Diet choice of a predator in the wild: overabundance of prey and missed opportunities along the prey capture sequence

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Abstract. Optimal diet theory (ODT) postulates that predators adjust their foraging decisions by calculating a prey value from the potential biomass gain, handling time, prey vulnerability and encounter rate. Tests of ODT have however so far mainly been restricted to laboratory settings. By video surveillance, we gathered a large data set of more than 2000 field observations of crab spider (*Misumena vatia*) encounters with potential prey. We then tested whether the complex ODT or two simpler models (prey identity and prey traits) best explain foraging decisions. Insect prey were killed with an average chance of 3.5% when alighting on an inflorescence harboring a spider. Spiders refused to attack suitable prey in 46–79% of encounters when prey was in attack range, indicating an over-abundance of prey relative to the needs of the spiders. Reduction of opportunities to capture prey along the prey capture sequence differed among pollinator groups, with syrphids and solitary bees showing strong avoidance of spiders early in the sequence and bumblebees resisting the final strike. Simple prey traits explained foraging decisions better than ODT, which was not supported. In the absence of food limitation, optimality decisions may be less stringent. The over-abundance of prey indicates that, in contrast to current theory, prey encounter rates are not the most important factor driving predator foraging decisions. Our results are highly coherent with those obtained in earlier field studies on patch leaving strategies and predator-prey encounters. Prey over-abundance and non-optimal predator behavior are apparently not uncommon in nature, and we highlight some of the implications for predator-prey theory.

Key words: attack rate; capture success; crab spider; encounter rate; handling time; *Misumena vatia*; optimal diet theory; predator avoidance; preference; prey size; prey value; vulnerability.

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INTRODUCTION

Diet preferences are ecologically important because non-random predation has important effects on the relative impacts of predators on different prey (Paine 1966, Sih et al. 1985). Encounter rate, prey size and vulnerability are all known to determine prey preference and thus the probability that a predator attacks and kills a prey. When a prey is abundant, predators more often encounter this type of prey, become more experienced in handling it (Murdoch 1969, Lawton et al. 1974, Endo and Endo 1994), and often prefer such prey species over those that are less abundant, i.e., they may develop a search image. This phenomenon is for example often implied in prey switching and can generate sigmoid functional responses (Murdoch 1973, Murdoch and

Oaten 1975). Prey size can also influence prey choice by predators, if prey show substantial variation in this respect. Larger prey are generally more profitable than smaller prey, because the gain in biomass is higher. However, as prey size increases, profitability for the predator may again decrease, because it is more difficult and thus costly to handle (= subdue, kill and eat) large prey than small prey (Paine 1976, Elner and Hughes 1978). Large prey also may be dangerous for the predator to attack, if the prey has the ability to fight back and hurt the predator (Eilam 2005). Thus, one would expect a dome-shaped function of preference with regard to prey size (Paine 1976, Elner and Hughes 1978, Wanzenbock 1995, Rutten et al. 2006). Finally, vulnerability of prey, i.e., the probability that a prey is captured given an attack, also modifies the decision of a predator to attack (Menge 1972, Ware 1972, 1973, Pastorok 1981). Prey vulnerability is a trait that can only be learned by previous experience in handling different prey types. However, vulnerability may also be partly a function of prey size in that very large prey (or very small prey; Gill 2003) are generally more difficult to subdue.

Since several decades, optimal diet theory (ODT) has been used to explain prey preference. ODT predicts that predators should hunt for prey items that generate high energetic values per unit of handling time (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Pyke et al. 1977). In fact, a predator's net energy intake for each prey species can be calculated as the product of the assimilatable energy of the prey and its vulnerability (Schoener 1971, Sih and Christensen 2001). Dividing the net energy intake by the handling time of this prey yields the prey's value (Sih and Christensen 2001):

$$\text{prey value} = \frac{(\text{assimilatable energy} \times \text{vulnerability})}{\text{handling time}}.$$
(1)

The higher a prey's value, the more profitable this prey is for a predator. Predators that optimize their foraging decisions according to ODT are attacking the prey with the highest prey value. Throughout the text we use the word "optimal" and its derivatives in the sense of being in accordance with ODT. ODT requires predators to trade-off potential gains of attacking a prey by the associated costs (including the potential of the attack to fail). This is a complex assessment including the weighing of multiple variables and it is assumed that predators are able to learn from experience to optimize the assessment. We therefore consider the prey value to be a complex trait. However, particularly invertebrate consumers may be limited in their cognitive capabilities to make quick and complex assessments of food quality (Bernays 2001). Alternatively, predators could decide whether or not to attack according to a simple hierarchy of preferences driven by prey identity (e.g., hierarchy threshold model; Courtney et al. 1989) or use simple prey traits (i.e., characteristics of individual prey, e.g., prey size, vulnerability). However, which of these three models, namely ODT, prey identity, or prey traits, explains best the behavior of a predator observed in nature, has, to our knowledge, never been tested.

Since all factors that potentially determine prey preference vary in natural prey populations, one needs to study the influence of all of them simultaneously. Thus, data on predator foraging decisions collected in natural environments are critical to understand preference, optimal behavior and natural selection pressures (Schenk and Bacher 2002, Schenk et al. 2005, Tschanz et al. 2007). Previous encounters with prey may influence decisions of predators. Forced predator-prey encounters like in most experiments under controlled conditions may thus generate misleading results. However, natural predator-prey encounter rates are difficult to observe in an unbiased way and in large numbers. Studies on the simultaneous influence of prey abundance, prey size and prey vulnerability are rare, and the few studies that exist either (1) come from artificial conditions or (2) lack good data on actual predator-prey encounter rates to determine the predator choice at a scale relevant for such studies, particularly for mobile prey (Sih and Christensen 2001, Barrette et al. 2009). The first aim of our study was thus to collect an unbiased data set of natural predator-prey encounters that enables us to measure field encounter rates, prey identity, size and vulnerability, and to test which of the three foraging models best explains predator foraging decisions.

