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# Ineffective crypsis in a crab spider: a prey community perspective

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Cryptic coloration is assumed to be beneficial to predators because of an increased encounter rate with unwary prey. This hypothesis is, however, very rarely, if ever, studied in the field. The aim of this study was to quantify the encounter rate and capture success of an ambush predator, in the field, as a function of its level of colour-matching with the background. We used the crab spider *Misumena vatia*, which varies its body colour and can thereby match the colour of the flower it hunts upon. We carried out a manipulative field experiment using a complete factorial design resulting in six different colour combinations of crab spiders and flowers differing in their degree of colour-matching. A rich and diverse set of naturally occurring insects visited the flowers while we continuously video-recorded the spider's foraging activity. This enabled us to test the crypsis, the spider avoidance and the flower visitor attraction hypotheses, all three supported by previous studies. Flower visitors of different groups either avoided crab spiders independent of colour-matching, such as solitary bees and syrphid flies, or ignored them, such as bumble-bees and honeybees. Moreover, colour-matched spiders did not have a higher encounter rate and capture success compared to the visually apparent ones. Thus, our results support the spider avoidance hypothesis, reject the two other hypotheses and uncovered a fourth behaviour: indifference to predators. Because flower visitors reacted differently, a community approach is mandatory in order to understand the function of background colour-matching in generalist predators. We discuss our results in relation to the size and sociality of the prey and in relation to the functional significance of colour change in this predator.

**Keywords:** capture success; *Misumena vatia*; generalist predator; colour-matching; spider avoidance; flower visitor attraction

## 1. INTRODUCTION

Cryptic animals are thought to avoid detection by their potential prey or their predators (Oxford & Gillespie 1998; Heiling *et al.* 2005). Thus, colour-matching predators are assumed to have an advantage over unmatched conspecifics, for example, in terms of an increased prey encounter rate or a higher prey capture rate. Astonishingly, this fundamental assumption has seldom been tested for prey (e.g. Majerus *et al.* 2000) and has never, to our knowledge, been assessed for cryptic predators. This is the overall aim of our work.

Adult females of several crab spider species in the Thomisidae are able to change their colour between white and yellow (in rare cases also pink/purple). This ability has been studied for over one century and was claimed to have evolved as a strategy to minimize the colour contrast on inflorescences where they wait for flower visitors (Angus 1882; Rabaud 1919; Gabritschewsky 1927; Weigel 1941; Morse 1979, 1981, 2007; Schmalhofer 2001; Théry & Casas 2002; Heiling & Herberstein 2004; Théry 2007). The duration of colour change to adapt body colour reported in these studies ranges from 2 to 20 days with a mean of 4–7 days; it is therefore a

morphological colour change (Oxford & Gillespie 1998; Insausti & Casas 2008, *in press*). In combination with this ability, these crab spiders are also reported to settle preferentially on inflorescences that match their body colour. Thus, white crab spiders mostly hunt on white inflorescences (e.g. 75% in Weigel 1941; 69% in Heiling *et al.* 2005), while yellow crab spiders almost exclusively forage on yellow inflorescences (e.g. 94% in Heiling *et al.* 2005).

However, the outcome of the latest works on this system has been increasingly disconcerting for the tenants of the crypsis hypothesis. Chittka (2001) found that only white spiders closely match the background colour of white inflorescences, while the other colour combinations of spiders and inflorescences are not matching (Chittka 2001; see also Heiling *et al.* 2005). Thus, it became questionable whether one should still consider these crab spiders as cryptic. These misgivings are in line with the studies of Heiling *et al.* (2003, 2005), who found that, under certain circumstances, the Australian crab spider *Thomisus spectabilis* may even be attractive to some flower visitors. The most recent systematic field survey conclusively showed that *Misumena vatia* is not cryptic in the visual system of bees, one of the most important prey, and that the striking cases of perfect colour-matching occur with low probability, not different from that obtained through a random assortment of spider and flower colours (Defrize *et al.* submitted). It is

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therefore mandatory to assess prey behaviour and the added value of the lack of chromatic contrast by manipulation rather than by simply observing the degree of matching, and by quantifying the rate of visits by flower visitors and the capture success of the spiders. This is the specific aim of our work.

