

0 Response of pollinators to the tradeoff between resource acquisition and predator avoidance 53

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10 Although the behaviour of animals facing the conflicting demands of increasing foraging success and decreasing predation risk has been studied in many taxa, the response of pollinators to variations in both factors has only been studied in isolation. We compared visit rates of two pollinator species, hoverflies and honeybees, to 40 *Chrysanthemum segetum* patches in which we manipulated predation risk (patches with and without crab spiders) and nectar availability (rich and poor patches) using a full factorial design. Pollinators responded differently to the tradeoff between maximising intake rate and minimising predation risk: honeybees preferred rich safe patches and avoided poor risky patches while the number of hoverflies was highest at poor risky patches. Because honeybees were more susceptible to predation than hoverflies, our results suggest that, in the presence of competition for resources, less susceptible pollinators concentrate their foraging effort on riskier resources, where competition is less severe. Crab spiders had a negative effect on the rate at which inflorescences were visited by honeybees. This effect was mediated through changes in the foraging strategy of honeybees, and could, in principle, be reversed by increasing nectar productivity of inflorescences. Our study shows that both pollinator species responded simultaneously and differently to variations in food reward and predation risk, and highlights the importance of studying the foraging strategies of pollinators in order to fully understand how plant–pollinator interactions are established. 65

25 Because of their role as pollen vectors, pollinators have the potential to influence the structure of plant communities. At the same time, however, plant–pollinator interactions represent just a step in more complex food webs and cannot be studied in isolation (Jordano 1987, Bascompte et al. 2003, Ings et al. 2009a). A proper understanding of plant–pollinator interactions therefore requires elucidating the factors determining the foraging choices of pollinators (Waser and Price 1998, Rodríguez-Gironés and Santamaría 2010). While the factors affecting foraging choices of pollinators can be studied both in the field and the laboratory (Pleasants 1981, Waddington 1981, 1995, Dukas and Morse 2003, Suttle 2003, Makino and Sakai 2007, Ings and Chittka 2009), details concerning the mechanisms responsible for the decision rules are best figured out under controlled laboratory conditions (Real 1981, Real et al. 1982, Chittka and Thomson 1997, Menzel 2001, Keasar et al. 2002, Chittka and Spaethe 2007). 80

45 The distribution of resources and predators are two of the main factors affecting choices of foraging animals. Everything else being equal, animals tend to adopt the foraging strategies that maximise their intake rate and minimise their exposure to predators. When those strategies leading to higher intake rates are associated with higher intake rates, however, animals will only be selected to choose the rich-risky strategy if the fitness returns of increasing intake rate are sufficient to compensate for the increased mortality rate (reviewed by Gilliam and Fraser 1987, Lima and Dill 1990, Brown and Kotler 2004). The tradeoff between maximizing the rate of resource harvesting and minimizing predation risk has been studied in many taxa, but in the context of pollination responses to resource availability (Pleasants 1981, Real and Rathcke 1991, Makino and Sakai 2007) and predation risk (Dukas and Morse 2003, Suttle 2003, Dukas 2005) have been studied in isolation. 85

90 Pollinating insects have long been used as a model system to test predictions from optimal foraging theory because of the strong direct links between resource acquisition and fitness in these animals (Heinrich 1979, Pyke 1979, Seeley 1985, Dreisig 1995, Bosch and Kemp 2004). The effect of predators on pollinator behaviour, on the other hand, was long neglected on the assumption that predation is too infrequent to affect the foraging strategy of pollinators (Pyke 1979, Miller and Gass 1985). Nevertheless, a number of studies over the last decade have shown that predators can affect the foraging strategy of pollinators at the inflorescence, plant and patch levels (Dukas 2001, 2005, Dukas and Morse 2003, Muñoz and Arroyo 2004). These studies have shown that, through their non-consumptive effects on pollinator behaviour (Dukas and Morse 2003, Gonçalves-Souza et al. 2008, Ings and Chittka 2009), predators may have top–down effects on plant fitness and even affect the structure of the plant–pollinator community (Suttle 2003, Gonçalves-Souza et al. 2008). A recent model has shown that pollinator's choice of foraging strategy should be affected by their susceptibility to predation, as well as the abundance 100

50 105

0 of resources and distribution of predators: less vulnerable
pollinators should concentrate their foraging effort on rich,
risky flowers and more vulnerable pollinators on poor, safe
flowers (Jones 2010), while an earlier model demonstrated
that social and solitary species should differ in their response
5 to predation risk (Clark and Dukas 1994). It is also known
that the tendency of bumblebees, *Bombus occidentalis*, to flee
from a model predator increases with the level of resources
at the hive (Cartar 1991). Yet no study has investigated
how pollinators trade off increasing resource acquisition and
10 minimising predation risk.

The response of pollinators to the interplay between
resource availability and predation risk may have ecologi-
cal and evolutionary implications. Thus, when predators
are relatively sedentary and flowers or inflorescences long-
lived (Morse 2007), resources will tend to accumulate in
15 areas where predation risk is high if pollinators avoid them.
Will the accumulation of resources tempt pollinators back
into predator-rich patches? A similar question can be raised
at the evolutionary time scale. Predators can show strong
preferences for some host plant species (Morse 2000, 2007,
20 Schmalhofer 2001). Any plant species that recurrently expe-
riences low reproductive success because it is used as hunting
platform by ambush predators might be selected to increase
reward production – at least if pollinators are willing to
25 increase their exposure to predation risk in order to increase
the rate at which they acquire resources. The purpose of this
paper is hence to study how pollinators trade off foraging
efficiency for avoidance of predation risk. To tease apart the
role of predators ambushing at flowers (hereafter referred to
30 as ambush predators) and resource availability from other
floral traits, instead of comparing visit rates at flower species
naturally differing in nectar production and the frequency
with which they harbour ambush predators, we compared
visit rates at flowers of a single species manipulated to differ
35 in their level of predation risk and resource availability. In
particular, this experiment allows us to answer the following
questions:

- 1) how do pollinators trade off between maximising intake
40 rate and minimising predation risk?
- 2) If pollinators avoid predator-rich areas, could inflores-
cences recover their attractiveness increasing their rate
of nectar production?