The prey capture sequence of a predator is usually split into several steps: encounter with

prey, attack and capture success (e.g., Sih and Christensen 2001). At each step the predator "loses" some of its potential prey items for different reasons: (1) the prey avoids encounter or detection by the predator; (2) the prey is not within the predator's attack range; (3) the predator decides not to attack; or (4) the attack fails. The losses at each step can vary among different prey types. Quantifying the losses at each step can pinpoint steps which are particularly sensitive to the overall hunting success of a predator. These critical steps are likely those on which natural selection acts most strongly, both for predator and prey. Pointing out those critical steps was the second aim of the study.

We collected data on the prey capture sequence by a sit-and-wait predator, the crab spider *Misumena vatia*, for some 2200 predator-prey interactions involving more than 100 different spiders in a natural setting. We placed outdoors crab spiders on three flower species that differed in their relative frequency of flower visitors (mostly pollinators; Brechbühl et al. 2010a). With the aid of continuous video surveillance, crab spiders were observed and their behavioral reaction towards different flower visitors at the different steps of the prey capture sequence was noted. This allowed a uniquely detailed analysis of foraging decisions of spiders in their natural environment, including the possibility to contrast predictions of ODT and simpler prey-choice models in an information-theoretic framework. If spiders optimized their foraging decisions according to ODT, we would expect that the prey value is the most important variable explaining their attack behavior. By contrast, if spiders base their foraging decisions on simpler rules, prey traits or simply prey identity would be the most relevant variables explaining attack behavior. The data we collected also allowed quantifying the successful transition from one step to the next in the prey capture sequence.

METHODS

We used data from video recordings of encounters of crab spiders with potential prey that were available from an experiment on the effects of spider crypsis. The full experimental set-up is described in Brechbühl et al. (2010a); in the following we briefly outline the parts relevant for the present study.

Experimental site and set-up

The experiment was carried out in the garden of the Zoological Institute (University of Bern, Switzerland) from May to August 2007. Adult female crab spiders were caught in wildflower fields around Bern by sweep-netting and kept in transparent plastic tubes (5 cm diameter) filled with moist soil (1–2 cm). Spiders were not weighed, but were approximately of equal size. The spiders caught were brought to a tool shed next to the experimental area, which was used as a rearing room. Once a week the spiders were fed with crickets (*Acheta domesticus*) ad libitum. Feeding ceased five days before being used in the experiment, to ensure that spiders all were in the same state of hunger.

Crab spiders were singly placed on equally-sized inflorescences of each of three plant species (*Anthemis tinctoria*, *Chrysanthemum frutescens*, *Knautia arvensis*) and their reactions to encounters with insects visiting the inflorescences were continuously monitored by wireless digital surveillance cameras (technical details of the surveillance system are described in Brechbühl et al. 2010b). Spiders were randomly assigned to the inflorescences. Simultaneously, we also monitored inflorescences without spiders to record natural flower visitation rates (10 × *A. tinctoria*, 10 × *C. frutescens*, 8 × *K. arvensis*; each for three consecutive days). Closed flower buds were covered with gauze bags before the experiments to prevent flower visitation. This was required because studies on honey bee (*Apis mellifera*) foraging behavior indicate that the probability of visiting a flower was influenced by previous visits from other pollinators (Williams 1998). After placing the crab spiders, the experimental inflorescences were inspected every two hours to verify that the spider was still present. If a crab spider had left the inflorescence, it was put back, or replaced by another *M. vatia* if it could not be re-located. Spider identity was recorded for the analysis.

Cameras recorded pictures of each experimental inflorescence continuously for three consecutive days. The plant species used in the experiment are not pollinated by night-active insects like moths (www.biolflor.de). For data
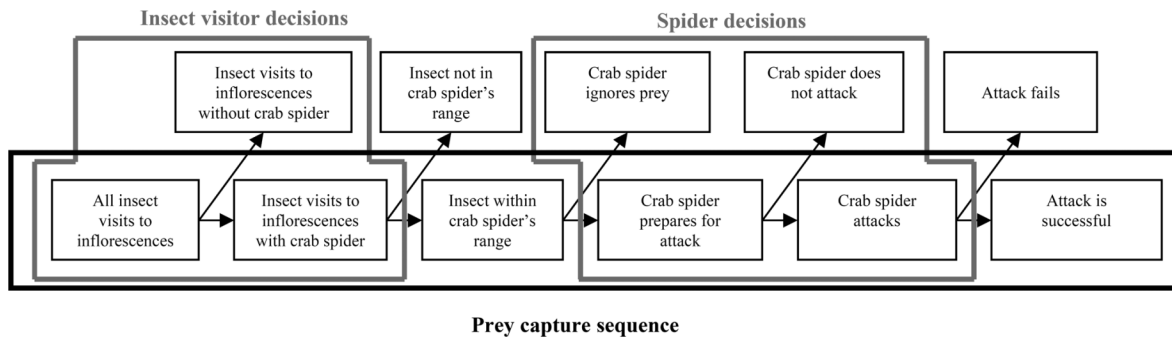
Prey capture sequence

Fig. 1. Scheme of the different steps of the prey capture sequence. At each step, arrows indicate either transitions to the next step of the sequence (horizontal arrows) or leaving the sequence (arrows pointing up); thus, at each step, crab spiders can "lose" a fraction of their potential insect prey.

analysis, we therefore used only data recorded from 9 am to 7 pm, when daylight pollinators, and thus crab spiders, were active.