We formulated three hypotheses: the crypsis hypothesis, the spider avoidance hypothesis and the flower visitor attraction hypothesis. According to the crypsis hypothesis, flower visitors cannot perceive colour-matching crab spiders on inflorescences or perceive them with more difficulty and errors. The spider avoidance hypothesis stipulates that inflorescences, harbouring a spider are generally avoided, regardless of colour-matching. According to the flower visitor attraction hypothesis, inflorescences harbouring a crab spider should be visited more often compared to spider-free inflorescences. All three hypotheses are contingent on the degree of colour-matching between crab spiders and inflorescences, and all three have received support in previous studies. However, these studies either focused on crab spiders hunting on flowers of the same colour, and therefore neglected the ability of these spiders to adapt their body colour, or the colour adaptation was taken into account, but the studies focused on large social bees only (Fritz & Morse 1985; Dukas 2001; Schmalhofer 2001; Heiling *et al.* 2003, 2005; Heiling & Herberstein 2004). Nearly all neglected the more species-rich, non-social flower visitors, such as solitary bees and syrphid flies (but see Schmalhofer 2001). The latter groups are also common visitors to flowers, and so are potential prey items for crab spiders, and several studies have suggested that flower visitor identity might play an important role in the responses shown towards spiders (Reader *et al.* 2006; Brechbühl *et al.* in press). Thus, including the entire flower visitor community is essential in studies regarding crab spider–flower visitor interactions.

In order to test the three hypotheses, we placed outdoors white and yellow crab spiders (*M. vatia*) on three different coloured flower species—white, yellow and violet—resulting in six different colour combinations of spiders and inflorescences. Responses from different local flower visitor species towards the settled crab spiders were then recorded using continuous video surveillance and compared to spider-free inflorescences. Furthermore, as more insect visits towards an inflorescence do not necessarily result in a higher capture success by crab spiders, we measured capture rates and biomass of captured prey as both may translate into fitness benefits for the spider.

## 2. MATERIAL AND METHODS

### (a) Study area and species

The experiment was set up in the garden of the Zoological Institute in Bern (Switzerland) from May to August 2007. Female spiders were caught in wildflower fields around Bern by sweep-netting and kept in *Drosophila* tubes (5 cm diameter) that were partially filled with soil (1–2 cm). The caught spiders were brought to the rearing room; a tool shed just beside the experimental area (unregulated climate). Once a week, the spiders were fed (*Acheta domestica*: 4–6 mm) and some water was sprinkled into the tubes.

Three native plant species were chosen: *Chrysanthemum frutescens* (white inflorescences; Asteraceae), *Anthemis tinctoria* (yellow inflorescences; Asteraceae) and *Knautia*

*arvensis* (violet inflorescences; Dipsacaceae), all of which are the regular hunting sites for *M. vatia* spiders (R. Brechbühl 2005–2009, personal observation). Seedlings were planted in plastic pots (16 l) in spring 2007. Twenty pots for each plant species were used, resulting in 60 pots with experimental plants. The experiment consisted of 20 patches distributed uniformly over the garden with a minimum distance of 3 m between them. Each patch included one pot of each of the three plant species, placed in a triangle as close together as possible.

Common flower visitor species were caught by sweep-netting in the experimental field, frozen at  $-20^{\circ}\text{C}$  and dried to determine their dry mass (mg) using a Mettler MT5 balance. We used the average dry mass of each flower visitor species or genus in order to estimate the captured biomass from capture rates.

### (b) Experimental design

We recorded the behaviour of flower visitors for nine different spider–inflorescence combinations in a complete factorial design (three spider treatments  $\times$  three flower species): either white or yellow crab spiders were individually placed on one inflorescence of each of the three flower species. The term ‘inflorescence’ is used here to describe a flowering display unit (i.e. the typical ‘flower head’ of the Asteraceae). In addition, we also had treatments of each flower species without spiders. The experiment was repeated ten times for *C. frutescens* and *A. tinctoria*, but only eight times for *K. arvensis* owing to the lower flower numbers of this plant species. In order to prevent flower visitation activities before the experiment, we covered flower buds with gauze bags until the recordings started. We included this manipulation because preliminary studies and other published work on *Apis mellifera* foraging behaviour (e.g. Williams 1998) indicated that the probability of acceptance of a flower by a bee was likely to be influenced strongly by previous visits from other flower visitors.

