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Original Article

Do crab spiders perceive Batesian mimicry in hoverflies?

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Many putative Batesian mimics only approximately resemble their supposed models, and such "imperfect" mimics are readily distinguished from defended species by humans and other vertebrates. One explanation for the existence of imperfect mimics is that the most important predators of many mimics have very different sensory and cognitive abilities from those of a typical vertebrate. In such circumstances, selection for more accurate mimicry, as perceived by humans, may be reduced. Little is known, however, about how invertebrate predators perceive and respond to mimicry in insect prey. Here, we investigate the foraging behavior of the crab spider *Synema globosum*, an important predator of flower-visiting insects at our field site, which frequently encounters both Batesian mimics (hoverflies—Diptera: Syrphidae) and their models (bees and wasps—Hymenoptera). In the field, we found that spiders can distinguish among dipteran and hymenopteran prey taxa, frequently attacking some models and mimics, but avoiding others. Laboratory experiments suggest that some apparently accurate mimic taxa are more likely to be avoided when spiders have prior experience of an aversive wasp model. Avoidance by spiders of black and yellow striped artificial prey suggests visual cues play a role in prey selection, but there was no evidence that olfactory cues are used to identify dangerous or noxious species. Overall, our results provide some support for the hypothesis that invertebrate predator behavior can generate selection on visual signals in putative Batesian mimics.

Key words: **aposematism, color patterns, evolution, imperfect Batesian mimicry, predator, selection, visual signals.**

INTRODUCTION

Batesian mimics are palatable and harmless species that resemble aversive or defended prey, many of which advertise their unprofitability to predators with aposematic warning signals (Bates 1862; Ruxton et al. 2004). They gain protection from attack by fooling predators into misidentifying them as unprofitable or dangerous. While for over a century Batesian mimicry has been considered a classic example of adaptive evolution, it has long been recognized that many supposed mimics only approximately resemble their putative models (Sherratt 2002; Gilbert 2005). This poses the question: if natural selection by predators favors the ever closer resemblance of a mimic to its model, why are so many mimics clearly "imperfect" (Edmunds 2000)? There are several possible answers to this question (reviewed in Gilbert 2005), with recent evidence suggesting that selection for perfect mimicry may be relaxed in palatable but relatively unprofitable prey (Penney et al. 2012), and that mimetic accuracy may be traded-off against thermoregulatory costs (Taylor et al., in review). However, there is no consensus about the most important factors influencing the precision with which mimics resemble their models (Gilbert 2005).

A widely recognized problem with studies of mimicry is that, although many mimics appear imperfect to human or other vertebrate eyes, the predators that are actually responsible for selection of mimetic phenotypes may include taxa (e.g., insects and spiders) with very different sensory and cognitive abilities (Stevens 2007). Thus, it is entirely possible that real-world predators perceive apparently imperfect mimics as being indistinguishable from aversive or defended prey (Cuthill and Bennett 1993). As yet, however, there is very little empirical evidence for differences in perception of prey signals among predators, especially in natural situations, and invertebrate predators in particular have been neglected in the literature on mimicry (but see Kauppinen and Mappes 2003; Rashed et al. 2005). This gap in our knowledge, combined with the fact that we know almost nothing about the relative importance of different current and historical causes of selection on warning and mimetic patterns in natural populations of invertebrates, seriously limits our ability to test hypotheses about the evolution of aposematism and mimicry.

It was noted as far back as the origin of the theory of Batesian mimicry that a wide range of predators avoided aposematic butterflies including dragonflies, mantids, and flies (see Carpenter and Ford 1933), but to date the majority of studies of predator perceptions of aposematism and Batesian mimicry have focused on birds (e.g., Mostler 1935; Dittrich et al. 1993; Ham et al. 2006) and other vertebrates (e.g., Nonacs 1985; Hetz and Slobodchikoff 1988;

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Osorio et al. 1999). Birds have been seen as important predators of a wide range of aposematic and mimetic prey taxa, as well as being easily trained and having a predictable behavioral repertoire, making them ideal study species. Early experiments demonstrated that avian predators have the potential to select for Batesian mimicry, but that they are not fooled by relatively imperfect mimics (Mostler 1935). These experiments showed that the more closely hoverflies (Diptera: Syrphidae) appeared to mimic hymenopteran models, the more protection they received from predation. They also showed that birds were less likely to attack certain mimics following experience with their proposed hymenopteran model. Overall, these experiments suggested that birds were generally deceived by mimics, but that the extent of protection enjoyed was dependent on the closeness of the mimic's resemblance to its model.

Although birds demonstrate some differences from humans in the perception of prey signals (Dittrich et al. 1993; Bain et al. 2007), and may have some cognitive and sensory limitation that impact on their ability to identify prey correctly (Chittka and Osorio 2007; Kikuchi and Pfennig 2010), many mimetic hoverfly species appear to gain little protection from birds as a result of their resemblance to their hymenopteran models (Dlusskii 1984). This would suggest that the potential for avian predation to select for inaccurate Batesian mimicry in invertebrate prey is limited. However, mimetic hoverflies are also attacked by many invertebrate predators (Howarth and Edmunds 2000), and these species are likely to view the mimetic patterns of their prey in a very different way from humans and other vertebrates.

In spite of the strong evidence for the visual and cognitive abilities of invertebrates (e.g., Tibbetts 2002; Dyer and Chittka 2004; Pohl et al. 2008), few studies have considered invertebrate predator responses to warning signals and to putative Batesian mimicry. Dejean (1988) found that hunting workers of the ant species, *Odontomachus troglodytes*, not only learned to avoid the warningly colored larvae of an African chrysomelid beetle but also retained this behavior for up to 28 days following an initial costly experience. Similarly, mantids can learn to avoid aposematic prey (Gelperin 1968) and extend their avoidance to similarly colored palatable mimics (Berenbaum and Miliczky 1984), and palatable, nonmimetic flies given artificial warning signals gained protection from predation by dragonflies (Kauppinen and Mappes 2003). Taken together, these studies strongly suggest that invertebrate predators have the potential to play a role in selecting for aposematism and Batesian mimicry (but see Rashed et al. 2005 for evidence to the contrary).

Spiders are probably important predators of many aposematic and mimetic invertebrates: we know, for example, that crab spiders (Thomisidae) are a major source of mortality in honeybees (*Apis mellifera*) in some circumstances (Reader et al. 2006). However, we have no direct estimate of the relative contributions of spiders and other predators (e.g., birds) to selection on invertebrate color patterns, and the extent to which spiders detect and respond to aposematism and mimicry remains almost completely unexplored. Spiders appear to be capable of learning to avoid signals associated with a cost (Vasconcellosneto and Lewinsohn 1984; Huang et al. 2011), and some species have been shown to have an innate aversion toward defended prey (Nelson and Jackson 2006). Most spiders are thought to have relatively poor vision and rely mainly on other senses such as olfaction and mechanoreception when foraging (Herbstein 2011). Thus, it has been suggested that spiders may select for prey warning signals and mimicry in other modalities (Vasconcellosneto and Lewinsohn 1984). However, some spiders do rely heavily on vision while hunting. Jumping spiders (Salticidae) have remarkably acute vision, which may be equivalent to that of some birds (Williams and McIntyre 1980). They are known to rely on visual cues for the identification of palatable prey, predatory threats, and other aspects of their environment (Harland and Jackson 2004). Furthermore, they have been proposed as important agents of selection on some mimetic signals; juveniles of myrmecomorphic salticids appear to benefit from Batesian mimicry of ants by avoiding attacks from larger salticids (Huang et al. 2011).