For each insect landing on an inflorescence with a spider, we distinguished from the video recordings between positive taxis of spiders (movement towards the potential prey) and indifferent behavior. Positive taxis involved three steps: in the first step, crab spiders spread their two anterior pairs of raptorial forelimbs. We called that behavior "preparation of attack", occasionally including a stalking behavior towards the insect (Morse 2007). The second step was attacking the prey ("attack"), spiders trying to catch the prey with their forelimbs in order to bite it. The third and last step, "capture success", is the outcome of the interaction. Indifferent behavior was assigned when the spider did not react to an insect visiting the inflorescence. The time during which spiders were eating prey was not considered for analysis of their reactions. After a spider captured a prey, it usually retreated from the top of the inflorescence to a place on its underside where it consumed the prey and it usually continued staying there even after finishing its meal; we presumed that during this digestive pause the spiders were not motivated to capture new prey. We only considered spiders for analysis after they returned to the upper side of the inflorescence.

Between observation periods, common pollinator species were caught by sweep-netting in the experimental field, frozen at −20°C and dried to determine their dry weight (mg; using a Mettler MT5 balance). We used the average dry-weight of each pollinator species or genus for further analysis. If a crab spider caught an insect prey, we determined the handling time (time feeding on the prey). Furthermore, flower visitors were determined to species or genus level from the video recordings. The prey encounter rate was calculated for each pollinator taxon as the number of pollinator visits per hour. 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.

We defined several steps at which crab spiders could "lose" a certain fraction of their potential prey (Fig. 1): (1) from the video recordings of inflorescences without crab spiders (controls) we obtained the naturally occurring rates of potential insect prey per time; (2) loss because insects avoided visiting inflorescences harboring a crab spider; (3) loss because the potential prey was not in the spider's hunting range (defined as at most two body lengths away from the spider; Morse 2007); (4) loss owing to the spider's decision not to prepare for an attack; (5) loss owing to the spider's decision not to attack the prey; and (6) loss because the attack failed. In order to estimate at which step crab spiders lose which proportion of their potential prey, we calculated percentages of loss for each step as:

$$\left(1 - \frac{\text{number of prey at step } n+1}{\text{number of prey at step } n}\right) \times 100.$$

Analyses

We tested for differences in crab spiders'

Table 1. Visitors to the experimental inflorescences: number of insects caught by the spiders; average individual dry-mass (±SE) of the different observed flower visitor taxa; N, number of weighed individuals per taxon; encounter rates per hour (±SE) on inflorescences harboring a crab spider; vulnerability of the different observed flower visitor taxa (no. caught prey/no. attacks); and, prey values (dry-mass × vulnerability/handling time).

Pollinator group	Insects caught	Dry mass (mg)	N	Encounter rate	Vulnerability	Prey value
Bumblebees	**2**	**98.2 ± 3.4**	**11**	**3.59 ± 1.1**	**0.05**	**1.8**
B. campestris	—	105.8 ± 0.7	2	0.27 ± 0.2	NA	NA
B. lapidarius	—	81.5 ± 0.3	2	0.06 ± 0.0	NA	NA
B. pascuorum	1	93.6 ± 7.4	3	1.07 ± 0.5	0.13	1.7
B. terrestris	—	108.8 ± 2.8	3	1.88 ± 0.8	NA	NA
Other Bombus	1	98.9 ± 0.0	1	0.29 ± 0.1	0.13	1.8
Honeybees	**14**	**29.5 ± 1.1**	**6**	**0.61 ± 0.2**	**0.32**	**5.1**
Solitary bees	**51**	**7.1 ± 1.1**	**18**	**2.75 ± 0.2**	**0.44**	**4.1**
Colletes sp.	3	15.6 ± 0.2	3	0.31 ± 0.1	0.3	4.4
Halictus sp.	2	6.2 ± 0.7	3	0.44 ± 0.1	0.11	2.4
Hylaeus sp.	31	5.3 ± 0.3	6	1.44 ± 0.4	0.48	3.9
Lasioglossum sp.	15	5.2 ± 0.5	6	0.58 ± 0.1	0.63	5.6
Other solitary bees	—	5.9 ± 0.0	1	0.00 ± 0.0	NA	NA
Hoverflies	**1**	**10.3 ± 2.5**	**13**	**0.23 ± 0.1**	**0.5**	**5**
Eristalis tenax	—	17.2 ± 2.6	5	0.10 ± 0.0	NA	NA
Sphaerophoria sp.	—	2.6 ± 0.4	3	0.04 ± 0.0	NA	NA
Syritta sp.	—	1.3 ± 0.1	3	0.02 ± 0.0	NA	NA
Other hoverflies	1	11.8 ± 0.3	2	0.06 ± 0.0	0.5	5.7
Others	**10**	**14.7 ± 2.2**	**16**	**1.23 ± 0.2**	**0.37**	**NA**
Ants	1	1.7 ± 0.2	6	0.36 ± 0.1	0.5	NA
Coleoptera	2	26.3 ± 11.8	3	0.37 ± 0.1	0.5	NA
Diptera†	5	7.7 ± 1.4	6	0.05 ± 0.0	0.71	11.7
Wasps	—	22.3 ± 0.0	1	0.11 ± 0.0	NA	NA
Undetermined	2	NA	NA	NA	NA	NA

