. Linn. Soc. Lon.* 23: 495–566.
- Beatty C, Bain R, Sherratt T, 2005. The evolution of aggregation in profitable and unprofitable prey. *Anim Behav* 70: 199–208.
- Blough DS, 1985. Discrimination of letters and random dot patterns by pigeons and humans. *Jour. Exp. Psychol: Anim. Behav. Process* 11:261–280.
- Bruce V, Georgeson MA, Green PR, 2003. *Visual Perception: Physiology, Psychology and Ecology*. London: Psychology Press.
- Chittka L, Osorio D, 2007. Cognitive dimensions of predator responses to imperfect mimicry. *PLoS Bio.* 5:e339.
- Cott HB, 1940. *Adaptive Coloration in Animals*. London: Methuen and Co, Ltd..
- Darst CR, Menendez PA, Coloma LA, Cannatella DC, 2005. Evolution of dietary specialization and chemical defense in poison frogs: A comparative analysis. *Am. Nat.* 165: 56–69.
- DeVries PJ, 1987. *The Butterflies of Costa Rica and Their Natural History*. Princeton: Princeton University Press
- Dittrich W, Gilbert F, Green P, Mcgregor P, 1993. Imperfect mimicry: A pigeon's perspective. *Proc. Roy. Soc. B* 251: 195–200.
- Ferrari MCO, Chivers DP, 2006. Learning threat-sensitive predator avoidance: How do fathead minnows incorporate conflicting information? *Anim. Behav.* 71: 19–26.
- Ferrari MCO, Gonzalo A, Messier F, Chivers DP, 2007. Generalization of learned predator recognition: An experimental test and framework for future studies. *Proc. Roy. Soc. B* 274: 1853–1859.
- Ferrari MCO, Messier F, Chivers DP, 2008. Can prey exhibit threat-sensitive generalization of predator recognition? Extending the Predator Recognition Continuum Hypothesis. *Proc. Roy. Soc. B* 275: 1811–1816.
- Franks DW, Sherratt TN, 2007. The evolution of multicomponent mimicry. *Jour. Theor. Bio.* 244: 631–639.
- Gilbert F, 2005. The evolution of imperfect mimicry. In: Fellowes MDE, Holloway GJ, Rolff J ed. *Insect Evolutionary Ecology*. Wallingford, UK: CABI, 231–288.
- Hetz M, Slobodchikoff CN, 1988. Predation pressure on an imperfect Batesian mimicry complex in the presence of alternative prey. *Oecologia* 76: 570–573.
- Honey RC, Bateson P, Horn G, 1994. The role of stimulus com-

- parison in perceptual learning: An investigation with the domestic chick. *Quart. Jour. Exp. Psychol.* 47B: 83–103.
- Holen O, Johnstone R, 2004. The evolution of mimicry under constraints. *Am. Nat.* 164: 598–613.
- Honig WK, Stewart KE, 1988. Pigeons can discriminate locations presented in pictures. *J. Exp. Anal. Behav.* 50, 541–551
- Jaenike J, 1990. Host specialization in phytophagous insects. *Ann. Rev. Ecol. Syst.* 21: 243–273.
- Johnstone R, 2002. The evolution of inaccurate mimics. *Nature* 418: 524–526.
- Lyon BE, 2003. Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature* 422: 495–499.
- Lindström L, Alatalo R, Mappes J, 1997. Imperfect Batesian mimicry: The effects of the frequency and the distastefulness of the model. *Proc. Roy. Soc. B* 264: 149–153.
- Lindström L, Alatalo RV, Lyytinen A, Mappes J, 2004. The effect of alternative prey on the dynamics of Batesian and Müllerian mimics. *Evol* 58: 1294–1302.
- Manfred F, Poggio T, 2002. *Perceptual Learning*. Cambridge: The MIT Press.
- Marshall G, 2009. On diaposematism, with reference to some limitations of the Müllerian mimicry. *Trans. Roy. Entomol. Soc. Lon.* 56: 93–142
- Moksnes A, Roskaft E, 1995. Egg-morphs and host preference in the common cuckoo *Cuculus canorus*: An analysis of cuckoo and host eggs from European museums and collections. *Jour. Zool.* 236: 625–648.
- Müller F, 1879. *Ituna* and *Thyridia*: A remarkable case of mimicry in butterflies (R. Meldola translation) *Procl. Entomol. Soc. Lon.* 1879: 20–29.
- Mundy ME, Dwyer DM, Honey RC, 2006. Inhibitory associations contribute to perceptual learning in humans. *Jour. Exp. Psychol.: Anim. Behav. Process* 32: 178–184.
- Mundy ME, Honey RC, Dwyer DM, 2007. Simultaneous presentation of similar stimuli produces perceptual learning in human picture processing. *Jour. Exp. Psychol: Anim Behav Process* 33: 124–138.
- Nilsson M, Forsman A, 2003. Evolution of conspicuous coloration, body size and gregariousness: A comparative analysis of lepidopteran larvae. *Evol. Ecol.* 17: 51–66.
- Pietsch TW, Grobecker DB, 1978 The compleat angler: Aggressive mimicry in an antennariid anglerfish. *Science* 201: 369–370.
- Pinheiro CEG, 2007. Asynchrony in daily activity patterns of butterfly models and mimics. *Jour. Tropic Ecol.* 23: 119–123.
- Pinheiro CEG, Meri Medri Í, Moreyra Salcedo AK, 2008. Why do the ithomiines (Lepidoptera, Nymphalidae) aggregate? Notes on a Butterfly Pocket in Central Brazil *Revista Brasileira de Entomologia* 52: 610–614.
- Radwan J, 2008. Maintenance of genetic variation in sexual ornaments: A review of the mechanisms. *Biomed Life Sci* 134: 113–127.
- Ruxton G, Franks D, Balogh ACV, Leimar O, 2008. Evolutionary implications of the form of predator generalisation for aposematic signals and mimicry in prey. *Evol.* 62: 2913–2921.
- Ruxton GD, Sherratt TN, Speed MP, 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford: Oxford University Press.
- Sherratt TN, 2002. The evolution of imperfect mimicry. *Behav. Ecol.* 13: 821–826.
- Sillén-Tullberg BS, 1988. Evolution of gregariousness in aposematic butterfly larvae: A phylogenetic analysis. *Evol.* 42: 293–305.
- Sillén-Tullberg BS, Leimar O, 1988. The evolution of gregariousness in distasteful insects as a defense against predators. *Am. Nat.* 132: 723–734.
- Skelhorn J, Rowland HM, Speed MP, Ruxton GD, 2010. Masquerade: Camouflage without crypsis. *Science* 327: 51.
- Skelhorn J, Ruxton GD, 2010. Predators are less likely to misclassify masquerading prey when their models are present. *Biol Lett.* 6: 597–599.
- Spottiswoode CN, Stevens M, 2010. Visual modeling shows that avian host parents use multiple visual cues in rejecting parasitic eggs. *Proc. Natl. Acad. Sci. USA* 107: 8672–8676.
- Stevens M, Yule DH, Ruxton GD, 2008. Dazzle coloration and prey movement. *Proc. Roy. Soc. B* 275:2 639–2643.
- Summers K, Clough M, 2001. The evolution of coloration and toxicity in the poison frog family (Dendrobatidae). *Proc. Natl. Acad. Sci. USA* 98: 6227–6232.
- Symonds M, Hall G, 1995. Perceptual learning in flavor aversion conditioning: Roles of stimulus comparison and latent inhibition of common stimulus elements. *Learn and Motivation* 26: 203–219.
- Webster RJ, Callahan A, Godin GJ, Sherratt TN, 2009 Behaviourally mediated crypsis in two nocturnal moths with contrasting appearance. *Phil. Trans. Roy. Soc. B* 364: 503–510.
- Zuzne L, 1970. *Visual Perception of Form*. New York: Academic Press.