Like salticids, crab spiders are cursorial (non-web-building) predators of various aposematic and mimetic invertebrates (Reader et al. 2006; Morse 2007). Relatively little is known about crab spider vision, but they are considered to be predominantly visual foragers, being able to resolve objects at a resolution similar to that achieved by the compound eyes of some insects (Schmalhofer and Casey 1999). Observations of the crab spider *Misumena vatia* suggest that it relies heavily on mechanoreceptors for prey detection and may attack prey relatively indiscriminately (Morse 2007). The ability of crab spiders, however, or any other spiders, to detect or respond to differences between defended and undefended, or mimetic and nonmimetic prey, has not been examined in detail (but see Tyshchenko 1961). Hence, the potential of spiders to select for Batesian mimicry remains unexplored, and the consequences of the differences between their sensory and cognitive abilities and those of vertebrates for the evolution of mimetic accuracy in prey such as hoverflies are unknown.

In this study, with a series of field and laboratory experiments, we explore the potential of a crab spider (*Synema globosum* Franganillo) to discriminate among aposematic, defended Hymenoptera and visually mimetic hoverflies. We ask whether venomous wasps and bees are aversive to spiders, and whether prior experience with such species makes spiders more likely to avoid their supposed Batesian mimics. Finally, we ask whether any discrimination among prey types is achieved through the use of visual or olfactory cues. Our ultimate objective is to shed light on the hypothesis that predators with relatively poor visual acuity compared with vertebrates could be responsible for the evolution of approximate or imperfect visual mimicry in their prey.

METHODS

Study system

We examined behavioral responses of *S. globosum* to common aposematic and mimetic prey, and artificial models of prey, at our field site in Sobreda de Caparica, Lisboa, Portugal (38°33′67″N, 009°11′34″W). Adult *S. globosum* are the most abundant flower-dwelling predators at our site in spring (Ibarra 2013) and are frequently observed attacking flower-visiting arthropods, including a range of mimetic hoverflies and other nonmimetic flies. Although *S. globosum* frequently kills honeybee workers (Reader et al. 2006), we have not observed it attacking any of the venomous social wasps (Hymenoptera: Vespidae) that visit flowers to feed on nectar and/or hunt for prey, the most common of which is the paper wasp *Polistes dominula* (also referred to as *P. dominulus*). *Polistes dominula* appears to be a threat to *S. globosum*: spiders were attacked and consumed by wasps when kept in captivity together.

For our experiments, we collected individuals of 7 species of Diptera and 2 species of Hymenoptera from flowers on which *S. globosum* is known to forage (Figure 1; Table 1). Four of the dipteran species have black and yellow or orange stripes on the abdomen and appear to be mimics of vespid wasps such as *P. dominula*, 1

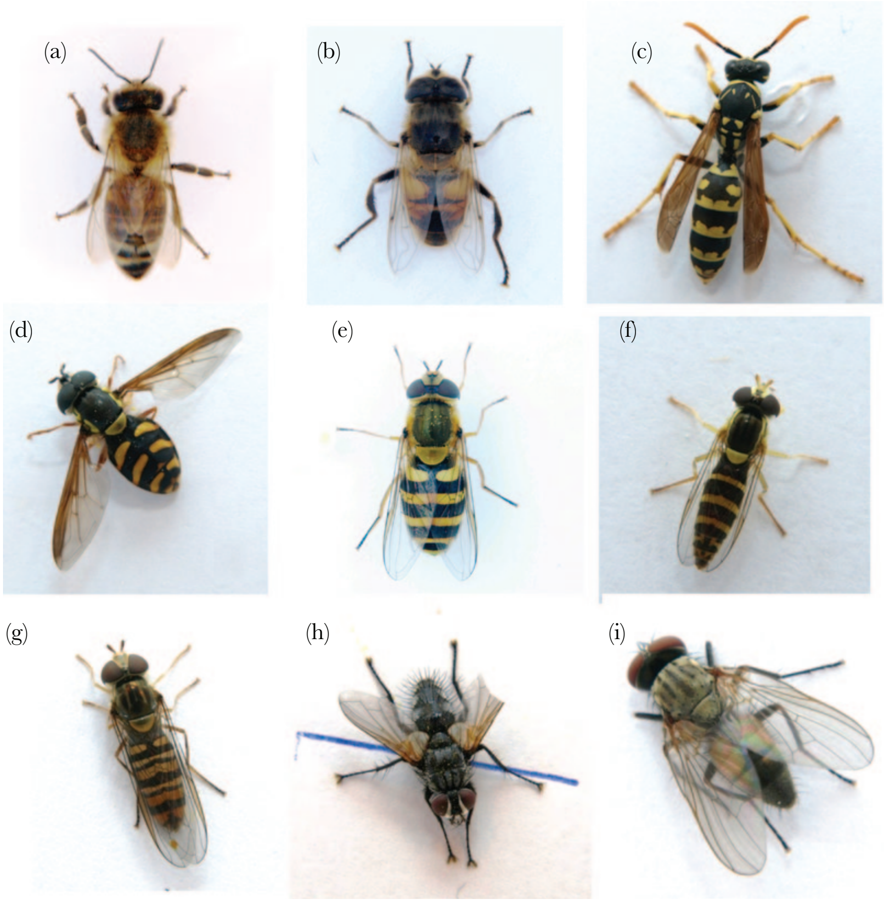

Figure 1

Nine insect species offered to crab spiders in experiments. (a) The honeybee (*Apis mellifera*) and (b) its mimic (*Eristalis tenax*). (c) The paper wasp (*Polistes dominula*). Wasp mimics in descending order of accuracy, as perceived by humans: (d) *Chrysotoxum intermedium*, (e) *Syrphus ribesii*, (f) *Sphaerophoria scripta*, and (g) *Episyrphus balteatus*. Nonmimetic flies: (h) *Sarcophaga carnaria* and (I) *Fannia canicularis*. Images a, b, and e are courtesy of Chris Taylor. Other images were taken by R.M.

is apparently a honeybee mimic, and 2 are apparently nonmimetic flies. Excluding the honeybee mimic (*Eristalis tenax*), we assigned the dipteran species a rank according to the accuracy with which human volunteers perceived they mimicked *P. dominula*. Twenty-seven students at the University of Nottingham were shown 1 photograph selected at random from 3 high-resolution color photographs of *P. dominula*, and 1 of 3 photographs (again, selected at random) of each of the 6 fly species. We used the best images of each species to which we had access, but the scale, lighting conditions, etc. of these images varied as was not always known. Volunteers were asked to rank the fly species in the photographs in order of resemblance to *P. dominula*. We did not emphasize the importance of any particular cues/criteria in scoring resemblance.