Note: NA indicates parameters that could not be computed because of lack of data.
† Without hoverflies.

decisions to proceed to the next step in the prey capture sequence with generalized linear mixed effects models. We compared three different classes of models, corresponding to the three foraging models described in the introduction, for their ability to explain variation in spiders' response towards potential prey and their capture success rates. In the prey identity models, flower visitor identity (bumblebee, honeybee, solitary bee, hoverfly, or other insect) was used as explanatory variable. In the prey traits models, prey mass, squared prey mass and vulnerability of the different flower visitor species were used as explanatory variables. We included the squared prey mass to allow for a dome-shaped relationship between prey mass and the spider's behavior and thus the possibility that insects of an intermediate mass are the preferred prey. In the ODT models, the prey value of the different insects was the explanatory variable. Prey value was calculated as average prey mass (as a proxy for assimilatable energy, Morse 1979; see also Sih and Christensen 2001) multiplied by prey vulnerability (estimated as capture success rate from

video recordings) divided by the average handling time (also estimated from video recordings; see Eq. 1) for each prey taxon (Table 1). In all three categories of models, we included as covariates the prey encounter rate for each prey type (see Table 1) and whether flower visitors were in the crab spider's hunting range.

Each predator-prey encounter was considered as an experimental unit and the spider's decision (yes/no) to proceed to the next step in the prey capture sequence was the response variable. We investigated the influence of the explanatory variables on the decision of spiders at different steps of the prey capture sequence (Fig. 1). Correlations with the spider's decision to "prepare for attack" were tested on all predator-prey encounters. For analyses of correlations with decisions to "attack", only those cases in which spiders previously prepared for an attack were considered. Analogously, for analyses of "success" only those cases in which spiders actually attacked were considered. It should be noted that to avoid circular reasoning, vulnerability (in the traits model) and prey value (in the ODT model)

were excluded as explanatory variables when testing for correlations with "success", because the average prey capture success rate was used in their calculations. Thus, no ODT model was fit for explaining capture success. However, optimality traits are not expected to influence prey capture success, since the outcome of an attack is not a consequence of the spiders' decisions, but simply its ability to capture a certain prey, which should depend on prey identity or prey traits, the experience of the spider in handling this type of prey (e.g., how often it is encountered), and the environmental setting (e.g., the spider's distance to the prey).

Behavioral data from the same spider individual cannot be regarded as independent data points. To account for this non-independence, the identity of the crab spider individuals was included as random factor in all models, assuming decisions of the same spider individual to be correlated, but assuming no correlation among outcomes of different spiders (Zuur et al. 2009). Models were fitted in the statistical software R (version 2.13.0; R Development Core Team 2011) using the function glmer from the package lme4 (version 0.999375; Bates and Maechler 2008), assuming a binomial distribution of the response variable and a logit link function.

We identified the factors that most likely determine spider's foraging decisions in an information theoretic framework for model selection (Burnham and Anderson 2002). Within each model class (prey identity, prey traits, ODT) we first fitted models with all possible combinations of explanatory variables; e.g., for the prey identity models we fitted models containing either only the prey identity, the prey range or the encounter rate, then models with all 2-way combinations of the three factors and finally a model containing all three factors; we did the same for the other two model classes (Tables 2–4). We also fitted a model without any explanatory variable, i.e., just with an intercept. We then ranked all models according to Akaikes information criterion (AIC). To determine the explanatory variables that best explain variation in the spiders' decisions at each step of the prey capture sequence, we selected all models that conformed to two rules (Richards 2008): First, we selected all models with a ΔAIC value ≤ 6, i.e., all models whose AIC value was at most 6 higher than the lowest AIC obtained. This threshold of ΔAIC ≤ 6 is much higher than the widely-applied rule-of-thumb of selecting all models with a ΔAIC value ≤ 2 proposed by Burnham and Anderson (2002), but it recently has been demonstrated that the most parsimonious model, defined as the one with the lowest expected Kullback-Leibler distance, which is a measure of the mean discrepancy between the model and the unknowable truth, may be missed otherwise (Richards 2005). As a second rule, we only selected a model if its AIC value was less than the AIC value of all the simpler models within which it is nested, in order to avoid selecting overly complex models (Richards 2008). The reasoning for this is that if an additional parameter provides little or no increase in model fit, then the more complex model with the additional parameter will have a ΔAIC-value less or equal to 2 to the simpler model; thus the more complex model fits the data equally well as the simpler model. However, in such cases the more complex model with the additional parameter should not be considered for ecological inference, since nothing is explained by the additional complexity (Burnham and Anderson 2002, Richards 2008).

We then estimated the value of all model parameters by model averaging among the set of candidate models chosen by the above model selection procedure (function modavg from the package AICcmodavg, version 1.18, in R; Mazerolle 2011). This method weights parameter estimates of more credible models (i.e., with lower AIC) higher than those with lower credibility. A parameter can be considered as having a significant effect on spiders' decisions if its confidence interval does not include zero. Parameters that were not part of any model chosen by model selection can be considered as having no relevant explanatory power.

RESULTS

We used 158 *M. vatia* spiders during our experiment. Of these, 105 encountered altogether 2198 insects visiting the experimental inflorescences (41 spiders on *A. tinctoria*, 27 spiders on *C. frutescens*, and 37 spiders on *K. arvensis*). With 821 visits, bumblebees were the most common flower visitors encountered by spiders, followed by solitary bees with 777 visits. While honeybees also occurred in considerable num-

Table 2. Models explaining the spiders' decision to prepare for an attack after encountering a prey ($N = 1304$), i.e., the first decision by the predator in the prey capture sequence (Fig. 1).