Ten digital surveillance cameras were used to continuously monitor experimental inflorescences for a period of three consecutive sunny days in summer 2007. We used cameras that transmitted pictures to a wireless server via an Internet access point. The technical details of the surveillance system are fully described elsewhere (Brechbühl *et al.* in press). We conducted the experiment during 10 different three-day periods, which were used as temporal blocks in the analysis (see below). At the beginning of each temporal block, individual pots were randomly assigned to spider treatments. Three replicates of each spider treatment were observed simultaneously, plus an additional randomly chosen treatment. In the morning of the first day at 11.00, crab spiders were placed on inflorescences. We tried to select equally sized inflorescences within flower species, but flower size (diameter) is used later as covariate in the analyses to account for the differences in size that still remained. The flowers used in the experiments were bound to bamboo sticks to minimize flower movements owing to wind, as the cameras were equipped with a movement sensor. After placing the crab spiders, the experimental inflorescences were checked every two hours (at 13.00, 15.00 and 17.00). If the crab spider had left the inflorescence, it was put back, or replaced by another *M. vatia* of the same colour if it could not be re-located (spiders on control flowers were removed). Spiders sometimes also hide beneath the petals of inflorescences, thereby complicating the issue of conspicuousness, but this

was only rarely the case in our experiment and we ignored this in the analysis. All crab spiders were used only once in the experiment. On days 2 and 3, the inflorescences were checked the same way as on day 1 (every two hours from 11.00 until 17.00). The experiment ended at 17.00 on day 3. Cameras recorded pictures continuously during the three day intervals. However, for data analysis, we used only data recorded from 09.00 to 19.00, when most of the flower visitors were active. Furthermore, we noted whether spiders caught prey and, if so, the identity of the prey.

We calculated the number and duration of visits to inflorescences per hour for each flower visitor taxon. Periods when spiders had left experimental inflorescences and periods during which cameras did not send pictures to the Internet because of connectivity problems were excluded.

Flower visitors were determined to species or genus level from the video recordings. In addition, we measured the height of each experimental inflorescence above the soil surface (cm) and its diameter (mm), and each patch received an  $x$ - and  $y$ -coordinate in order to account for the spatial heterogeneity in insect visits.

### (c) *The hypotheses*

Given our setup, we can predict the outcome of the experiments according to the three hypotheses. In the crypsis hypothesis, spiders with the same colour as the flower and spider-free flowers should gain more insect visits than unmatched pairs. Accordingly, white crab spiders on white inflorescences and yellow spiders on yellow inflorescences should have a higher foraging success than the converse colour combinations. The two colours of crab spiders on violet inflorescences should gain the same amount of prey, as they are both conspicuous. In the spider avoidance hypothesis, we would expect considerably more insect visits on spider-free inflorescences. However, the foraging success should not depend on the colour combinations of crab spiders and inflorescences. Finally, in the flower visitor attraction hypothesis, contrasting spiders should have an appealing effect on flower visitors. Thus, we would expect more visits on inflorescences harbouring spiders than on control inflorescences. Here, again, we would not expect differences between different colour combinations of spiders and inflorescences.

### (d) *Statistical analysis*

We tested for the preferences of different flower visitor groups with linear mixed effects models (function `lme` in the statistical software R v.2.7.2; R Development Core Team 2007) fitted by maximum likelihood with flower species and spider treatment (yes or no, independent of the spider's colour) and their interaction as fixed factors. In a second analysis, in which we used only data from inflorescences harbouring crab spiders, we tested (i) whether flower visitors showed higher or lower visitation rates to inflorescences on which the crab spider's colour matched the background colour of the flowers and (ii) whether crab spiders profited from colour-matching in terms of the number and dry mass of flower visitors caught. Here, spider colour, flower colour and their interactions were used as independent variables. The number of flower visitor visits per hour, the duration of visits per hour and the dry mass caught per hour (all log-transformed to conform to the assumptions of normality) were used as dependent

variables. Inflorescence height, diameter of the inflorescences and the spatial patch position ( $x$ - $y$  variables) were covariates in all analyses. The temporal block was included as a random factor. It should be noted that in some cases, we analysed the data for one flower species only, if no or very few visiting events occurred on the other flower species (e.g. for bumble-bees that exclusively visited *K. arvensis*; see appendices SA and SB, electronic supplementary material). We started with a full model, containing all variables, and used a backward procedure to obtain minimum adequate models by removing variables that did not improve the fit of the model (tested by the Bayesian information criterion (BIC), Schwarz 1978). All calculations were done in R v.2.7.2.