Experiment 1: prey preference

A field experiment was carried out to determine if crab spiders distinguish among prey types and to establish the palatability of the defended model species (*P. dominula* and *A. mellifera*). Between 09:00 and 18:00 on 19 sunny days between 3 April and 5 May 2008, live model and mimic species were offered to *S. globosum* found foraging on flowers in the field and their subsequent response recorded. Individuals of 7 prey species (Table 1) were caught with a sweep net no more than 24 h before the experiment and temporarily stored in specimen tubes. Immediately before the experiment, each individual was stunned using carbon dioxide gas, its wings were removed, and a piece of very fine metal wire (350 mm long and 0.125 mm in diameter) tied between its head and thorax. The removal of the wings ensured that the prey were easier to manipulate and minimized the extent of any auditory or behavioral cues that might influence spider behavior. Each individual was suspended on its wire from a 30-cm wooden stick and offered to a different spider ($n = 180$; 139 females and 41 males). An individual of a randomly selected prey taxon was “dangled” 5–10 mm above the center of a haphazardly selected flower with a resident spider. Random selection of prey types meant that sample sizes were not necessarily equal. Individuals were dangled for 5 min or until they were killed by the spider. In addition to whether prey were killed and consumed by spiders, 7 distinct spider behaviors were recorded during trials (Table 2). During the course of Experiment 1, it became clear that “retreat” actually encompassed 2 distinct behaviors, one of which was subsequently redefined “bungee.”

Experiment 2: can spiders learn aversion to mimetic prey?

In order to control the previous experiences and hunger of the crab spiders, all subsequent experiments were carried out under laboratory conditions at our field station. Spiders used in laboratory experiments were collected from flowers in the field, stored

Table 1

Prey types used, their mimetic status, the experiments in which they were used, and their ranked mimetic accuracy as perceived by humans (see main text)

Species/prey type	Mimetic status	Experiments	Mimetic rank (1 = most accurate)
Polistes dominula (paper wasp) (L. 1758)	Model	All	NA
Chrysotoxum intermedium (Meigen 1822)	Wasp mimic	All	1
Syrphus ribesii (L. 1758)	Wasp mimic	1 and 2	2
Sphaerophoria scripta (L. 1758)	Wasp mimic	1 and 2	3
Episyrphus balteatus (De Geer 1776)	Wasp mimic	2	4
Apis mellifera (honeybee) (L. 1758)	Model	1	NA
Eristalis tenax (L. 1758)	Honeybee mimic	1	NA
Sarcophaga carnaria (L. 1758)	Not mimetic	1 and 2	5
Fannia canicularis (L. 1758)	Not mimetic	1, 2, and 3	6
C. intermedium paint control	Wasp mimic	3	NA
C. *intermedium* black	Not mimetic	3	NA
Artificial black	Not mimetic	3 and 4	NA
Artificial yellow	Not mimetic	3	NA
Artificial back and yellow stripes	Wasp mimic	3	NA

Table 2

Behaviors performed by *Synema globosum* during experiments

Behavior	Description
Leave flower	Leaving the plant completely and not returning
Bungee	Jumping from the flower and dangling on a line of silk
Retreat	Moving away from the prey (and, in Experiment 1 only, bungeeing)
Display	Spreading and lifting fore-limbs while orientated toward prey
Approach	Orientation and movement toward the prey
Tickle	Gently touching the prey with its front legs
Grapple	Frantic touching of the prey and occasional jumping
Attack	Mounting and biting of the prey

Note that retreat and bungee were not differentiated in Experiment 1.

individually in 9-cm Petri dishes, and kept on a natural light:dark cycle. Prior to their use in experiments, they were starved for at least 4 days to increase their motivation to hunt.

The first laboratory experiment tested whether prior experience with an aposematic, aversive model species affected spider behavior when subsequently presented with mimetic and nonmimetic palatable prey. Field observations and the results of Experiment 1 indicated that *P. dominula* and hoverfly mimics of wasps were the most suitable species for this test: although *S. globosum* readily attacks and consumes *A. mellifera*, it rarely if ever attacks *P. dominula* and in fact often flees from a flower on encountering this species. Thus, we tested 1) whether spiders exposed to *P. dominula* were less likely to attack wasp mimics subsequently and 2) whether any such acquired aversion to wasp mimics was stronger toward hoverfly species that are considered by humans to be more accurate mimics.

Over 27 days in April–June 2008 and March–May 2009, spiders (n = 259; 188 females and 71 males) were randomly allocated to either "wasp" or "no-wasp" treatments and placed in a clean Petri dish under a desk lamp with a 60-W bulb for 10 min. Individuals in the wasp treatment were housed with a live adult *P. dominula* (with wings removed). In a few cases, spiders were injured or killed by wasps, in which case they were discarded. After 10 min, spiders were removed from dishes and placed onto a fresh flower of *Chrysanthemum segetum* standing in a sample tube filled with water, in a Perspex experimental arena (30 × 20 × 20 cm). *Chrysanthemum segetum* was chosen because crab spiders were often seen foraging on it the field and it did not wilt easily. The spider was given 10 min to settle on the flower, after which a fly specimen from 1 (randomly selected for each trial) of 6 species (4 wasp mimics and 2 nonmimics; see Table 1) was dangled above the center of the flower as above. Random selection of treatments for individual spiders meant that sample sizes were not necessarily equal. Spider behaviors were recorded as before (Table 2). On rare occasions, spiders did not settle on the flower; these individuals were discarded. For this experiment, prey were frozen until dead immediately prior to being presented to spiders, in order to remove mechanosensory stimuli. Preliminary tests revealed that spiders were equally likely to attack live and dead prey.

Experiment 3: visual cues

The next experiment was designed to establish whether *S. globosum* relies on visual cues while hunting and whether, after experience with a wasp, they show aversion toward visual signals designed to mimic the black and yellow banding on vespid abdomens. Over 15 days in May 2008 and in March and April 2009, we presented spiders with dead flies and artificial "prey" consisting of 10-mm-long cylindrical pieces of modeling clay (Staedtler® Fimo®). Both real and artificial prey were manipulated to produce mimetic and nonmimetic forms. Artificial prey were either black clay with black stripes, yellow clay with black stripes, or yellow clay with yellow stripes. All stripes were painted using a fine brush and Revell® enamel model paint (yellow matt #15 and black matt #8). A groove cut approximately 2 mm from one end of each cylinder acted as the "neck" to allow metal wire to be fastened in place (as above). The flies used were the hoverfly *Chrysotoxum intermedium*, which was deemed the most accurate mimic of *P. dominula* by human volunteers, and the nonmimetic fly *Fannia canicularis* (Table 1). Their wings and legs were removed. Two "altered" forms of *C. intermedium* were also used for comparison with artificial prey and to control for possible effects of paint on spider behavior: they had either their yellow markings or their black markings painted over using black paint (as above). Spiders (n = 98; 69 females and 29 males) were exposed to wasps as in the wasp treatment in Experiment 2 and then transferred to flowers in the experimental arena. They were offered artificial prey of a randomly selected type, as above, for 3 min or until the spider attacked. Spider behavior was recorded as before (Table 2). Random selection of the prey type for each individual spider meant that sample sizes were not necessarily equal.

Experiment 4: olfactory cues

The final experiment was designed to determine whether *S. globosum* uses olfactory cues while hunting, and whether there is olfactory mimicry in the apparently accurate visual wasp mimic *C. intermedium*. All prey in this experiment were cylindrical pieces of black modeling clay. Each cylinder was randomly assigned an odor treatment: wasp, honeybee, wasp mimic, or nothing. Odor was transferred using a similar method to that used by Wood and Ratnieks (2004). Each cylinder was placed in a sample tube with a live wasp (*P. dominula*), honeybee (*A. mellifera*), wasp mimic (*C. intermedium*), or nothing and shaken for 10s. We shook the tube sufficiently to prevent the live animals from avoiding contact with the artificial prey, but not so vigorously that they were obviously harmed. The experiment was carried out over 15 days in April 2010. Each spider (n = 238; 161 females and 77 males) was randomly assigned to a "wasp" or "no-wasp" treatment and exposed to *P. dominula* for 10min as in Experiment 2. Spiders were then transferred to a flower in the experimental arena and offered a prey cylinder from a randomly chosen odor treatment for 3min or until it was attacked. Behaviors exhibited by the spiders during trials were recorded as before (Table 2).