45 The purpose of this study is not so much to learn how spatial
heterogeneity in resource availability and predation risk
affects plant–pollinator interactions in a particular commu-
nity, as to understand the factors affecting the foraging strat-
egies of pollinators. This insight can then be incorporated
50 into models and used to understand the ecological assem-
blage and evolutionary trajectories of pollination networks
(Rodríguez-Gironés and Santamaría 2005, 2010).

55 Methods

Study site and species

We conducted our experiment in May 2007 in an aban-
60 doned crop field at ‘la Raña’ (39°41'51"N, 5°27'55"W)

within ‘Las Villuercas-Ibores’ region in Extremadura, south-
western Spain. The most common flowering plants at our
study site were *Chrysanthemum segetum* (Asteraceae), *Orni-*
thopus compressus (Papilionaceae), *Anthemis* sp. (Asteraceae),
65 *Hedypnois cretica* (Asteraceae), *Leontodon taraxacoides* (Aster-
aceae), *Echium plantagineum* (Boraginaceae), *Silene gallica*
(Caryophyllaceae) and *Calendula arvensis* (Asteraceae). We
selected the field site because of the abundance of *C. segetum*
inflorescences: they are commonly used by crab spiders as
70 hunting platform and are visited by a large number of nec-
tar- and pollen-collecting insects, including Hymenoptera,
Diptera, Coleoptera and Lepidoptera. In what follows, we
consider only the interactions between honeybees *Apis mel-*
lifera (Apidae), hoverflies *Eristalis tenax* (Syrphidae), hereaf-
75 ter ‘hoverflies’ and *C. segetum*, as they were the only ones
sufficiently common for statistical analysis.

We used adult females of two crab spider species, *Thomisus*
onustus and *Synema globosum* (Thomisidae), as ambush
predators in our experiment. Crab spiders are sit-and-wait
80 ambush predators and use their enlarged powerful raptorial
front legs to capture their prey (Morse 2007). *Thomisus onus-*
tus and *S. globosum* prey mainly on bees and flies and were
locally abundant in our field site.

85 Experimental treatments

We selected 40 1 × 1 m² patches with high density of
C. segetum for the experiment and mowed a 1.5 m wide strip
of vegetation around each patch to decrease the number
of crab spiders leaving the patch by bridging (Corcobado
90 et al. 2010). We grouped patches in ten blocks of four nearby
patches each and allocated patches at random to the follow-
ing treatments: rich-risky patches, poor-risky patches, rich-
safe patches and poor-safe patches, with one patch of each
type per block. On 6 May we counted the number of pol-
95 linators per patch four times, at 09:30, 11:30, 15:30 and
17:30. After the last count we counted and removed all the
spiders we found in all the patches. We counted the number
of *C. segetum* inflorescences per patch on 6, 13, 20 and 29
May and 1 June. 100

On 7 May we added seven *T. onustus* and three *S. globo-*
sum females to each risky patch. From then on, we removed
all spiders we found in safe patches during the experiment
and we added crab spiders to risky patches whenever we
105 found less than three individuals in a patch during the
observations.

For the nectar treatment we added 50 µl of 15% (w/w)
sucrose solution to 40 haphazardly selected *C. segetum* inflo-
rescences (not harbouring spiders) in each rich patch twice
per day, starting at 09:00 and 14:00. We used low concen-
110 tration nectar because of the speed at which water evapo-
rated from the exposed droplets. We chose the number of
inflorescences to which we added sucrose solution and the
amount of sucrose added per inflorescence so as to double
nectar availability in rich and poor patches. Sucrose solu-
115 tion was added with a repeater micropipette on the disc of
inflorescence heads. Each day, twenty patches were observed
between 10:00 and 13:00, and the remaining 20 after 15:00.
In each half of the day we observed the 20 patches where
nectar had been more recently added to minimize changes in
120 nectar concentration.