## 3. RESULTS

During our experiment, a total of 8358 insect visits were observed on the inflorescences (table 1). Solitary bees were the most frequent visitors and made up almost half of all visitation events (3984 visits). Within the group of solitary bees, *Hylaeus* sp. (1927 visits) and *Lasioglossum* sp. (1118 visits) were the most common visitors, but two other genera also occurred in considerable numbers (*Halictus* sp. and *Colletes* sp.). The second most common visitors were bumble-bees, with 1906 visits, dominated by *Bombus terrestris*. Honeybees, with 706 visits, and syrphid flies, with 433 visits, also foraged regularly on the experimental inflorescences (table 1). All the other insect visitors either occurred in small numbers or were not typical pollinators (e.g. ants). We therefore concentrated our analyses on four flower visitor groups: bumble-bees, honeybees, solitary bees and syrphid flies.

The time spent by the flower visitors on the inflorescences was correlated with the number of visits (linear regression:  $n = 90$  inflorescences,  $r^2 = 0.47$ ,  $p < 0.001$ ). Thus, attractive inflorescences not only gained more insect visits, but were also visited for longer. As the results for the average number of insect visits and the average duration revealed similar results, we only present the results for the average number of visits in the paper (duration is treated in the electronic supplementary material). Bumble-bees and honeybees showed a clear preference for *K. arvensis* compared to the other two flower species used in the experiment. In fact, *K. arvensis* was the most often visited flower species by all groups (3704 visits) and a visit lasted on average  $24.0 \pm 2.8$  s. Solitary bees and syrphid flies preferred *A. tinctoria*, the inflorescences of which were visited second most (3353 visits;  $14.7 \pm 1.8$  s/visit). With 1301 visits, *C. frutescens* gained the fewest visits, but the longest ( $26.2 \pm 5.8$  s/visit).

We did not observe a uniform spatial distribution of the flower visitors, meaning that certain patches were preferred by different flower visitor taxa. This heterogeneity was seen when analysing the data for all flower visitors together (appendix SA, electronic supplementary material), but disappeared when the flower visitor groups were split into subgroups and genera. Furthermore, bumble-bees generally preferred taller inflorescences and solitary bees showed a slight preference for inflorescences with a larger diameter in their duration of visits (appendices SA and SB, electronic supplementary material).

Table 1. Visitors to the experimental inflorescences: the total number of visits to experimental inflorescences (with and without crab spiders); the total number of visits to inflorescences harbouring a hunting crab spider; the number of insects caught by the spiders; the chance of being caught during a random visit towards an inflorescence harbouring a crab spider; and the average individual dry mass (in mg  $\pm$  SE) of the different observed flower visitor taxa (in brackets, the number of weighed individuals per taxon).

	visits total	visits with spiders	insects caught	% caught	dry mass (mg)
bumble-bees	1906	821	2	0.24	98.2 $\pm$ 3.4 (11)
<i>Bombus campestris</i>	284	59	—	—	105.8 $\pm$ 0.7 (2)
<i>Bombus lapidarius</i>	26	15	—	—	81.5 $\pm$ 0.3 (2)
<i>Bombus pascuorum</i>	374	208	1	0.48	93.6 $\pm$ 7.4 (3)
<i>Bombus terrestris</i>	1089	470	—	—	108.8 $\pm$ 2.8 (3)
other <i>Bombus</i>	133	69	1	1.45	98.9 $\pm$ 0.0 (1)
honeybees	706	242	14	5.79	29.5 $\pm$ 1.1 (6)
solitary bees	3984	777	51	6.56	7.1 $\pm$ 1.1 (18)
<i>Colletes</i> sp.	357	67	3	4.48	15.6 $\pm$ 0.2 (3)
<i>Halictus</i> sp.	557	162	2	1.23	6.2 $\pm$ 0.7 (3)
<i>Hylaeus</i> sp.	1927	403	31	7.69	5.3 $\pm$ 0.3 (6)
<i>Lasioglossum</i> sp.	1118	145	15	10.34	5.2 $\pm$ 0.5 (6)
other solitary bees	25	0	—	—	5.9 $\pm$ 0.0 (1)
syrphid flies	433	57	1	1.75	10.3 $\pm$ 2.5 (13)
<i>Eristalis tenax</i>	164	21	—	—	17.2 $\pm$ 2.6 (5)
<i>Sphaerophoria</i> sp.	106	8	—	—	2.6 $\pm$ 0.4 (3)
<i>Syritta</i> sp.	89	7	—	—	1.3 $\pm$ 0.1 (3)
other syrphid flies	74	21	1	4.76	11.8 $\pm$ 0.3 (2)
others	1329	301	10	3.32	14.7 $\pm$ 2.2 (16)
ants	392	93	1	1.08	1.7 $\pm$ 0.2 (6)
Coleoptera	390	60	2	3.33	26.3 $\pm$ 11.8 (3)
other Diptera	81	18	5	27.78	7.7 $\pm$ 1.4 (6)
wasps	349	99	—	—	22.3 $\pm$ 0.0 (1)
undetermined	117	31	2	6.45	—
total	8358	2198	78	3.55	24.5 $\pm$ 4.0 (64)