Statistical analysis

For analysis, we characterized spider responses to prey in 2 different ways. First, where possible, we considered whether or not prey were killed in a trial as a binary response variable. In experiments with dead or artificial prey, we considered whether or not prey were attacked at least once, instead of whether they were killed. Second, we considered the frequency with which each different behavior (Table 2) occurred in each trial. Because the frequencies of some behaviors were clearly correlated, we used principal components analysis (PCA) to derive a smaller number of uncorrelated response variables with which to describe these data. We extracted all principal components (PCs) with eigenvectors of greater than 1.0 for use in subsequent analysis.

The effects of spider sex, prey taxon or type, treatment (exposure to *P. dominula*), and prey mimetic accuracy on the 2 types of response variable were analyzed using either binomial or Gaussian generalized linear models (GLMs) or linear mixed-effects models (GLMMs). For all experiments, we fitted GLMs, in which spider sex and prey taxon/type were fixed factors, and there were no random effects. Where appropriate, treatment was also fitted as a fixed factor. In Experiments 1 and 2, we explicitly tested the effect of mimetic accuracy using a GLMM, with prey taxon as a random factor and prey mimetic accuracy (ranked) as a fixed covariate. Model fitting and simplification followed Zuur et al. (2009). The significance of fixed effects was assessed by testing the effect of deleting terms sequentially, starting with the highest order interactions, from a saturated model with likelihood ratio, *F*-ratio, or chi-square tests. PCA and model fitting were done using the packages glmer and stats in R Version 3.0.1 (R Core Team 2015). Post hoc comparisons of prey taxa were performed using the package phia. Where relevant, planned comparisons were applied with a custom contrast matrix.

RESULTS

Experiment 1: prey preference

When offered prey in the field, spiders were significantly more likely to kill and consume some taxa than others (binomial GLM: χ^2_7 = 89.434, P < 0.001; Figure 2). Spiders never killed *P. dominula*, but readily consumed most dipteran prey, except for the honeybee mimic *E. tenax*. Female spiders were significantly more likely to kill prey (62.6% of 139) than males (25% of 40) (χ^2_1 = 8.6142, P = 0.003), but there was no interaction between sex and prey taxon (χ^2_7 = 7.953, P = 0.337). Considering only the data for the wasp mimics and control fly species, the effect of spider sex was no longer significant (GLMM: χ^2_1 = 1.579, P = 0.209), spiders were not significantly more likely to kill less accurate mimics (χ^2_1 = 0.295, P = 0.587), and there was no interaction between sex and accuracy (χ^2_1 = 1.480, P = 0.224).

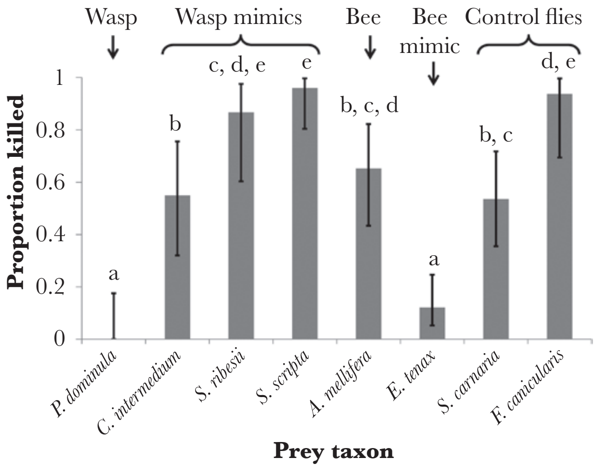

Figure 2
Differences in the proportion (±95% confidence interval) of prey killed and consumed by spiders offered different prey taxa in the field. Letters above bars indicate results of post hoc tests: species that share a latter were not significantly different (P > 0.05).

PCA of spider behavior yielded 2 PCs with eigenvalues greater than 1 (Table 3). The first (PC1) correlated positively with the frequencies of all behaviors except "attack" and "left flower" and hence can be interpreted as a general index of activity exhibited by spiders when they encountered prey. The second (PC2) correlated positively with the number of attacks observed, and negatively with the number of times the spider left the flower on which it was sitting, and hence contrasts the most positive and the most negative reactions by spiders to prey, with positive scores indicating positive reactions.

Spiders behaved differently toward different prey taxa. Scores on PC1 and PC2 were significantly different among prey taxa (PC1: $F_{7,171}$ = 6.204, P < 0.001; PC2: $F_{7,170}$ = 2.591, P = 0.015), with spiders being most active and least likely to react positively to *P. dominula*, and least active but most likely to respond positively to the nonmimic *F. canicularis* and the relatively inaccurate wasp mimic *Sphaerophoria scripta* (Figure 3). There was a significant difference between male and female spiders in PC2 scores ($F_{1,170}$ = 10.396, P = 0.002), with males being less positive toward prey (mean = −0.460; standard error of the mean [SEM] = 0.196) than females (mean = 0.132; SEM = 0.075), but not in PC1 scores ($F_{1,170}$ = 0.013, P = 0.910). There was no interaction between the effects of sex and taxon on either PC (PC1: $F_{7,163}$ = 1.717, P = 0.108; PC2: $F_{7,163}$ = 1.879, P = 0.076). Considering only the data for the wasp mimics and control fly species, male spiders were both more active (GLMM for PC1: χ^2_1 = 8.433, P = 0.004) and less positive toward prey (PC2: χ^2_1 = 7.302, P = 0.007). However, there was no significant effect of mimetic accuracy on either measure of

Table 3

Results of PCA of behavioral responses by spiders to prey offered in the field in Experiment 1, and in the laboratory in Experiments 2, 3, and 4

	Experiment 1		Experiment 2			Experiment 3			Experiment 4		
Original variable	PC1	PC2	PC1	PC2	PC3	PC1	PC2	PC3	PC1	PC2	PC3
Display	0.751	0.095	0.551	0.347	−0.044	0.772	0.268	0.230	0.821	0.304	0.097
Retreat	0.884	0.003	0.894	0.025	−0.114	0.849	−0.078	0.019	0.836	−0.270	0.053
Approach	0.874	0.145	0.620	0.190	0.550	0.749	−0.139	−0.01	0.836	−0.136	−0.070
Tickle	0.704	−0.189	0.717	0.140	−0.123	0.471	−0.160	−0.636	0.436	0.106	−0.174
Grapple	0.409	0.261	0.511	0.167	−0.498	0.634	0.402	0.297	0.698	0.395	0.219
Attack	−0.196	0.729	−0.459	0.713	0.059	−0.194	0.661	0.405	−0.109	0.809	−0.141
Bungee	NA	NA	0.236	−0.235	0.789	0.198	−0.751	0.285	0.332	−0.441	−0.452
Left flower	0.041	−0.745	0.165	−0.812	−0.193	−0.097	−0.621	0.541	−0.010	−0.213	0.839
Variance explained	40.17%	17.44%	31.96%	17.85%	15.54%	32.34%	20.87%	13.55%	35.88%	15.57%	12.79%

Correlation coefficients are shown indicating the strength and direction of the relationships between extracted PCs (with eigenvectors > 1.0) and the original variables describing the frequencies with which particular behaviors (see Table 2) were observed. Note that retreat and bungee were not differentiated in Experiment 1.