Prey identity models	Prey traits models			ODT models	Confounding variables		
Pollinator identity	Prey weight	(Prey weight)^2	Prey vulnerability	Prey value	Encounter rate	Prey within hunting range	ΔAIC
x						x	0.0*
x					x	x	0.3
	x				x	x	3.1*
	x		x		x	x	5.1
	x					x	5.6 *
	x		x			x	7.4
			x		x	x	9.8
					x	x	9.8
				x	x	x	10.3
				x		x	10.7
						x	11.4
			x			x	12.5
		x			x	x	55.8
	x	x			x	x	57.3
		x	x		x	x	58.0
	x	x	x		x	x	59.5
		x				x	59.9
	x	x				x	61.9
		x	x			x	61.9
	x	x	x			x	63.9
x							415.0
x					x		416.9
	x	x					418.5
	x	x			x		419.5
	x	x	x				419.7
		x			x		419.9
		x					420.0
		x	x				420.9
	x	x	x		x		420.9
		x	x		x		421.4
	x				x		421.9
	x						422.3
				x			423.1
	x		x				423.6
	x		x		x		423.6
				x	x		424.4
							425.4
					x		425.7
					x		425.7
			x		x		427.2
			x				427.3

Notes: Models are ranked by their ΔAIC value. "x" denotes if a variable was included in the model. Asterisks (*) indicate models considered for model averaging of parameters, i.e., those whose ΔAIC ≤ 6 and whose AIC value is less than the AIC value of all the simpler models within which it is nested.

bers (242 visits), hoverflies as the fourth major group only occasionally visited the experimental inflorescences (57 visits). The other insect visitors observed either occurred in small numbers or were not typical plant pollinators (e.g., ants). A detailed list of visits is given in Table 5.

Behavioral responses of M. vatia spiders toward flower visitors

Preparation of attack.—Of the 1304 cases of spider encounters with potential prey we could use in the analysis (i.e., where we had the information on all explanatory variables), *M. vatia* spiders prepared for an attack at 432 encounters, however, the prey was in the spider's range in only 354 of these cases. The model selection procedure identified only three models that should be kept for ecological inference (indicated by an asterisk in Table 2). All of these models found that spiders prepared for attack more often when prey was within the spiders' hunting range (Table 6). The most credible model, which had the lowest AIC, had apart

Table 3. Models explaining the spiders decision to attack a prey after having prepared for the attack ($N = 432$), i.e., the second decision by the predator in the prey capture sequence (Fig. 1).

Prey identity models	Prey traits models			ODT models	Confounding variables		
Pollinator identity	Prey weight	(Prey weight)^2	Prey vulnerability	Prey value	Encounter rate	Prey within hunting range	ΔAIC
			x			x	0.0*
	x		x			x	1.4
			x		x	x	1.7
		x	x			x	1.8
	x		x		x	x	3.1
		x	x		x	x	3.5
	x					x	3.5*
				x	x	x	3.6*
				x		x	4.2*
	x	x				x	4.5
		x				x	4.5*
	x				x	x	4.9
						x	5.0*
x						x	5.7
		x			x	x	5.7
					x	x	6.0
					x	x	6.0
	x	x			x	x	6.1
	x	x	x			x	7.2
x					x	x	7.3
	x	x	x		x	x	9.1
				x	x		169.0
			x				171.1
			x		x		171.9
				x			172.0
x					x		172.6
	x		x				173.0
		x	x				173.1
x							173.5
					x		173.7
					x		173.7
	x		x		x		173.7
							174.0
		x	x		x		174.0
	x	x	x				175.1
		x			x		175.4
	x				x		175.4
	x						175.5
		x					175.6
	x	x	x		x		175.7
	x	x			x		177.2
	x	x					177.7

Notes: Models are ranked by their ΔAIC value. "x" denotes if a factor was included in the model. Asterisks (*) indicate models considered for model averaging of parameters, i.e., those whose ΔAIC ≤ 6 and whose AIC value is less than the AIC value of all the simpler models within which it is nested.

from the prey range only the prey identity as explanatory variable. The other two models suggested that prey weight and encounter rate may also predict decisions of spiders to prepare for an attack. Model averaging revealed that spiders are less likely to prepare for an attack for prey that are often encountered, but that prey weight did not have a significant influence on this decision (Table 6). Crab spiders prepared significantly more often for an attack towards honeybees, solitary bees and hoverflies than towards bumblebees (Table 6). Thus, only the prey identity model received support at this stage of the prey capture sequence.

Attack.—Of 432 insect visits where crab spiders prepared for an attack, spiders attacked in 182 cases. The model selection procedure identified six models that should be kept for ecological inference (indicated by an asterisk in Table 3). Again the prey being within the spiders' hunting range was an important predictor of attack in all of these models (Table 6). The most credible

Table 4. Models explaining the spiders capture success after having attacked a prey ($N = 182$), i.e., the outcome of the prey capture sequence (Fig. 1).