#### (a) Responses to crab spiders

Solitary bees and syrphid flies strongly avoided inflorescences harbouring crab spiders, independent of colour combinations, and spent significantly less time on these inflorescences (figure 1; appendix SA, electronic supplementary material). Within the solitary bees and syrphid flies, we found differences between the observed genera. While the solitary bees *Hylaeus* sp. and *Lasioglossum* sp. avoided spider-harboured inflorescences, the other two observed genera (*Colletes* and *Halictus*) did not significantly reduce their visits to inflorescences with crab spiders (figure 1). Although the number of visits of *Colletes* bees did not significantly decrease towards spider-harboured inflorescences, they spent less time on them (appendix SA, electronic supplementary material). In the group of syrphid flies, only two of the three observed taxa (the *Syritta* and *Sphaerophoria* genera) avoided spiders. They visited inflorescences harbouring crab spiders less frequently and for shorter durations than spider-free inflorescences. No reaction towards crab spiders was observed for *Eristalis tenax* (figure 1).

By contrast, none of the observed bumble-bee species or honeybees showed a reaction towards *M. vatia* spiders. In both groups, the average number and duration of visits did not significantly differ between inflorescences with and without crab spiders (figure 1; appendix SA, electronic supplementary material). Furthermore, it is noteworthy that in our study, all flower-visiting groups either avoided or ignored crab spiders, but were never attracted to them (appendix SA, electronic supplementary material).

#### (b) Responses to different colour combinations of crab spiders and inflorescences

When analysing the data of inflorescences harbouring crab spiders only, and focusing on the different colour combinations of spiders and inflorescences, we found no evidence that crab spiders profit from adapting their colour to that of inflorescences (figure 2; appendix SB, electronic supplementary material). Neither white crab spiders on white inflorescences nor yellow spiders on yellow inflorescences gained significantly more insect visits compared to the respective unmatched colour combination. On the violet *K. arvensis* inflorescences, no significant differences between white and yellow crab spiders were observed. The average duration of the visits yielded similar results as the average number of visits (appendix SB, electronic supplementary material).

#### (c) Prey capture success

Crab spiders were able to catch and feed on 78 insects. As 2198 visits occurred on spider-harboured inflorescences (when a spider was present), the chance of a visiting insect being caught was on average 3.55 per cent (table 1). Although we observed only 18 visits of non-syrphid flies to inflorescences harbouring a crab spider, these had the highest probability of being caught (27.78%). Their small sizes prevented us from identifying them to the family or the genus level. Honeybees (5.79%) and solitary bees (7.40%) were also relatively common prey items. During the experiment, only two bumble-bees (0.24%) and one syrphid fly (1.75%) were caught (table 1).