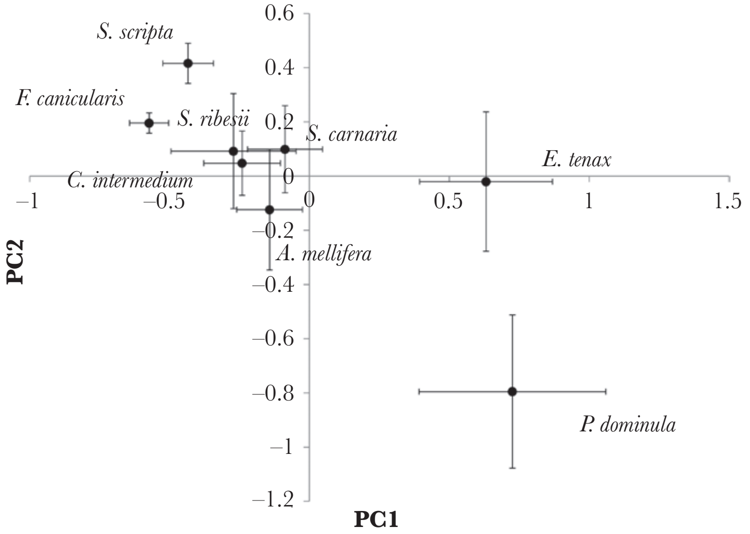

Figure 3

Differences in behavior of spiders toward different prey taxa offered to them in the field in Experiment 1. Behavioral responses are characterized by means (±SEM) of 2 PCs (PC1 and PC2) derived from PCA of the frequencies of 7 different behaviors observed in the field (see Table 3). High scores on PC1 indicate high frequencies of most behaviors except "attack" and "left flower." High scores on PC2 indicate high frequencies of "attack" and low frequencies of "left flower." Post hoc tests for PC1 showed that *Polistes dominula* and *Eristalis tenax* were significantly different from all other taxa ($P < 0.05$), but that there were no pairwise differences among other taxa. Post hoc tests for PC2 showed that *P. dominula* was significantly different from all other taxa, but that there were no pairwise differences among other taxa.

behavior (PC1: $\chi^2_1 = 0.136$, $P = 0.713$; PC2: $\chi^2_1 = 0.001$, $P = 0.999$) and no interaction between accuracy and sex (PC1: $\chi^2_1 = 0.304$, $P = 0.581$; PC2: $\chi^2_1 = 3.124$, $P = 0.077$).

Experiment 2: can spiders learn aversion to mimetic prey?

When offered hoverflies with varying levels of mimetic accuracy, and nonmimetic flies, in the laboratory, spiders with prior experience of *P. dominula* were slightly less likely to kill prey (63.6% of 129) than spiders without such experience (72.3% of 130), but this effect was not significant (binomial GLM: $\chi^2_1 = 2.354$, $P = 0.125$). The probability that a spider killed a prey item was significantly affected by taxon ($\chi^2_1 = 36.714$, $P < 0.001$; see Figure 4), with the relatively accurate mimic *C. intermedium* being killed least often, and the nonmimetic fly *F. canicularis* being killed most often. Spider sex did not significantly affect the probability of prey being killed ($\chi^2_1 = 3.145$, $P = 0.076$). None of the interactions among the main effects on the probability that spiders killed a prey item was significant ($P > 0.3$ in all cases). It is worth noting that, although most prey taxa were attacked at similar frequencies in the 2 treatments, the most accurate mimic taxon was about half as likely to be attacked by spiders if they had previously been exposed to *P. dominula*. However, when the data were reanalyzed with a mixed model, there was no significant effect of mimetic accuracy on the probability of prey being killed (binomial GLMM: $\chi^2_1 = 2.674$, $P = 0.102$) and no significant interactions involving accuracy ($P > 0.1$ in all cases). Tests of the other main effects and interactions in the mixed model yielded qualitatively identical results to the GLM (results not shown).

PCA of spider behaviors in Experiment 2 produced 3 PCs with eigenvalues greater than 1 (see Table 3). The first 2 PCs were similar to those produced in Experiment 1: the first correlated positively

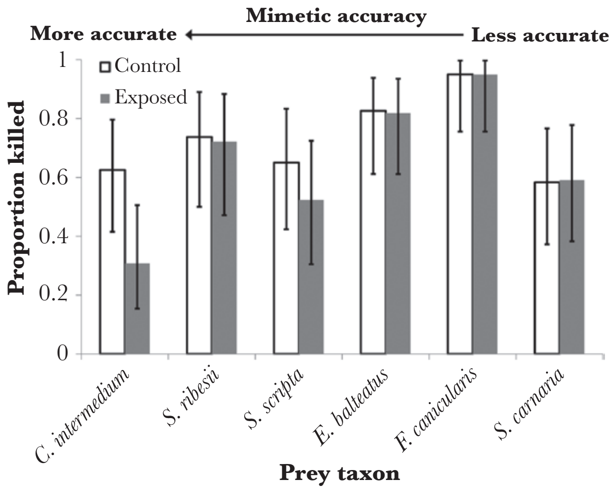

Figure 4

The effects of previous exposure to the aversive model *Polistes dominula*, and prey mimetic accuracy, on the probability (±95% confidence interval) that spiders attacked prey of various taxa offered to them in the laboratory in Experiment 2.

with all behaviors except "attack," and the second contrasted the frequency of attacks with the frequency with which spiders left flowers. The third PC correlated most strongly (positively) with "bungee," a behavior that was not distinguished from "retreat" in Experiment 1.

Analysis that modeled the effect of prey taxon as a fixed factor (GLMs) showed that there were no significant effects of prior exposure to *P. dominula*, spider sex, or prey taxon, or their interactions, on PC1 (Table 4; Figure 5). There were, however, significant main effects of prey taxon and treatment on PC2 (Figure 6). Spiders behaved most positively toward *Syrphus ribesii* and most negatively toward *C. intermedium*. In addition, spiders were less likely to attack prey, and more likely to flee them, if they had previously been exposed to wasps. There were no significant interactions involving these main effects on PC2. The behaviors captured by PC3 showed a complex response to the different explanatory variables, with a significant 3-way interaction in addition to a main effect of taxon (Figure S1, Supplementary Information). In general, spiders were least likely to "bungee" (i.e., had the lowest PC3 scores) in response to *C. intermedium* and most likely to exhibit this behavior in response to *S. ribesii*. The significant 3-way interaction reflects contrasting patterns in male and female PC3 scores, particularly toward *S. ribesii*, *S. scripta*, and *Episyrphus balteatus*: prior exposure to wasps had a relatively positive effect on the male propensity to "bungee" in response to S. *ribesii* and *E. balteatus*, and a relatively negative effect on the male propensity to "bungee" in response to *S. scripta*, when compared with the equivalent effects of exposure on females.

The mixed model analysis, which included a fixed effect of mimetic accuracy, did not reveal any significant main effects on any of the PCs but did indicate a significant interaction between treatment and mimetic accuracy: spiders that had been previously been exposed to the aversive model species were relatively more active in response to more accurate mimics, in comparison with less accurate or nonmimetic prey (Figure 5).