Prey identity models	Prey traits models		Confounding variables		
Pollinator identity	Prey weight	(Prey weight)^2	Encounter rate	Prey within hunting range	ΔAIC
	x			x	0.0*
	x		x	x	1.9
	x	x		x	2.0
x			x	x	2.9*
		x		x	2.9*
x				x	3.4*
	x	x	x	x	3.7
		x	x	x	4.5
	x				6.6
				x	7.2
				x	7.2
x			x		8.0
			x	x	8.2
	x		x		8.2
	x	x			8.5
		x			9.1
x					9.7
	x	x	x		9.9
		x	x		10.5
					13.3
			x		13.8

Notes: Models are ranked by their ΔAIC value. "x" denotes if a factor was included in the model. Asterisks (*) indicate models considered for model averaging of parameters, i.e., those whose ΔAIC $\leq$ 6 and whose AIC value is less than the AIC value of all the simpler models within which it is nested.

Table 5. Visitors to the experimental inflorescences harboring a crab spider and percentages of losses of potential prey items at different steps of the prey capture sequence.

		Loss (%)				
Pollinator group	Visits to flowers with spiders	Compared to flowers without spiders	Because not in range	Through not preparing for attack	Through not attacking	Through not being successful
Bumblebees	821	7.6	76	42.6	63.7	95.1
B. campestris	59	60.7	81.4	18.2	77.8	100
B. lapidarius	15	11.7	60	16.7	0	100
B. pascuorum	208	11.1	81.7	52.6	55.6	87.5
B. terrestris	470	7.2	73.8	47.2	72.3	100
Other *Bombus*	69	155.4	72.5	15.8	50	87.5
Honeybees	242	7.6	61.6	21.5	46.6	64.1
Solitary bees	777	47.7	73.5	21.4	31.5	54.1
Colletes sp.	67	38.4	79.1	7.1	38.5	62.5
Halictus sp.	162	18.1	71.6	23.9	48.6	88.9
Hylaeus sp.	403	36.6	72.2	23.2	27.9	50
Lasioglossum sp.	145	56.9	76.6	17.6	17.9	34.8
Other solitary bees	0	NA	NA	NA	NA	NA
Syrphid flies	57	51.6	87.7	28.6	60	50
Eristalis tenax	21	27.7	95.2	100	NA	NA
Sphaerophoria sp.	8	74.7	100	NA	NA	NA
Syritta sp.	7	70.5	100	NA	NA	NA
Other syrphid flies	21	43	71.4	16.7	60	50
Others	301	5	66.8	49	47.1	63
Ants	93	7.1	66.7	71	77.8	50
Coleoptera	60	11.8	71.7	64.7	33.3	50
Diptera†	18	38	44.4	10	22.2	28.6
Wasps	99	20.5	68.7	35.5	55	100
Undetermined	31	NA	NA	NA	NA	NA

Note: NA indicates parameters that could not be computed because of lack of data.
† Without hoverflies.

Table 6. Parameter estimates (mean and 95% confidence interval) for the different steps of the predation sequence.

Parameter	Preparation for attack		Attack		Capture success	
	Mean	95% CI	Mean	95% CI	Mean	95% CI
Prey within hunting range	3.70*	3.27, 4.13	4.50*	3.48, 5.51	16.5	−2831, 2865
Encounter rate	−0.45*	−0.85, −0.04	0.56	−0.11, 1.24	0.85	−0.11, 1.81
Prey identity model						
Honeybees	0.79*	0.09, 1.49	—	—	2.34*	0.42, 4.26
Solitary bees	0.85*	0.23, 1.47	—	—	2.35*	0.4, 4.3
Hoverflies	2.77*	1.51, 4.04	—	—	1.79	−2.1, 5.68
Others	0.65	−0.97, 2.28	—	—	4.64*	1.8, 7.47
Prey traits model						
Weight	−0.01	−0.02, 0	−0.01	−0.021, 0.0004	−0.03*	−0.05, −0.01
Weight^2	—	—	0.00	−0.0002, 0.00002	−0.00023*	−0.00042, −0.00004
Prey vulnerability	—	—	2.36*	0.6, 4.12	NA	NA
Optimal diet theory model						
Prey value	—	—	15.62	−1.18, 32.42	NA	NA

Notes: For the prey identity models, the different pollinator groups were compared to bumblebees, which served as control group and are thus not listed. Estimates were obtained by model averaging over the set of best-fitting models determined by model selection. Parameters with confidence intervals (CI) that do not include zero have a significant influence on the spiders' decision or prey capture success and are marked with an asterisk (*). A dash indicates that these parameters were not included in the set of best-fitting models and thus could not be estimated. Prey vulnerability and prey value were excluded from models explaining capture success (indicated by NA: not applicable).

model additionally had the prey's vulnerability as explanatory variable, which was the only factor apart from the hunting range that had a significant influence on the spiders' decision to attack a prey (Table 6). Thus, the prey traits model was the only model supported at the attack stage of the prey capture sequence.

Success.—Overall, crab spiders caught 78 insects, thus, 35.5% of the 220 attacks were successful; an insect was caught with an average chance of 3.5% when alighting on an inflorescence harboring a spider. For the analysis, we used 182 cases where we had information on all parameters fitted in the models. Three models were kept by model selection for ecological inference (Table 4). Prey identity and traits, but not the spiders experience with certain prey types (encounter rate) nor the distance to the prey significantly determined capture success of attacking crab spiders (Table 6). Both the prey weight and the squared weight were negatively related to capture success, indicating a hump-shaped relationship between prey weight and capture success, with very large and very small prey being difficult to catch. Honeybees, solitary bees and other flower visitors were generally easier to catch than bumblebees and hoverflies; from the latter two groups only three individuals were caught by crab spiders (two bumblebees and one hoverfly).