0	We observed each patch for 15 min per day. We counted the number of pollinators present in the patch upon arrival of the observer and we recorded the number of insects visiting the patch and the number of inflorescences visited by each insect during the observation period. We	61
5	also recorded the number of spiders in the patch and how many of them were consuming prey at the start of the observations. Finally, we recorded the number of spider attacks and prey captures.	65
10	Strength of manipulations	70
15	The strength of the predation-risk manipulation was determined comparing the number of crab spiders present in risk and safe patches during the experiment with their natural density, which was estimated from the number of crab spiders we encountered on patches before the start of the experiment.	75
20	To determine whether spiders concentrated on patches with more resources, we used a paired t-test to compare the average number of spiders observed per patch between rich and poor patches. We further compared the number of spiders that we had to add to or remove from rich and poor patches.	80
25	To assess the strength of the nectar enrichment manipulation, we assumed that nectar production rate by <i>C. segetum</i> is similar to that of <i>C. coronarium</i> in Greece, where each disk floret produces 0.01 µl of 47% (w/w) nectar per day (Petani-	85
30	dou and Smets 1995). Because there are approximately 300 disk florets per inflorescence in <i>C. segetum</i> (Howarth and Williams 1972), nectar productivity must be about 3 µl per inflorescence. Nectar productivity per patch was therefore estimated as the number of <i>C. segetum</i> inflorescences times 3 µl of 47% (w/w) per inflorescence. We used an ANOVA to test whether rich and poor patches differed in the number of inflorescences (averaged over the five counts) and hence in	90
35	the amount of resources they produced.	95
	Effect of predation risk and resource availability – patch level	
40	For each patch, we averaged over five days of observations (15–19 May) the number of pollinators (honeybees and hoverflies) arriving to the patch during the observations, the number of inflorescences visited by each pollinator within the patch and the number of open inflorescences. These average	100
45	values were entered into mixed effects models to determine the effect of treatment and inflorescence abundance on pollinator behaviour. Each model included nectar presence (poor vs. rich patches), spider presence (safe vs risky patches) and their interaction as fixed factors, block (10 levels) as random	105
50	factor and number of inflorescences per patch as a covariate. The dependent variables were the number of pollinators (honeybees or hoverflies) and the average number of inflorescences visited per pollinator within the patch. To achieve	110
55	homogeneity of variances, we square-root transformed the number of inflorescences that each pollinator visited. Interactions between the number of inflorescences per patch and treatment (resource availability and/or predation risk) are not reported because they were never statistically significant and models including these interactions always lead to increases	115
60	in the AIC value greater than two units (Akaike 1973).	121
	Effect of predation risk and resource availability – inflorescence level	
	We first analysed the effect of predation risk and resource availability on the average number of visits that inflorescences received. For each patch, we divided the total number of visits recorded during the observations (averaged over the five days of observations) by the number of inflorescences in the patch, thus obtaining the average number of visits per inflorescence. We analysed separately the data for honeybees and hoverflies, using mixed effects models that included nectar presence (poor vs rich patches), spider presence (safe vs risky patches) and their interaction as fixed factors and block (10 levels) as random factor. We used Box-Cox transformations to achieve homogeneity of variances, with $\lambda = 0.35$ for the honeybees and $\lambda = 0.5$ (equivalent to the square-root transformation) for the hoverflies.	
	We next focused on the response of pollinators to the presence of predators on the inflorescences they approached. To determine whether pollinator species and patch resource availability affected the probability of landing on predator-harbouring inflorescences we used a generalized linear mixed effects model with a binomial distribution and identity link function. For each inflorescence visited in risky patches throughout the period of observations, the type of inflorescence chosen (with or without predator) was used as dependent variable in the analysis. Resource availability (rich vs poor patches) and pollinator species (honeybees vs hoverflies) were the fixed factors, block (10 levels) was used as random factor and the proportion of inflorescences harbouring spiders was used as covariate. If pollinators chose inflorescences at random, irrespective of the presence of spiders, there should be a linear relationship, with slope of one, between the proportion of inflorescences harbouring spiders and the probability of choosing a spider-harbouring inflorescence. If pollinators avoided inflorescences with spiders, the probability of choosing a spider-harbouring inflorescence might increase with the proportion of inflorescences harbouring spiders, but the slope of the relationship would be smaller than one. To test whether pollinators avoided spiders, we performed a Wald's Z test on the slope (Dobson and Barnett 2008), the null hypothesis being slope = 1.	
	Effect of spider encounters on patch departure	
	Whenever a pollinator landed on a spider-harbouring inflorescence, we scored the response of the spider according to one of the following categories: indifference if the spider did not respond to the arrival of a pollinator, approach if the spider oriented and moved in the direction of the pollinator, strike if the spider attempted to capture the pollinator with its forelegs and failed to contact the pollinator, struggle if the spider enclosed the pollinator with its forelegs but the pollinator managed to escape and kill if the spider managed to capture the pollinator. If the pollinator was not killed, we further recorded whether the next inflorescence it visited was within the same patch. We used a generalised linear mixed effect model with binomial distribution to determine the factors affecting patch departure (stay vs leave patch). The model included spider response (still, approach, strike and struggle), resource availability (rich vs poor patches) and	

0 pollinator species (honeybees vs hoverflies) as fixed factors
 and block (10 levels) as random factor.

Susceptibility to predation

5 We compared the susceptibility to predation of honeybees
 and hoverflies in two ways. First we used Fisher's exact test to
 compare 1) the proportion of honeybees and hoverflies that
 were attacked by spiders after landing on spider-harboring
 inflorescences, and 2) from the attacked individuals, the pro-
 10 portion that were actually captured. In this analysis, we only
 included those pollinators that landed on spider-harboring
 inflorescences while we were observing the patch. In a sec-
 ond analysis, we estimated susceptibility to predation as the
 number of honeybees or hoverflies that were being consumed
 15 by spiders when we arrived to a patch, normalised by the rate
 at which pollinators of the corresponding species visited the
 patch. (For each patch, we obtained a single value averag-
 ing over all observations.) This surrogate of susceptibility was
 then compared (honeybees vs hoverflies) with a Wilcoxon
 20 matched-pairs test.

Unless otherwise specified, all results are reported as aver-
 age \pm SD, where averages refer to least squares means.

Results

Strength of manipulations

Because *Chrysanthemum segetum* inflorescences in our patches
 30 received over 99% of honeybee and hoverfly visits to experi-
 mental patches during the observations, as a first approxi-
 mation we can ignore other plant species when estimating
 resource availability per patch. There were no significant
 differences ($F_{1,38} = 0.128$, $p = 0.721$) between the num-
 35 ber of *C. segetum* inflorescences at rich (175.4 ± 65.5) and
 poor patches (182.3 ± 55.5). At 3 μ l of nectar per inflores-
 cence, the average patch offered 537 μ l of nectar. Given that
 the density of 15% and 47% sucrose solution is 1.06 and
 1.22 $\text{g}\cdot\text{cm}^{-3}$, respectively, the 50 μ l of 15% sucrose solution
 40 that we added to 40 inflorescences per rich patch correspond
 to 554 μ l of 47% nectar, implying that we essentially dou-
 bled the amount of nectar available at rich patches. On aver-
 age, we added nectar to 22% of *C. segetum* inflorescences.

Before the manipulation, there were 0.014 ± 0.012 crab
 45 spiders per inflorescence, with a range of 0 to 6 spiders per
 patch. During the observations, the number of spiders per
 inflorescence in risky patches was 0.023 ± 0.009 , with 0 to
 7 spiders per patch. Therefore the distribution of the num-
 ber of crab spiders per patch had similar ranges in risky and
 50 un-manipulated patches, although the average spider density
 in risky patches was 65% higher than the natural density in
 the area. We found and removed only 5 spiders from the
 safe patches throughout the experiment, so safe patches were
 essentially predator-free.

55 The average number of spiders per patch was similar
 in poor (3.50 ± 0.65) and rich (3.42 ± 0.72) patches.
 The difference was not statistically significant ($t_9 = 0.30$,
 $p = 0.77$). During the observations, we added one spider
 per patch, with the exception of one rich and one poor patch
 60 to which we added four spiders. Likewise, of the five spiders

we removed from safe patches, two were in poor patches and
 three in rich patches. Hence, rich and poor patches did not
 differ in their level of predation risk, or in the number of
 spiders they attracted.