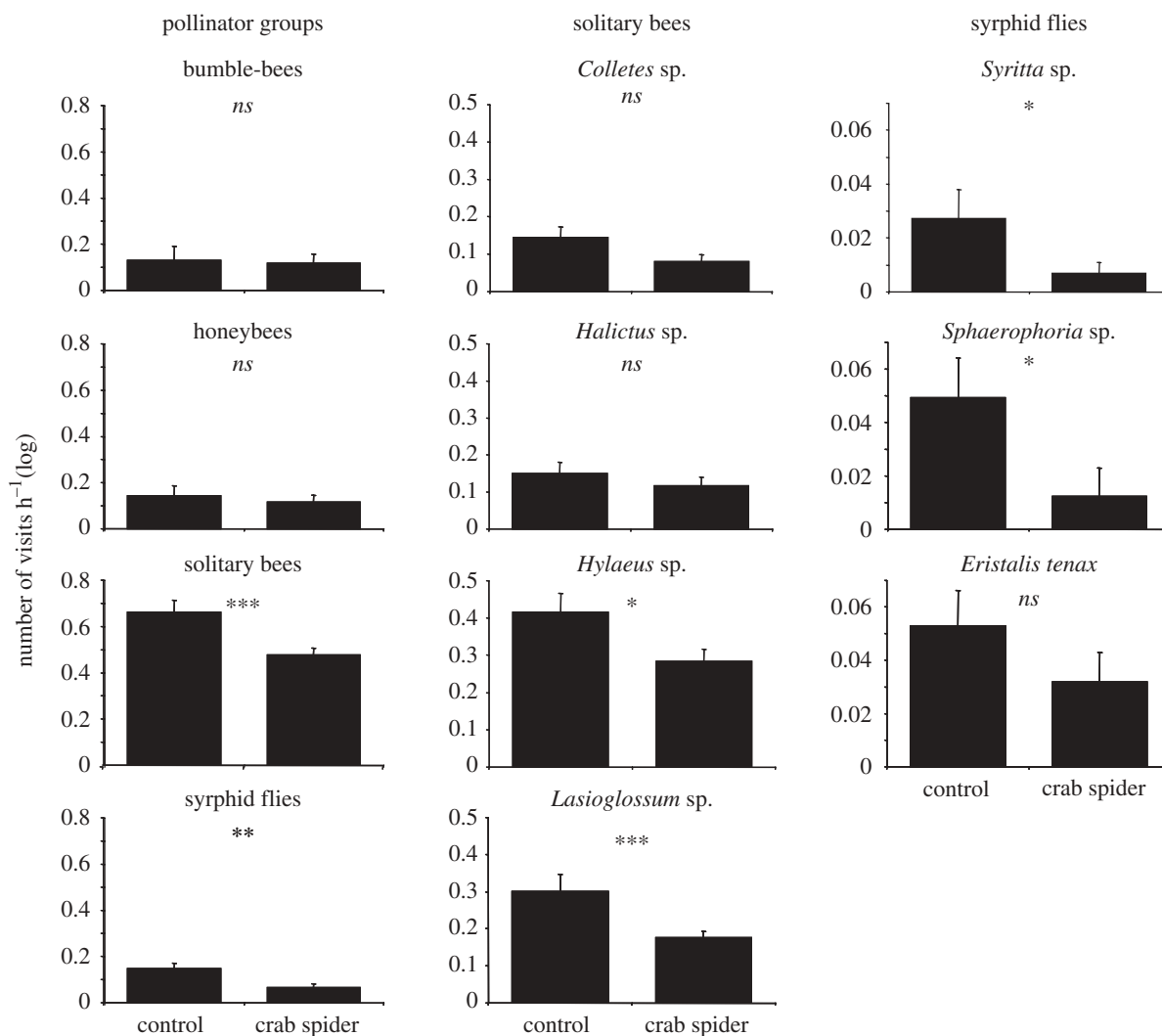


Figure 1. Total number of visits per hour (mean + SE; log-transformed) according to spider treatment (control, crab spider) of the different flower visitor groups, solitary bee taxa and syrphid fly taxa: \* $p < 0.05$ ; \*\* $p < 0.01$ ; \*\*\* $p < 0.001$ ; for exact values see appendix SA, electronic supplementary material.

Colour-matched crab spiders did not catch significantly higher prey biomass (lme:  $t < 0.71$ ,  $p > 0.48$ ). Furthermore, crab spiders caught more insects (dry mass) on inflorescences with a larger diameter (lme:  $t = 3.88$ ,  $p < 0.001$ ). All the other variables did not remain in the minimum adequate models. Flower species did not appear as a significant factor, but there were clear differences in prey biomass caught on different flower species (figure 3), explained mostly by the differences in the diameter of the inflorescences of the three species (*A. tinctoria*:  $30.2 \pm 1.0$  mm; *C. frutescens*:  $35.2 \pm 0.8$  mm; *K. arvensis*:  $38.8 \pm 1.9$  mm).

#### 4. DISCUSSION

Of the three hypotheses tested, we found support for only one: the spider avoidance hypothesis. If flower visitors reacted at all, they generally avoided crab spiders hunting on inflorescences, independently of the colour combination of spiders and inflorescences. While solitary bees and syrphid flies support this spider avoidance hypothesis, bumble-bees and honeybees displayed a fourth behaviour: they were indifferent to crab spiders, despite a high likelihood that they were able to detect them.