Reductions of prey opportunities at different steps of the prey capture sequence

Losses of prey capture opportunities that crab spiders suffered at the different steps of the prey capture sequence are summarized for the four most important flower visitor groups in Fig. 2 and Table 5. Differences in the amount of losses among pollinator groups were highly significant at each step of the prey capture sequence (chi-square test, all $p < 0.0001$). The mere presence of a crab spider already prevented about half of the solitary bees and hoverflies from landing on an inflorescence; relative losses (in %) at this step in bumblebees and honeybees, however, were comparatively small (Fig. 2, Table 5). As most of the flower visitors alighting on an inflorescence harboring a spider never came to within its hunting range (61.6–87.7%; Table 6), the relative losses at this step were on average the highest. Relative losses owing to the decision of not preparing to attack flower visitors within the hunting range were between 21.4% and 42.6% and were on average the smallest. However, spiders prepared less often for attacking bumblebees that were in their attack range (losses 42.6%) than for the members of the other three pollinator groups (honeybees, solitary bees, hoverflies: losses ~25%; Table 6). Relative losses through not attacking ranged between 31.5% and 63.7%, with smaller prey (e.g., solitary bees)
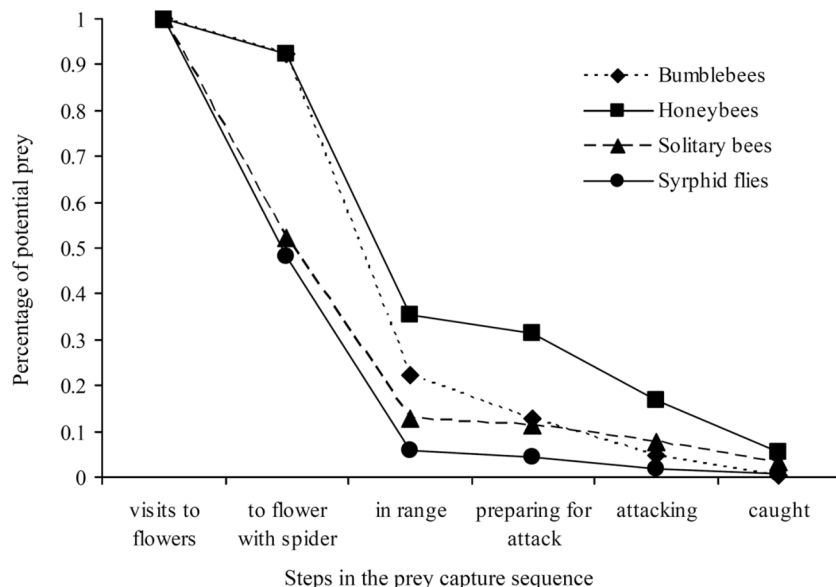
Fig. 2. Losses (in %) at different steps of the prey capture sequence (see Fig. 1) arranged according to flower visitor taxon.

generally being more often attacked than larger prey (e.g., bumblebees). Missed attacks accounted for relative losses between 50% (syrphids flies) and 95.1% (bumblebees).

DISCUSSION

This is to our knowledge the first time that the entire predation sequence was described and analyzed in detail for a predator without artificial restraints on prey composition and encounter rates. Results show that decisions of the spiders are driven by different criteria at different steps of the sequence. In the beginning of the attack sequence, prey identity was used to decide whether to prepare for an attack, while subsequently prey vulnerability (a simple prey trait) determined whether to execute the attack. Finally, success, which is not a decision of the spider and thus not expected to be influenced by optimality criteria, depended on prey size (in a dome-shaped way) and prey identity. Prey value, the trait that should determine foraging decisions according to ODT, never appeared in any credible model for the preparation of attack and was clearly less well supported than prey vulnerability in models explaining attack (Table 6). Since prey value and prey vulnerability were

correlated (Table 1: prey value = 10.6 × vulnerability + 0.6, $R^2 = 0.71$), the appearance of prey value in some of the models chosen for ecological inference on attack decisions may simply reflect the clear effect of prey vulnerability, which was used in its calculation (Eq. 1). In fact, the strong correlation between prey value and vulnerability comes from the almost perfect correlation between prey weight and handling time (Fig. 3; handling time = 7.28 × weight, $R^2 = 0,995$, $N = 8$). This linear correlation remained almost unchanged if we excluded the extreme value of the bumblebees (handling time = 7.29 × weight, $R^2 = 0,915$, $N = 7$). A linear relationship between prey mass and handling time also fitted better (according to the R^2 values) than exponential or power relationships that were found in other studies (e.g., Paszkowski and Moermond 1984, and references therein). In summary, our data do not support optimality traits to guide attack probability in crab spiders. From the predator's point of view, just an assessment of how easy it will be to catch the prey (i.e., the prey's vulnerability) appears to be sufficient. We therefore conclude that there is no strong evidence that crab spiders optimize their foraging decisions in a complex natural setting; simpler prey traits explained better their foraging behavior in
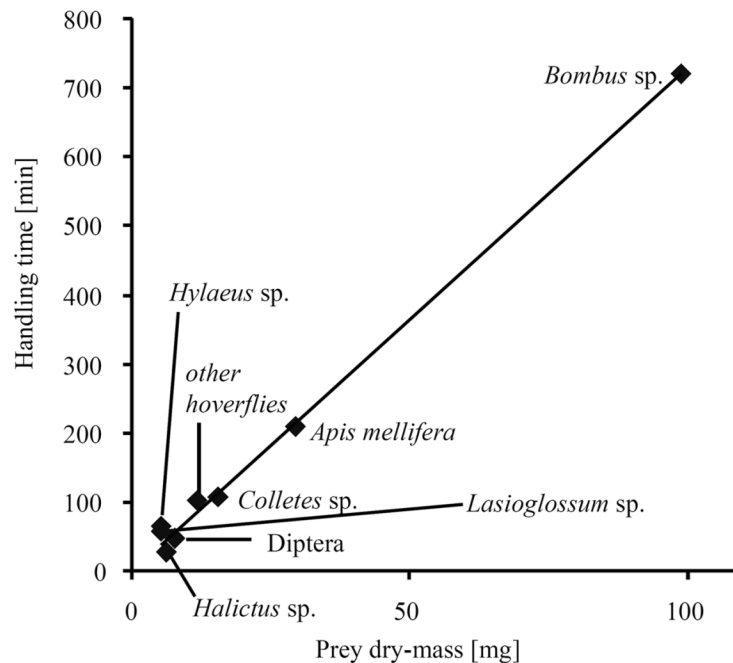
Fig. 3. Linear regression of handling time and prey dry-mass.