65 Although resource availability and predation risk affected
 the average number of pollinators visiting patches, they did
 not affect the range of visitors we encountered. Before the
 onset of the experimental manipulation, the number of visi-
 tors we encountered upon arrival to a patch was between
 0 and 5 for honeybees and between 0 and 3 for hoverflies. 70
 During the application of experimental treatments, the
 number of visitors we encountered upon arrival to patches
 was between 0 and 4 for both honeybees and hoverflies – so
 pollinator activity at experimental patches was well within
 75 natural levels.

**Effect of predation risk and resource
 availability – patch level**

Honeybees preferred rich to poor patches ($F_{1,9} = 68.79$,
 80 $p < 0.001$) and safe to risky patches ($F_{1,9} = 42.73$,
 $p < 0.001$), and their preference for rich patches was higher
 in safe than in risky patches (interaction term: $F_{1,9} = 13.70$,
 $p = 0.001$): the number of honeybees visiting rich-safe
 patches was more than double than the number of honey-
 bees visiting poor-safe patches, while the number of honey-
 bees visiting rich-risky patches was only 78% higher than the
 number visiting poor-risky patches (Fig. 1a). Patches with
 more inflorescences attracted more honeybees ($F_{1,26} = 14.66$,
 85 $p < 0.001$).

Honeybees visited more inflorescences per patch in safe
 than in risky patches ($F_{1,9} = 19.62$, $p = 0.002$), and in rich
 than in poor patches ($F_{1,9} = 22.26$, $p = 0.001$). The effect
 of the interaction between resource availability and preda-
 tion risk on the number of inflorescences that honeybees
 90 visited per patch was not statistically significant ($F_{1,9} = 1.79$,
 $p = 0.21$; Fig. 1b). The number of inflorescences that honey-
 bees visited before leaving a patch increased with the number
 of inflorescences in the patch ($F_{1,26} = 9.79$, $p = 0.004$).

Hoverflies preferred poor to rich patches ($F_{1,9} = 6.94$,
 95 $p = 0.01$). Although the main effect of predation risk was
 not statistically significant (risk vs poor patches: $F_{1,9} = 0.00$,
 $p = 0.96$), the interaction between resource availability and
 predation risk had a statistically significant effect on the num-
 ber of hoverflies visiting patches ($F_{1,9} = 4.33$, $p = 0.047$).
 100 Although the numbers of hoverflies visiting rich-safe and
 poor-safe patches was similar, more hoverflies visited poor-
 risky than rich-risky patches. The number of hoverflies visit-
 ing patches was therefore smallest at rich-risky and highest at
 poor-risky patches (Fig. 2a). The number of hoverflies visit-
 105 ing patches increased with the number of inflorescences in
 the patch ($F_{1,26} = 6.03$, $p = 0.02$).

None of the factors studied had a clear effect on the num-
 ber of inflorescences that hoverflies visited per patch. Hov-
 110 erflies tended to visit more inflorescences in patches where
 inflorescences were more abundant, but this trend was not
 statistically significant ($F_{1,26} = 3.43$, $p = 0.075$). Likewise,
 although the average number of inflorescences that hoverflies
 visited per patch was higher in rich than in poor patches, in
 safe than in risky patches, the effects of resource availabil-
 115 ity ($F_{1,9} = 2.87$, $p = 0.12$) and predation risk ($F_{1,9} = 4.03$,
 120

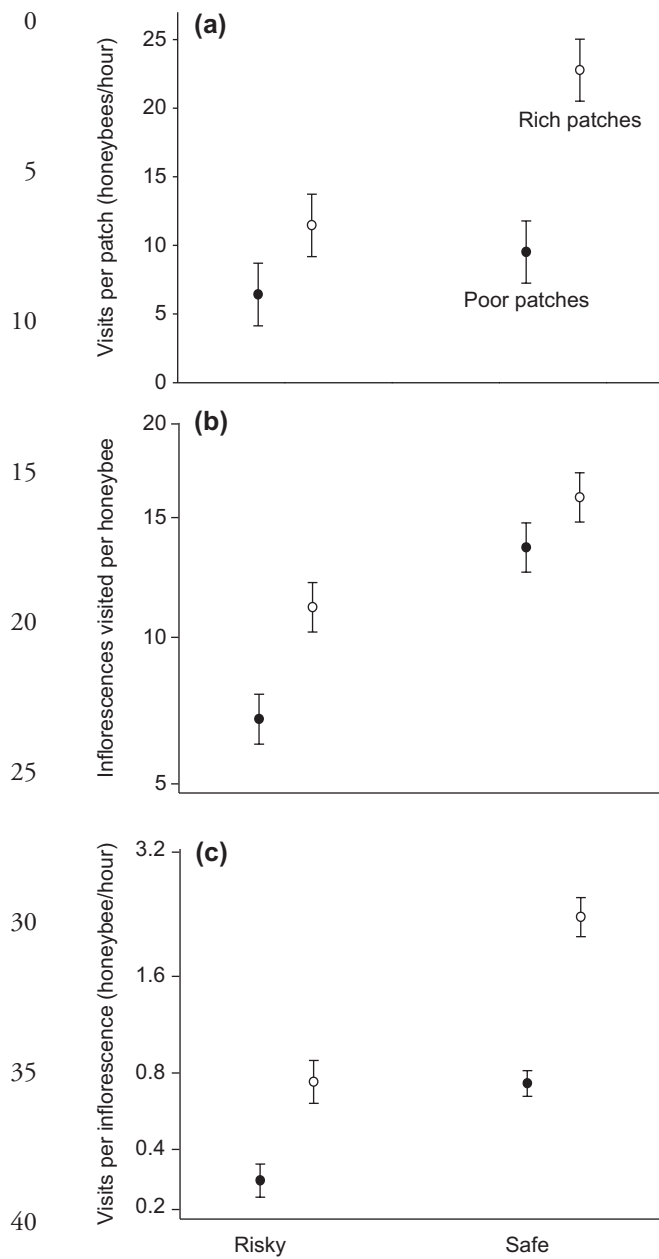


Figure 1. (a) Average rate (hour⁻¹) at which honeybees, *Apis mellifera*, visited patches; (b) average number of inflorescences that individual honeybee visited before leaving the patch, and (c) rate (hour⁻¹) at which the average inflorescence was visited by honeybees. Circles represent least-squared means ± SE for the four treatments (rich and poor, safe and risky patches; 10 replicas).