Experiment 3: visual cues

When spiders previously exposed to *P. dominula* were offered real and artificial prey whose visual appearance was more or less

Table 4

Results of analysis of the effects of spider sex, prey taxon or mimetic accuracy, and treatment (whether spiders were exposed to a wasp before encountering prey), and their interactions, on PCs describing the behavioral responses of spiders to prey in the laboratory in Experiment 2 (see Table 3)

	GLM with fixed effect of taxon									GLMM with fixed effect of accuracy								
	PC1			PC2			PC3			PC1			PC2			PC3		
Term	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*	LR	df	*P*	LR	df	*P*	LR	df	*P*
Sex	0.061	1,252	0.806	0.664	1,251	0.416	3.782	1,252	0.053	1.036	1	0.309	1.037	1	0.309	0.755	1	0.385
Taxon/accuracy	0.924	5,253	0.466	3.562	5,253	**0.004**	5.573	5,253	**<0.001**	1.639	1	0.201	0.727	1	0.394	2.084	1	0.149
Treatment	0.062	1,251	0.803	5.055	1,252	**0.025**	0.498	1,251	0.481	3.410	1	0.065	1.489	1	0.222	2.369	1	0.124
Sex × taxon/accuracy	0838	5,240	0.524	0.466	5,241	0.802	1.089	5,246	0.367	0.756	1	0.385	2.301	1	0.129	0.327	1	0.568
Sex × treatment	0.138	1,245	0.710	0.001	1,240	0.995	1.820	1,241	0.110	0.162	1	0.687	0.027	1	0.869	2.394	1	0.122
Taxon/accuracy × treatment	1.213	5,246	0.304	0.649	5,246	0.663	0.798	5,240	0.373	5.131	1	**0.024**	0.149	1	0.699	2.686	1	0.101
Sex × taxon/accuracy × treatment	2.235	5,235	0.052	0.910	5,235	0.968	4.520	5,235	**<0.001**	2.348	1	0.125	0.206	1	0.650	0.858	1	0.354

Models were fitted with a Gaussian error structure and included either a fixed effect of prey taxon (GLMs) or a fixed effect of mimetic accuracy and a random effect of prey taxon (GLMMs). Effects were assessed by *F*-tests or likelihood ratio (LR) deletion tests during model simplification. Significant *P* values are highlighted in bold.

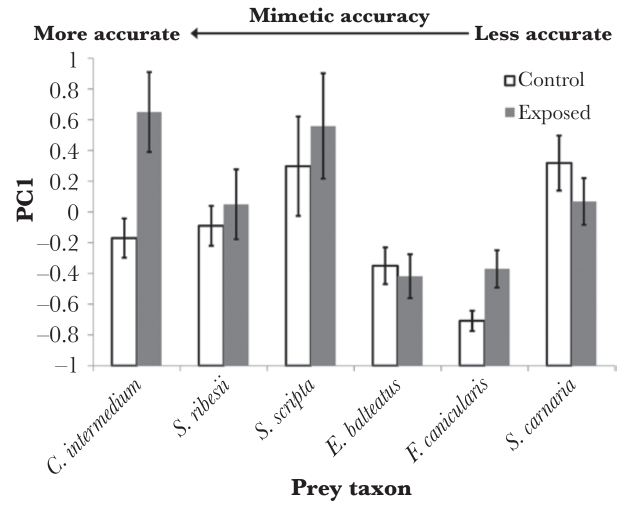

Figure 5

The effects of previous exposure to the aversive model *Polistes dominula*, and prey mimetic accuracy, on spider behavior when offered different prey taxa in the laboratory in Experiment 2. Spider behavior is described by mean PC1 scores (±SEM) derived from PCA of the frequencies of 8 different behaviors observed in the field (see Table 3), with high scores indicating spiders that were more active and less likely to attack prey.

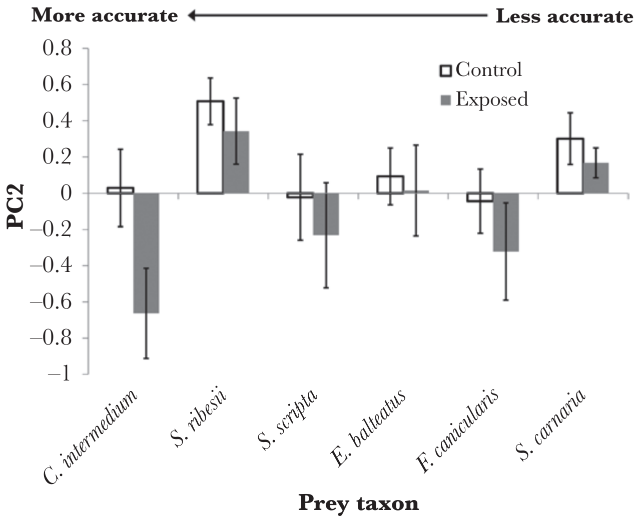

Figure 6

The effects of previous exposure to the aversive model *Polistes dominula*, and prey taxon, on spider behavior when offered different prey taxa in the laboratory in Experiment 2. Spider behavior is described by mean PC2 scores (±SEM) derived from PCA of the frequencies of 8 different behaviors observed in the field (see Table 3), with high scores indicating spiders that were more likely to attack prey and less likely to flee from them.

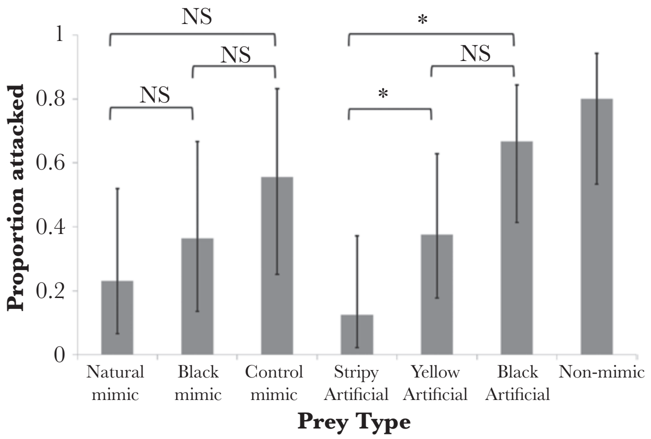

Figure 7

The effects of prey type on the proportion of spiders (±95% confidence interval) that attacked real and artificial prey in the laboratory in Experiment 3. Prey types were: Natural Mimic (the accurate wasp-mimic *Chrysotoxum intermedium*; $n = 13$), Black Mimic (*C. intermedium* with its yellow stripes painted black; $n = 11$), Control Mimic (*C. intermedium* with its black stripes painted black; $n = 9$), Stripy Artificial (yellow clay with black stripes; $n = 16$), Yellow Artificial (yellow clay with yellow stripes; $n = 16$), Black Artificial (black clay with black stripes; $n = 18$), and Nonmimic (the nonmimetic fly *F. canicularis*; $n = 15$). Planned comparison tests are indicated above the bars for pairs of prey types of particular interest (NS: $P > 0.05$; *$P < 0.05$).

similar to the aversive model species, the probability that they would attack was significantly affected by prey type (binomial GLM: $\chi^2_6 = 21.173$, $P = 0.002$; Figure 7). Unmanipulated hoverfly mimics with black and yellow stripes (*C. intermedium*) and stripy artificial prey were the least likely to be attacked. According to planned comparisons, artificial prey without stripes were significantly more likely to be attacked than those with stripes. Hoverflies with their yellow or black stripes painted black were more likely to be attacked than unpainted equivalents, although not significantly so. Unmanipulated, nonmimetic control flies were the prey type most likely to be attacked. Spider sex (GLM: $\chi^2_1 = 0.034$, $P = 0.854$), and the interaction between sex and prey type (GLM: $\chi^2_6 = 8.212$, $P = 0.223$), did not significantly affect the probability of attack.