Avoidance could be either innate or learnt. Recent work has shown that bumble-bees and honeybees can learn to avoid crab spiders, but only after they have had exposure to predation attempts, and the same might apply to flies (Ings & Chittka 2008; Abbott & Dukas 2009). Unfortunately, we have no information about the origin or the age of the bees that visited our garden. However, we have no reason to believe that the different flower visitor groups differed in their level of experience with crab spiders, as they experienced the same environment. Even if honeybees and bumble-bees, and maybe other flower visitors as well, are capable of learning to avoid predators, it remains to be shown how often this situation arises in nature. In our study, we artificially increased crab spider densities throughout the flowering season at the experimental site and still we did not find indications for the avoidance of spider-harboured flowers by bumble-bees and honeybees. There may also be less evolutionary pressure in social insects to develop an avoidance reaction, because the death of a worker only marginally reduces its fitness (Hamilton's rule; Clark & Dukas 1994). A third reason may lie in the different body sizes of the flower visitor groups (Dukas & Morse 2003, 2005). The bumble-bees might be better protected from

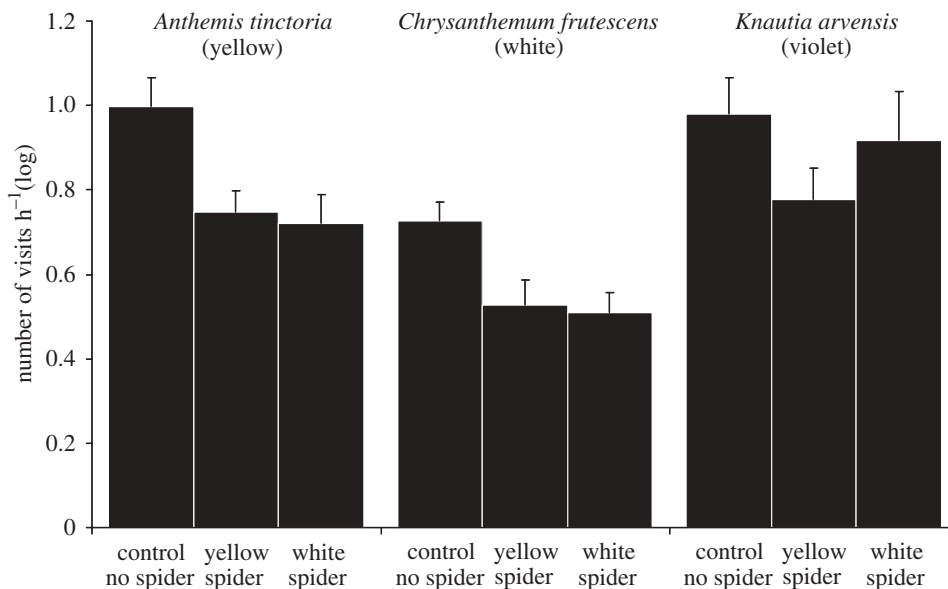


Figure 2. Total number of insect visits (mean + SE; log-transformed) towards control inflorescences and different colour combinations of crab spiders and inflorescences.

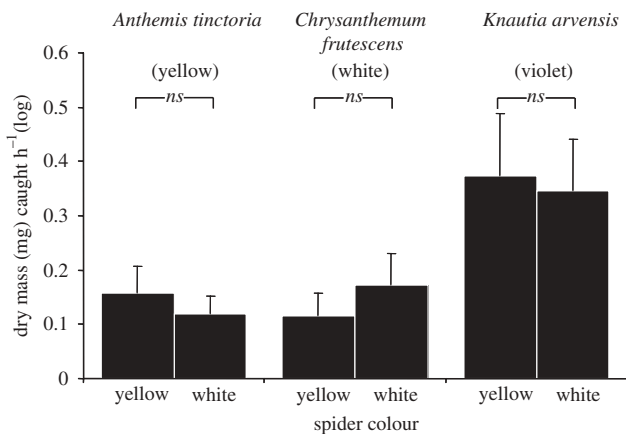


Figure 3. Dry mass (mg) caught per hour (mean + SE; log-transformed) by white and yellow crab spiders on differently coloured inflorescences.

predation by their size alone, which is three times greater than that of the other flower visitors. As a consequence, bumble-bees were very frequent visitors but had the lowest probability of being captured.