$p = 0.076$) did not reach statistical significance (Fig. 2b). The interaction between resource availability and predation risk had no discernable effects on the number of inflorescences that hoverflies visited per patch ($F_{1,9} = 0.05$, $p = 0.82$).

Effect of predation risk and resource availability – inflorescence level

Both the number of honeybees visiting patches and the number of inflorescences that each honeybee visited per patch were greater in rich than poor patches, in safe than risky patches (Fig. 1a–b). As a result, there were statistically significant

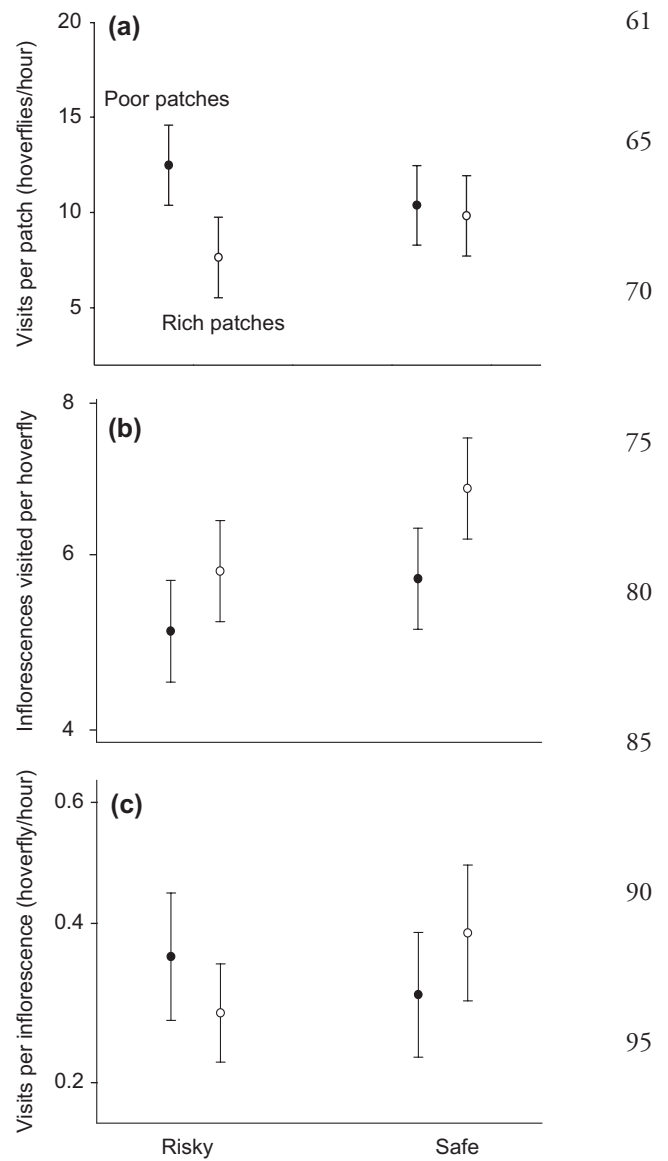


Figure 2. (a) Average rate (hour⁻¹) at which hoverflies, *Eristalis tenax*, visited patches; (b) average number of inflorescences that individual hoverflies visited before leaving the patch, and (c) rate (hour⁻¹) at which the average inflorescence was visited by hoverflies. Circles represent least-squared means ± SE for the four treatments (rich and poor, safe and risky patches; 10 replicas).

effects of resource availability ($F_{1,9} = 54.19$, $p < 0.0001$) and predation risk ($F_{1,9} = 74.93$, $p < 0.0001$), but not of their interaction ($F_{1,9} = 3.28$, $p = 0.10$), on the rate at which inflorescences were visited by honeybees. Note that inflorescences in risky-poor patches received less than half the number of honeybee visits per unit time than inflorescences in safe-poor patches, but inflorescences in risky-rich patches received as many honeybee visits as in safe-poor patches (Fig. 1c).

The pattern was different for hoverflies, as the number of inflorescences visited per hoverfly was lowest in the patches that received the greatest number of hoverfly visitors (Fig. 2a–b). This combination resulted in inflorescences receiving similar rates of hoverfly visits in all patch types (Fig. 2c). Neither resource availability ($F_{1,9} = 0.02$,

0 $p = 0.90$), predation risk ($F_{1,9} = 0.29$, $p = 0.60$) or their interaction ($F_{1,9} = 2.16$, $p = 0.18$) had statistically significant effects on the rate at which inflorescences were visited by hoverflies.

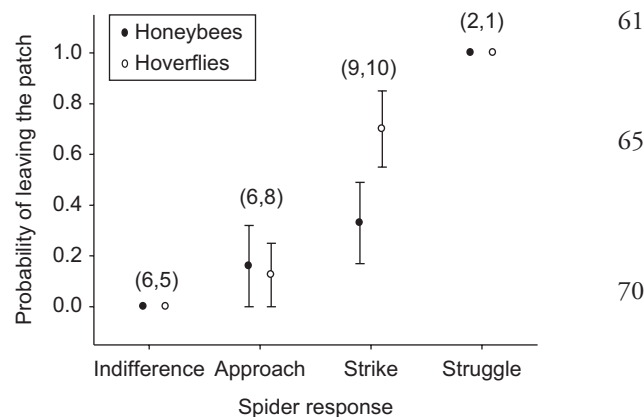
5 We now focus on those inflorescences where spiders were hunting. The probability that visitors to risky patches landed on spider-harboured inflorescences was not significantly affected by patch type (rich or poor), pollinator species (honeybee or hoverfly) or their interaction (all $p \geq 0.2$). However, due to the small number of visits to inflorescences with spiders (61 out of 8081 pollinator visits) the test has relatively little power and the null hypotheses must be retained with caution. Despite the low proportion of visits to spider-harboured inflorescences, the probability of landing on a spider-harboured inflorescence increased with the proportion of inflorescences within a patch which harboured spiders ($p < 0.0001$). The slope of this relationship, 0.33 (SE 0.06), was significantly smaller than one ($W = -11.13$, $p < 0.001$), indicating that both honeybees and hoverflies avoided spider-harboured inflorescences. Avoidance of spider-harboured inflorescences becomes also apparent when we note that the proportion of inflorescences harbouring spiders in risky patches, 0.02, was greater than the proportion of visits to spider-harboured inflorescences in risky patches, 0.0075. If honeybees and hoverflies were selecting inflorescences at random, the probability that they selected 61 or fewer spider-harboured inflorescences out of 8081 landings would be 5.6×10^{-20} (binomial test).