As in Experiment 2, PCA produced 3 PCs with eigenvalues greater than 1, the first 2 of which had similar correlations with the raw variables describing spider behavior (Table 3). None of these PCs was significantly affected by prey type (Gaussian GLM for PC1: $F_{6,89} = 0.941$, $P = 0.470$; PC2: $F_{6,89} = 1.967$, $P = 0.079$; PC3: $F_{6,89} = 0.750$, $P = 0.611$), although PC2 (contrasting the propensity to attack with the tendency to leave the flower) showed patterns consistent with the above analysis of spider attacks: stripy artificial prey scored lower than those without stripes, and the same was true for hoverflies, whereas unmanipulated control flies had the most positive scores (Figure S2, Supplementary Infromation). There were no significant effects of spider sex ($F_{1,88} < 3.0$, $P > 0.05$) or the interaction between sex and prey type ($F_{6,82} < 1.5$, $P > 0.1$) on PC scores.

Experiment 4: olfactory cues

When offered artificial prey bearing the odor of models (*P. dominula* and *A. mellifera*) and mimics (*C. intermedium*), or no odor, in the laboratory, there were no significant effects of prior experience with *P. dominula* (binomial GLM: $\chi^2_1 = 1.689$, $P = 0.194$), odor type ($\chi^2_3 = 1.609$, $P = 0.657$), or spider sex ($\chi^2_1 = 1.568$, $P = 0.211$) on the probability that spiders would attack. Neither were there any significant effects of any interactions among these effects on the probability that spiders would attack prey ($\chi^2_{1 \text{ or } 3} < 5.0$, $P > 0.1$).

As in Experiments 2 and 3, PCA produced 3 PCs with eigenvalues greater than 1 the first 2 of which had similar correlations with the raw variables describing spider behavior (Table 3). None of these PCs was significantly affected by odor type or prior experience with *P. dominula* (Table 5). However, PC1, but not PC2 and PC3, was significantly affected by spider sex, with male spiders

Table 5

Results of analysis of the effects of spider sex, prey odor, and treatment (whether spiders were exposed to a wasp before encountering prey), and their interactions, on PCs describing the behavioral responses of spiders to prey in the laboratory in Experiment 4 (see Table 3)

	PC1			PC2			PC3		
Term	*F*	df	*P*	*F*	df	*P*	*F*	df	*P*
Sex	13.745	1,236	<0.001	0.245	1,236	0.622	1.638	1,236	0.202
Odor	1.320	3,232	0.269	0.031	3,232	0.993	0.855	3,233	0.465
Treatment	2.379	1,235	0.124	1.023	1,235	0.313	0.416	1,229	0.520
Sex × odor	1.979	3,226	0.118	0.998	3,226	0.395	2.022	3,230	0.116
Sex × treatment	0.014	1,225	0.905	0.105	1,225	0.746	3.223	1,228	0.074
Odor × treatment	1.328	3,229	0.266	0.961	3,229	0.412	0.432	3,225	0.730
Sex × odor × treatment	2.025	3,222	0.111	0.871	3,222	0.457	4.130	3,222	0.243

Effects were assessed by *F*-tests at deletion during simplification of a Gaussian general linear model.

scoring more highly, indicating higher frequencies of most behaviors (especially display, retreat, and approach) than were seen in females. There were no significant interactions among the effects of prior experience, odor type, and sex on any of the PCs.

DISCUSSION

The results of our experiments demonstrate that the crab spider *S. globosum* has clear prey preferences and suggest that those preferences are influenced by the visual appearance of prey, but not by olfactory cues. In addition, there was limited evidence that prior experience with an aversive model species altered spider behavior toward more accurate Batesian mimics of that model. Overall, our results provide support the idea that invertebrate predators can play a role in the evolution of the visual appearance of their prey and shed some light on the hypothesis that differences between invertebrate and vertebrate sensory and cognitive processes result in relaxed selection on mimetic perfection in prey that are subject to predation by invertebrates.

Prey preferences

The existence and nature of prey preferences in crab spiders are poorly reported. The large, flower-dwelling species *M. vatia* apparently shows very little discrimination among prey types, and the frequencies of prey taxa in its diet are thought simply to reflect variation in prey availability (Morse 2007). By contrast, our results show that *S. globosum* readily distinguished among prey species in the field, completely avoiding *P. dominula*, while killing and consuming nearly all individuals of some dipteran taxa. *Synema globosum* therefore has the potential to exert selection pressure on prey phenotypes via the cues it uses to identify prey types. Other studies have shown that even when spiders are able to discriminate among prey types, this discrimination may not affect selection because even rejected prey were left irreparably injured or dead (see Vasconcellosneto and Lewinsohn 1984). In the case of *S. globosum*, however, our observations showed that none of the prey that were bitten were later rejected, and all rejected prey were left unharmed. Therefore, especially given its abundance and likely impact on prey populations (Reader et al. 2006; Ibarra and Reader 2014), the results of our experiments suggest that *S. globosum* does indeed have the potential to select for visual or other traits in aposematic and mimetic prey.

The putative model wasp species *P. dominula* was never attacked in the field experiment. Furthermore, encountering *P. dominula* caused the spiders to become very active, often leaving the flower completely during the prey presentation period. This suggests that *P. dominula* was aversive to *S. globosum* either because it is unprofitable, distasteful, or dangerous. Birds may avoid vespid wasps because their abdomens are distasteful (Mostler 1935), but circumstantial evidence points away from this explanation for avoidance of *P. dominula* by *S. globosum*: although other spiders have been shown to attack unpalatable prey before rejecting it moments later (Vasconcellosneto and Lewinsohn 1984), we have only seen *S. globosum* attack *P. dominula* once (during exposure in the laboratory in Experiment 2), and on this occasion the spider appeared to feed unperturbed until the wasp was completely consumed. Instead, the main deterrent associated with *P. dominula* appears to be its aggressive and/or predatory nature. In the laboratory, it frequently bit or attempted to sting *S. globosum*, killing spiders on several occasions, and in the field *P. dominula* is often seen hunting invertebrate prey on or around flowers that harbor *S. globosum*. It is therefore high plausible that learned or evolved avoidance of *P. dominula* is adaptive in *S. globosum*.

In contrast to the results for *P. dominula*, the other aposematic, defended insect we offered to *S. globosum* in Experiment 1—the honeybee—was readily attacked and consumed, a fact that helps to explain the levels of mortality that spiders impose on honeybees in our field site (Reader et al. 2006). For this reason, we excluded the honeybee and its mimic *E. tenax* from subsequent experiments in which we were interested in responses to mimicry of aversive prey. The honeybee's defenses are apparently not a threat to *S. globosum*, which underlines the likely importance of *P. dominula*'s aggressive predatory behavior, rather than the possession of a sting per se, in determining spider prey choice. The almost complete avoidance of *E. tenax*, which to humans is a good mimic of the honeybee, in Experiment 1 is puzzling. It suggests that, although visual appearance may play a role in some circumstances (e.g., as in Experiment 3), other factors affect spider prey choice significantly. Which cues were used to identify *E. tenax* as unpalatable, and the reason why it is unpalatable, remain a mystery that only further experimentation can unlock.