Supplementary Material: Discriminative Predation

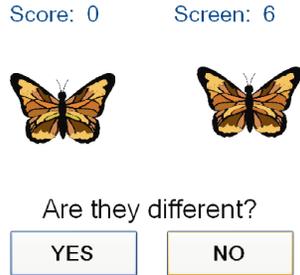


Fig. S1 Example screenshot from interactive

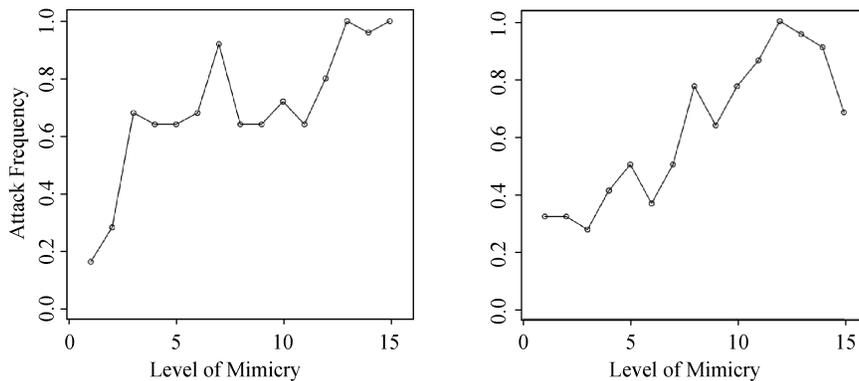


Fig. S2 The frequency of ‘attacks’ (yes clicks) for the first 15 screens (total number of attacks for each mimicry level normalized between 0 and 1) for (a) simultaneous treatment, (b) sequential treatment

The closest mimicry level achievable (without perfection) is 1 while is the furthest achievable is 15.

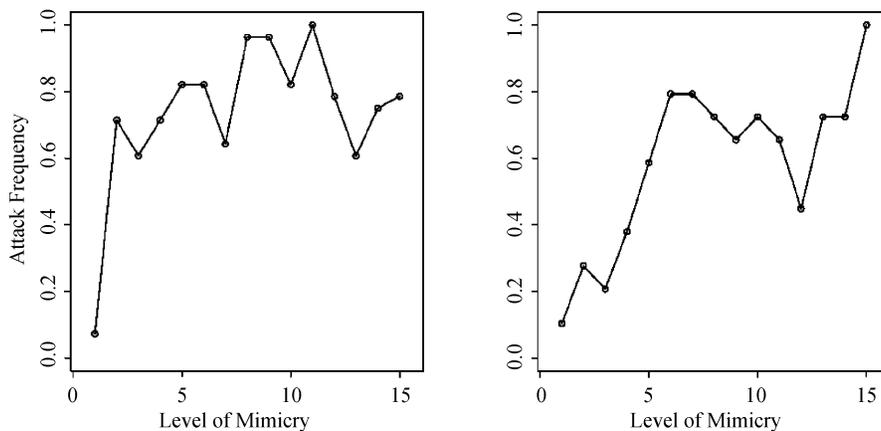


Fig. S3 The frequency of ‘attacks’ (yes clicks) for the final 15 screens (total number of attacks for each mimicry level normalized between 0 and 1) for (a) simultaneous treatment, (b) sequential treatment

The closest mimicry level achievable (without perfection) is 1 while is the furthest achievable is 15.