In addition to the differences in flower visiting behaviour between flower visitor groups, we also found differences within these groups: some members of the solitary bee and syrphid fly groups strongly avoided crab spiders (e.g. *Lasioglossum* sp. and *Syrirta* sp.), but others did not show significant avoidance reactions (e.g. *Halictus* sp. and *E. tenax*). This general result is in line with an increasing number of other studies mentioning that crab spider and flower visitor identities (also flower species) have to be taken into account in order to fully understand predator–prey–plant interactions (e.g. Reader *et al.* 2006; Brechbühl *et al.* in press). As the flower visitors were continuously video-recorded, we gained some indications of what might be responsible for the behavioural differences within the flower visitor groups. The syrphid flies of the genus *Syrirta* and *Sphaerophoria*, for example, displayed characteristic hovering and systematic examination of an

inflorescence before landing. They usually avoided a flower when a crab spider was present. In contrast, this hovering behaviour was not observed in *E. tenax*, which did not show avoidance reaction towards spiders. Inside the group of solitary bees, the behavioural avoidance reaction towards crab spiders could be observed before landing (spiders might be a visual cue) and also after landing (solitary bees spent less time on spider-harbouring inflorescences). The latter behaviour has been shown in a study with vertebrate ambush predators (lizards), where flower visitors fled as soon as they were attacked and thus spent less time on plants beside which lizards were hunting (Muñoz & Arroyo 2004). Therefore, a prey community approach is mandatory to understand crypsis in a generalist predator, as each prey has evolved specific visual abilities and behavioural responses to the same stimulus.

We found no support for the other two hypotheses (crypsis hypothesis and spider attraction hypothesis). Focusing first on the crypsis hypothesis, *M. vatia* spiders clearly did not profit from having the same colour as the inflorescence on which they were settled. Colour-matched spiders did not have more encounters with flower visitors and, more importantly, they did not have a higher foraging success in terms of the biomass captured. Bearing in mind the predominance of the crypsis hypothesis in the literature for over a century, this is a surprising result, but one which is in line with the findings of Chittka (2001), who often found poorly matching spiders, and Defrize *et al.* (submitted), who observed a very low degree of perfect matching in the field. As in our study system, most large flower visitors (bumble-bees and honeybees) were observed on the violet *K. arvensis* inflorescences, crab spiders should place themselves on these inflorescences in order to be most successful (most dry mass caught per hour), despite not matching there. Prey capture success seems therefore not to depend on the degree of colour-matching, but much more on the insects visiting the inflorescences—a fact that Morse & Fritz (1982) have reported a long time ago.

As we found no evidence that colour change would increase predation success, why do these spiders change their body colour? The colour change might be a protection mechanism against radiation (Venner & Casas 2005; Insausti & Casas 2008, *in press*; Théry & Casas 2009). The photo-protection role of these colour pigments (ommochromes) has been shown in insect eyes (Langer 1975; Stavenga 1989). As these crab spiders settle themselves for long periods on top of the inflorescences, a protection against intense sunlight might be necessary, most of all because they have a transparent cuticle. Thus, incidental colour adaptation (crypsis) might only be a by-product, with the driving force being the protection of the crab spiders against radiation. However, as flower colour choice in the field is not random (Weigel 1941; Heiling *et al.* 2005), protection against radiation alone cannot explain the colour adaptation of the spiders. Another argument that has been suggested is predator avoidance. If crypsis is involved in predator avoidance, one would expect higher predation rates on non-matching colour combinations. However, in three years of video observations (Brechbühl *et al.* *in press*; R. Brechbühl 2006–2008, personal observation), we only recorded one predation event (by a bird—a black redstart *Phoenicurus ochruros*), despite the presence of a multitude of potential predators at the experimental site—among others, spider wasps (Pompilidae), common and paper wasps (Vespidae), a variety of birds and assassin bugs. Although our study is restricted to one site only, we doubt that crypsis plays a major role in avoiding predation.

The third hypothesis tested in this work—the flower visitor attraction hypothesis (Heiling *et al.* 2003, 2005)—found no support in our study system. However, in contrast to the crab spider species (*T. spectabilis*) used by Heiling *et al.* (2003, 2005), *M. vatia* does not reflect ultraviolet light (Chittka 2001; Théry & Casas 2002).

In conclusion, we found no support for the two hypotheses of crypsis and flower visitor attraction. The spider avoidance hypothesis gained support for several flower visitor species; in particular solitary bees and different fly species, and a fourth mechanism, indifference to spiders, was found for the large social bees. Thus, deriving conclusions from the study of only a subset of flower visitor species is fraught with difficulties, and a community approach towards crypsis in a generalist predator seems mandatory.

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