In 2 of our 4 experiments, sex had a significant effect on spider responses to prey. There was no evidence that prey preferences were different between males and females, but males were in general less likely to attack prey in the field and more active (rather "skittish") when presented with artificial prey in the laboratory. These differences could be explained by the pronounced sexual size dimorphism (Blanckenhorn 2005) that is seen in many spiders, including *S. globosum* (full grown females are about 7 times the mass of males; Corcobado et al. 2010). Typically, smaller male spiders have a different diet from larger females (Walker and Rypstra

2002). Furthermore, males often spend the majority of the time searching for and guarding females and invest less energy and time in foraging for themselves (e.g., Givens 1978) than females, whose reproductive fitness is closely related to foraging success (Walker and Rypstra 2002). As a result, male *S. globosum* may have been more interested in fleeing the confines of the experimental arena than they were in finding a meal. Their smaller body size did not, however, obviously constrain prey choice: just like females, males showed a relative preference for the largest popular prey type (honeybees) compared with some of the smaller prey in Experiment 1, for example.

Responses to Batesian mimicry

Our results provide some support for the hypothesis that *S. globosum* perceives and responds to Batesian mimicry in its prey. Results from the laboratory (Experiment 2) showed that, overall, spider attack rates and other measures of behavior toward hoverflies that mimic wasps did not correlate strongly with mimetic accuracy, as perceived by humans. However, recent prior exposure to the aversive model *P. dominula* resulted in some changes in behavior that were most marked toward the hoverflies that most closely resemble the model. Although the relatively large (ca. 50%) decline in the frequency of attacks by spiders exposed to the model on the best mimic (*C. intermedium*) was not significantly different from the change in the attack rate on other prey species, there was a significant interaction between the effects of mimetic accuracy and exposure to the model on spider activity levels. The high levels of spider activity that characterized their response to the model species in Experiment 1 were mirrored in exposed spiders offered relatively accurate mimics (especially *C. intermedium*) in Experiment 2. One explanation for this pattern is that exposed spiders generalized from learned responses to wasp cues, resulting in them avoiding or trying to escape from those particular prey taxa that humans perceive to be accurate Batesian mimics. Hence, although the statistical support for the observed pattern is somewhat equivocal, and we do not know what the effects on prey fitness would be in the wild, our data do provide some tentative suggestions that spiders might respond to Batesian mimicry (see also Tyshchenko 1961). There are, however, alternative explanations for the observed patterns. Rather than facilitating learning about wasp-related cues, a recent encounter with a potential predator may "prime" *S. globosum* for danger, making it more likely to exhibit innate avoidance behaviors in subsequent encounters with certain prey types. This priming might not be specific to *P. dominula* and might have nothing to do with aposematism or mimicry. We would have to repeat the experiment with a control treatment in which spiders were exposed to a different insect (e.g., one that was not aposematic and not dangerous) in order to explore the possibility further.

Although we found some evidence that mimetic accuracy as perceived by humans may affect spider behavior, there are several reasons why we might expect spiders to rank mimics differently from vertebrates. In addition to differences in sensory and cognitive capabilities, spiders probably also view their insect prey from a different angle from that typically experienced by birds or humans. In our study, humans evaluated the accuracy of mimics from photographs taken from above, while spiders were beneath their prey as they were "dangled" onto flowers. Because prey appear very different from below, this could substantially change the accuracy of any perceived mimicry from the spider's perspective, but the significance of any such change remains unknown without testing the effect of prey orientation on human and spider behavior.

There were other limitations to the ranking exercise we used to assess mimetic accuracy of the insect taxa we used in our experiments. For example, we were not able to standardize the scale of the images we showed to human volunteers, and hence reliable information about body size was not available to them, in contrast to the situation for spiders in the experiments. Overall, therefore, we are cautious about the interpretation of our analyses that included mimetic accuracy as a predictor, and we think the most important message from our study is that spiders responded differently to different prey taxa and different artificial prey types in a way that highlights the *potential* of spiders as agents of selection on color patterns in mimetic and aposematic insects.

The importance of visual, olfactory, and other cues

The results show that *S. globosum* relies at least partly on vision when hunting. Although the preferences demonstrated in the field (Experiment 1) may have been influenced by olfactory and/or mechanosensory information associated with live prey, Experiment 3 showed that spiders also discriminated among artificial prey that varied only in color. The results from Experiment 3 also suggest that *S. globosum* responds to typical aposematic signals: following previous wasp experience, the spiders attacked black and yellow striped artificial prey significantly less often than the completely yellow and completely black artificial prey. It remains unclear whether the important cue here was variation in hue (yellow vs. black) or simply luminance (contrast between dark and light stripes), but evidence for true color vision in crab spiders (Thomisidae) is limited (Insausti et al. 2012).

There was no evidence that *S. globosum* distinguished among the different odor treatments in Experiment 4. The results thus suggest that crab spiders do not utilize olfactory signals to detect the aversive model *P. dominula* or its mimics. This could be because the olfactory signals of wasps have not evolved under selection by predators and are not as readily learned and remembered as aposematic color signals are thought to be (Stevens 2007; Svadova et al. 2009). Alternatively, *S. globosum* may not rely heavily on olfactory signals while foraging, as appears to be the case in the closely related crab spider, *M. vatia* (Morse 2007).

The laboratory experiments presented here were designed to eliminate behavioral, auditory, and mechanosensory stimuli emitted by prey. Under natural conditions, these stimuli may contribute to decision making by crab spiders, and hence they may play a role in determining the adaptive value of wasp mimicry by hoverflies. There is evidence of behavioral mimicry in some hoverfly species (Rotheray and Gilbert 2011), but the only published evidence suggests that hoverflies do not mimic the sounds of their hymenopteran models (Rashed et al. 2009). Observations of the behavior of the *M. vatia* suggest that it depends largely on mechanoreceptors when hunting (Morse 2007), but we know little about variance in the kind of vibrations produced among the potential prey of crab spiders. In order to understand fully the potential of predators such as crab spiders to influence the evolution of prey morphology and behavior, further investigation of the importance of cues in each sensory modality is required.

CONCLUSION

Overall, this study provides evidence that spiders have the ability to differentiate among prey using visual cues, and therefore that they have the potential to exert selection on prey morphology, including perhaps aposematic and mimetic color patterns. Previous studies of Batesian mimicry in insects have tended to assume that the predators responsible for the evolution of warning patterns and their mimetic equivalents are vertebrates. Given that invertebrates are important predators of flower-visiting insects and several other groups containing aposematic and mimetic species, our results suggest that the evolutionary significance of selection on aposematic and mimetic patterns by invertebrate predators is worthy of more detailed consideration. The very different sensory and cognitive abilities of invertebrate predators such as spiders could easily result in patterns of selection that are not well predicted by human or avian behavior, and hence our results are broadly consistent with the hypothesis that the perceived degree of perfection of a Batesian mimic may be in "the eye of the beholder" (Cuthill and Bennett 1993). Crucially, in our community of models and mimics, and in most others, the relative contributions of different types of predator to selection on mimetic patterns remain unknown. The phenotype of a Batesian mimic should represent a net evolved response to selection imposed by all predators. Careful consideration of the importance and selectivity of predation from all sources is therefore needed to understand properly how and why mimetic signals appear as they do.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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