30 Effect of spider encounters on patch departure

30 The tendency of honeybees and hoverflies to leave the patch following a non-lethal encounter with a spider increased as the response of the spider escalated from indifference through approach and strike to struggle (Fig. 3). The effect of spider response on the probability of leaving the patch was highly significant (deviance = 21.10, DF = 3, $p = 0.0001$). All honeybees and hoverflies remained in the patch after encountering a spider that did not react to their landing, and left the patch after a struggle with a crab spider. On the other hand, neither visitor species (honeybee vs hoverfly) nor patch type (rich vs. poor patches) had statistically significant effects on the probability of leaving the patch upon an encounter with a spider (species: deviance = 0.72, DF = 1, $p = 0.40$; resource availability: deviance = 0.85, DF = 1, $p = 0.36$).

45 Susceptibility to predation

45 Over 13 days of observations, we recorded 33 honeybees and 28 hoverflies landing on inflorescences harbouring crab spiders. Of these, 20 honeybees (60.61%) and 16 hoverflies (57.14%) were attacked by the spider. Spiders were therefore equally likely to attack honeybees and hoverflies (Fisher's exact test, two-tailed: $p = 0.80$). Of the 20 honeybees attacked, 9 (45%) were killed, while only 4 (25%) hoverflies were captured by spiders. Although the difference in susceptibility was not statistically significant (Fisher's exact test, two-tailed: $p = 0.30$), the probability of detecting a significant difference with our sample size would be very low. Even if the observed capture frequencies (45% vs 24%) represented the real susceptibility to predation of honeybees



75 Figure 3. Proportion of honeybees and hoverflies leaving the patch after a non-lethal encounter with a crab spider, plotted against the response of the spider. Sample sizes are indicated as (number of honeybees, number of hoverflies). Error bars represent SE, and are omitted when all individuals within a group showed the same response.

80 and hoverflies, over 80 honeybees and 80 hoverflies would have to be attacked before the probability of detecting a significant difference in success rate reached 50% (as calculated from 2000 Monte Carlo simulations for each sample size). A more powerful test of susceptibility to predation is therefore obtained comparing the number of honeybees and hoverflies that spiders were eating when we arrived to the patches, normalised by the visit rate of the corresponding species. When we compared those prey that spiders were consuming at the start of the observations, the proportion of visiting pollinators captured by spiders was higher for honeybees (0.15 ± 0.12) than for hoverflies (0.04 ± 0.03), the difference being significant according to the Wilcoxon matched-pair test ($Z = 3.88$, $p < 0.001$, $n = 20$). However, it is important to note that *A. mellifera* honeybees have a higher dry mass (29.5 ± 1.1 mg) than *E. tenax* hoverflies (17.2 ± 2.6 mg), which will possibly result in a longer spiders' handling time for bees compared to hoverflies (Brechtbühl et al. 2010). A proper comparison of honeybee and hoverfly susceptibility to predation therefore requires dividing the number of spiders consuming each prey type by the handling time of that prey type or, equivalently, dividing the number of spiders consuming honeybees by the ratio 'handling time for honeybees' / 'handling time for hoverflies'. Using a ratio of 1.7 for the correction (which assumes a linear relationship between dry body mass and handling time, $29.5/17.2 = 1.7$) we still find a highly significant difference between honeybee and hoverfly susceptibility ($Z = 3.21$, $p = 0.001$, $n = 20$). Indeed, the ratio of handling times would have to be greater than 2.5 for the susceptibilities not to be significantly different at the 5% level (Fig. 4).

115 Discussion

115 To the best of our knowledge, this is the first study of how pollinators trade off intake rate and predation risk. It allows us to answer the two questions we raised at the beginning of the study. 1) Honeybees and hoverflies responded to variations in predation risk and foraging success, albeit in completely

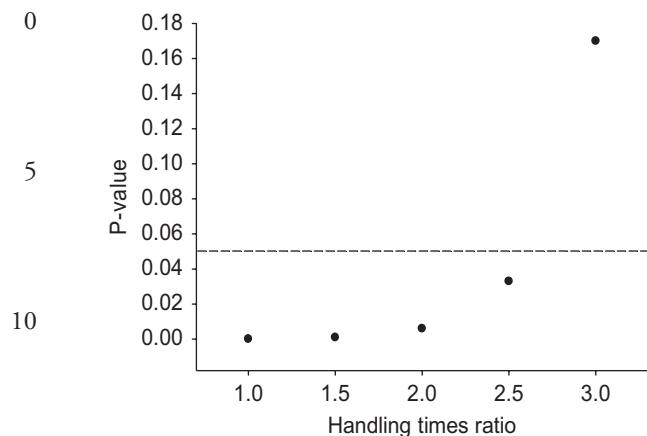


Figure 4. p-values for the comparison between honeybee and hoverfly susceptibility to predation (Wilcoxon matched pair test) versus the value by which the number of spiders consuming honeybees was divided to correct for the difference in handling times. Values greater than 1 imply that handling times are greater for honeybees than for hoverflies. The dashed line indicates the 0.05 significance level.

different ways. The most susceptible pollinators, honeybees, avoided risky patches, particularly if their profitability was low (Fig. 1a), while less susceptible hoverflies visited most often low-quality risky patches (Fig. 2a). 2) In the absence of nectar addition, honeybee visit rates were lower for inflorescences in risky than in safe patches. Nevertheless, inflorescences in risky-rich patches received as many honeybee visits per unit time as inflorescences in safe-poor patches (Fig. 1c). Since our treatments did not affect the rate at which inflorescences were visited by hoverflies (Fig. 2c), we can conclude that, while ambush predators make inflorescences less attractive to the pollinator ensemble, inflorescences can recover their attractiveness increasing nectar production rate.

Ambush predators can have positive and negative effects on the reproductive success of the plants they use as hunting platforms (Suttle 2003, Romero and Vasconcellos-Neto 2004, Gonçalves-Souza et al. 2008). When pollination limits the reproductive success of the plant, plants with ambush predators are likely to experience a decrease in seed set (Higginson et al. 2010). Because ambush predators like crab spiders preferentially adopt certain flowers and inflorescences as hunting platforms (Morse 2007), it has been suggested that they can affect the population dynamics of their host plants (Suttle 2003). The effect of crab spiders on their community will be all the most pronounced when, as we found, pollinators avoid not only spider-harboring inflorescences, but their entire neighbourhood. At the evolutionary time scale, however, our results suggest a mechanism through which flower species regularly associated with ambush predators could attract pollinators despite the increased predation risk: increasing reward production. Nectar availability in rich patches was roughly double than in natural patches. It is worth noting that, due to the way in which the experimental manipulation was conducted, bees probably perceived rich patches less than 'twice as good' as poor patches. First of all, at the time when nectar was added it was relatively diluted (15% w/w) and therefore unattractive to bees. Although nectar would become more attractive as sugar concentration increased through water evaporation, the amount of sugar at

flowers also decreased through nectar consumption. Furthermore, bees are risk-averse foragers: they prefer to visit patches where all flowers have similar amounts of nectar rather than patches with the same average amount of nectar per flower but higher inter-flower variance (Waddington et al. 1981, Real 1981, Real et al. 1982). Because the proportion of *C. segetum* inflorescences to which we added nectar was on average 0.22, rich patches, as perceived by pollinators, were not as good as a hypothetical patch where each inflorescence would have had twice as much nectar as in a normal patch. As a result, our nectar manipulation did not increase pollinator activity unrealistically in rich patches, but was sufficient to compensate for the presence of predators: inflorescences in safe-poor and risky-rich patches received similar amounts of honeybee (Fig. 1c) or hoverfly (Fig. 2c) visit rates.

It is worth mentioning that the relationship between nectar availability and pollinator attractiveness in the presence of ambush predators can be quite complex. In our study, spiders did not respond to the nectar manipulation: we had to add as many spiders to poor-risky and rich-risky patches, indicating that spiders were not more likely to leave poor than rich patches, and we had to remove as many spiders from poor-safe and rich-safe patches, indicating that spiders were not more likely to move to rich than poor patches. Nevertheless, other studies have shown that crab spiders show a preference for more rewarding plant individuals (Heiling and Herberstein 2004) and species (Schmalhofer 2001). If flowers regularly used as hunting platforms by spiders increased nectar productivity to attract more pollinators, and the arrival of additional pollinators attracted more spiders (Jones 2010, Abbott 2010), the system might enter a coevolutionary arms race with uncertain endpoint.

Different patterns at different spatial scales

At the flower level, honeybees and hoverflies showed similar responses: both species avoided spider-harboring inflorescences. We found no significant differences between species in the probability of landing on spider-harboring inflorescences while foraging in risky patches. Furthermore, the rates observed for honeybees ($33/4405 = 0.0075$) and hoverflies ($28/3676 = 0.0076$) were so similar that any statistically significant difference that could be detected increasing sample size would be biologically irrelevant. Honeybees and hoverflies also reacted similarly to non-lethal encounters with crab spiders. They tended to remain in the patch if the crab spider responded weakly to their presence, and to leave the patch after an attack (Fig. 3). The two species therefore exhibited strong anti-predator behaviour at the inflorescence level, and at this spatial scale the anti-predator response was not affected by resource availability in the patch. Despite these similarities, when we analysed the foraging strategies of honeybees and hoverflies at the patch level we found striking differences in the number of individuals visiting patches (Fig. 1a, 2a). Between-species differences in patch-level response can have their origin in mechanistic and functional differences.

Mechanisms: patch choice

Honeybees are central-place foragers. Numerous observations on marked bees indicate that workers concentrate their

0 foraging effort on a restricted area that they revisit trip after
trip, even though each trip may include visits to inflores-
cences not belonging to the bee's core territory (Ribbands
1949, Free 1966). Moreover, individual honeybee and
bumblebee workers have important learning and memory
5 capabilities that affect their foraging behaviour (Menzel
2001, Keasar et al. 2002, Giurfa 2007, Ings et al. 2009b)
and they can learn to avoid specific flowers, flower species
and even areas where they have been attacked (Abramson
1986, Dukas 2001, Ings and Chittka 2008, 2009). Recent
10 laboratory experiments conducted under controlled condi-
tions have shown that learning can play a key role in preda-
tor avoidance (Ings and Chittka 2008, 2009). Therefore,
through the process of learning, rich and safe patches will be
included in the foraging territories of more honeybees than
15 poor and risky patches – explaining why more bees visit rich
than poor patches, safe than risky patches (Fig. 1b).

Much less is known about the foraging ecology of hover-
flies. Males acquire mating territories and are therefore
residential (Wellington and Fitzpatrick 1981). If males
20 avoided spider-harboured inflorescences and left patches
upon attack by crab spiders, male territories would concen-
trate in safe patches. However, we rarely observed hoverflies
behaving territorially. Most of our observations concerned
foraging individuals that arrived to the patch and left it after
25 visiting a few inflorescences. Because the flight pattern of
foraging *E. tenax* is characterised by a strong directionality
(Gilbert 1983), non-territorial hoverflies are likely to wander
through their environment without forming special attach-
ments to any particular location. If this is the case, hoverflies
30 will have little or no information concerning the quality of
the patches they approach. The number of hoverflies arriving
to a patch must therefore be a function of the attractiveness
of the patch, as assessed from whatever information hover-
flies can obtain at a distance. Because resource availability
35 per flower and abundance of crab spiders cannot be detected
at a distance, if hoverflies have no information concerning
the patches they approach they must rely on other cues to
select patches. Hoverflies showed a preference for patches
with more *C. segetum* inflorescences – a trait that can be per-
40 ceived from afar. As we discuss below, hoverflies may also
have used the presence of other pollinators as a cue to assess
the suitability of patches (Morse 1981).

45 **Functional considerations: predator avoidance**

From a functional point of view, honeybees may be avoid-
ing risky patches because of their higher susceptibility to
predation. Although there were no obvious differences in
the ability of honeybees and hoverflies to detect and avoid
50 spider-harboured inflorescences, honeybees were more vul-
nerable to predation than hoverflies once they landed on a
spider-harboured inflorescence. Schmalhofer (2001) sug-
gested that the low representation of syrphids on the diet
of *Misumenoides formosipes*, relative to honeybees, might be
55 due to the clumsiness of honeybees (Fritz and Morse 1985)
and the extreme agility and speed of syrphids (Barth 1991).
Whatever the reason for the difference in susceptibility
to predation between honeybees and hoverflies, susceptibility
to predation is known to affect the predator-avoidance response
60 of pollinators, in agreement with theoretical models (Jones

2010). For example, Dukas and Morse (2003) reported that 61
while small and easily handled pollinators like *B. ternarius*
and *A. mellifera* avoided crab spiders (*Misumena vatia*),
larger pollinators like *B. terricola* and *B. vagans* did not show
any anti-predatory response (see also Dukas and Morse 65
2005). Gonçalves-Souza et al. (2008) also found that not
all pollinator species responded equally to the presence of
an artificial crab spider sitting on *Rubus rosifolius* flowers:
while hymenopterans tended to avoid flowers harbouring
70 the artificial crab spider, lepidopterans did not show such a
response. These authors suggest that the absence of predator-
avoidance mechanisms in butterflies could be due to their
unpalatability. Indeed, we have observed in the field crab
spiders eschewing butterflies after grabbing them with their
75 forelegs. According to these and our study, pollinators suf-
fering a low predation risk will show a weak anti-predatory
response, while pollinators that are more vulnerable to pre-
dation will show stronger anti-predator behaviour.

80 **Functional considerations: resource competition**

Exploitation competition is known to play an important role
in pollinator communities. To cite some examples, where
Bombus appositus and *B. flavifrons* competed for the nectar
produced by *Delphinium barbeyi* and *Aconitum colombianum*, 85
B. appositus concentrated its foraging effort on flowers of
D. barbeyi and *B. flavifrons* on flowers of *A. colombianum*,
but when one species was temporarily removed, the remain-
ing bumblebee species increased visitation to the other flower
species (Inouye 1978). In an experiment with marked bum- 90
blebees, Thomson et al. (1987) found that when some bees
were removed, remaining bees shifted their foraging activ-
ity towards the removal areas, thus increasing their forag-
ing efficiency. Likewise, competition with honeybees forced
B. occidentalis colonies to change their foraging strategy, allo- 95
cating a greater fraction of their foragers from pollen to nectar
collection (Thomson 2004). It is therefore possible that the
high number of hoverflies visiting poor-risky patches reflects
the fact that hoverflies are selecting to forage at those patches
where honeybee activity is lower. Nevertheless, it is unclear 100
whether hoverflies and honeybees compete through the
exploitation of resources or some form of territoriality: hover-
flies, *Melanostoma mellinum*, foraged preferentially on flowers
and patches where bumblebees, *B. terricola* and *B. vagans*, had
been excluded, and avoided returning to flowers from which 105
they had been displaced by bumblebees (Morse 1981). It is
therefore possible that, in our experiment, hoverflies were not
choosing poor-risky patches to maximise their fitness. They
may be simply excluded from rich-safe patches by honeybees.
It is important to elucidate the mechanisms of resource com- 110
petition between pollinator groups if we are to understand
how pollination networks are structured.

Finally, other than competition for resources, honeybees
and hoverflies may be reacting differently to our experimental
treatments because they have different requirements. Honey- 115
bees must collect enough resources to sustain the growth of
the colony during spring and summer, bringing enough pol-
len and nectar to feed non-foraging workers and developing
larvae, and to keep the colony alive over the fall and winter
(Seeley 1985). Hoverflies, on the other hand, require only
120 resources for their own needs (including egg production, but

0 not larval growth). This life-history difference means that,
 to make ends meet, hoverflies can exploit resources where
 the average rate of gain is relatively low, while bees require
 much richer resources. Indeed, bumblebees rarely visit
 5 flowers where their average rate of gain is less than 0.02 W
 (Heinrich 1975), while hoverflies accept resources with net
 energy intake rate of about 0.01 W (Gilbert 1983). If the
 productivity of *C. segetum* patches is just above the thresh-
 old for productive honeybee exploitation, a small increase in
 10 predation risk may suffice to tip the balance between exploi-
 tation and neglect. By itself, however, it does not explain
 why hoverflies visited poor-risky patches at a higher rate than
 poor-safe and rich-safe patches. A combination of several
 factors (use of information, avoidance of competition and
 15 low energetic requirements) may be required to explain the
 complex pattern of patch use by hoverflies.

Conclusion

20 Our results show that hoverflies and honeybees responded
 differently to spatial variability in levels of resource availabil-
 ity and predation risk at the patch level, although both spe-
 cies strongly avoided spider-harboured inflorescences and
 left patches following an attack. Although we have suggested
 25 some mechanisms that can affect these behavioural differ-
 ences, laboratory experiments, controlling for the previous
 exposure to food reward and predation risk of individual
 pollinators, are needed to elucidate the specific mechanisms
 by which pollinators respond to variability in predation risk
 30 and food reward simultaneously. Whatever the mechanisms
 involved, ambush predators are likely to affect reproductive
 success of the flowers they use as hunting platforms (as sug-
 gested by Ings and Chittka 2009), but will also interfere with
 pollen flow in their immediate neighbourhood. It follows
 35 that the reproductive success of a plant will not only depend
 on its phenotypic traits, but also on those of its neighbours.
 Therefore, the spatial scale at which predators and resource
 availability affect pollinator behaviour must be included in
 any ecological or evolutionary analysis of how predators affect
 40 plant-pollinator interactions. In conclusion, our study high-
 lights the importance of studying the foraging strategies of
 pollinators at different spatial scales in order to fully under-
 stand how plant-pollinator interactions are established.

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