the field. The lack of evidence for an optimal foraging strategy we observed at the single prey encounter level is quite coherent with the results obtained by Kareiva et al. (1989) on patch time allocation by the same species. They found that spiders were leaving inflorescences nearly irrespective of their visiting rate by pollinators. An analysis using stochastic models revealed that the gain profile for behaving optimally was exceedingly flat, explaining thereby why a random leaving strategy was sufficient. Similarly, Morse (1979) failed to find support for several predictions of optimal foraging theory in the crab spider *M. calycina*, e.g., like in our study spiders did not specialize on the most profitable prey.

The importance of prey vulnerability in the spiders' decision to attack indicates that crab spiders learn from experience how easy it will be to catch different prey, because vulnerability is difficult to assess otherwise. Although vulnerability was negatively correlated with prey mass (vulnerability = $-0.004 \times$ prey mass + 0.496; $R^2 =$ 0.56), prey mass did not explain foraging decisions of spiders to a relevant extent. Thus it appears that crab spiders learn from experience and are capable of making decisions with a certain level of complexity and flexibility, which

may enable them to make optimality decisions in situations where they would be advantageous.

The quantification of losses of potential prey along the prey capture sequence showed, from the prey point of view, that the prey groups with the highest vulnerability (syrphids and solitary bees) avoided visits to flowers with crab spiders altogether, or at least tried to stay out of direct attack range of the spiders (steepest losses of potential prey at the beginning of the sequence). In contrast, the prey group with the lowest vulnerability (bumblebees) had the highest losses at the end of the sequence. Indeed, syrphids flies are generally more vulnerable to crab spiders than bumblebees (e.g., Morse 1979) and show pronounced hesitation behavior to land on flowers occupied by different crab spiders (*Thomisus* sp.: Yokoi and Fujisaki 2009; *Xysticus* sp.: Brechbühl et al. 2010b). This indicates that selection acts for vulnerable species to avoid the proximity of predators. Moreover, low capture success rates imply that a large proportion of the flower visiting insects in the field might have previously experienced an unsuccessful attack, depending on the density of prey, spiders and flowers. The reduced foraging behavior triggered by fear following missed predatory attempts by

spiders on herbivores has been found to impact many key processes at the community and ecosystem levels, up to nutrient flow (Schmitz 2008).

One of the most astonishing results was the high percentage of missed opportunities for spiders to catch prey. Losses through not attacking, given that the potential prey was within attack range, ranged from 46.2 % (solitary bees) to 79.2 % (bumblebees). These values were calculated by looking at losses from the steps "insect within range" to "attacked". Our findings explain why previous authors claimed that crab spiders are apparently inefficient hunters (Morse 1979, 1981, Schmalhofer 2001, Dukas and Morse 2003, Robertson and Kelmash Maguire 2005, Reader et al. 2006, Brechbühl et al. 2010a). Morse (1979) also found the crab spider *M. calycina* refusing to attack in 37.2% of the cases. However, these studies were conduced from the point of view of the prey. Even if chances for a single prey of being caught are indeed small (e.g., between 3.5% and 4.8%; Morse 1979, Reader et al. 2006, Brechbühl et al. 2010a), the chances for a spider to catch a prey are rather large, approximately one prey individual within a day (on average one prey individual every 10.8 hours: 10 hours of observations per day $\times$ 3 experimental days $\times$ 28 replicates/78 prey caught). Given the low metabolic rate of spiders, one prey of intermediate size per day might be sufficient for survival, however reproduction requires the rare incidence of catching a large prey (Venner and Casas 2005). Hence, the high abundance of prey and the low metabolic rate may make up for the low probability of successfully attacking a prey. Only comprehensive studies conducted in the field with unrestricted encounters of the entire prey community by a predator species can lead to the reconciliation of the often diverging points of view of prey and predators.

Our findings are in line with previous studies in which we used long-term video surveillance to show that in nature, actively-hunting generalist predators will also often refuse to attack apparently suitable prey (Bacher and Luder 2005). The huge fraction of missed opportunities we observed here indicates that prey is over-abundant; predators thus may not need to take every opportunity to catch prey. In the study presented here, spiders encountered on average at least 1.5 prey per hour (calculated from Brechbühl et al. 2010a: in total 2198 visits to flowers with spiders/ 2 spider treatments/28 replicates/26 observation hours; note that this is an underestimation since it includes observation time during which spiders left the flowers and time during which cameras did not transmit pictures due to technical problems). This may also explain why encounter rates with different prey were not significantly determining decisions to attack in our experiment; in fact, spiders were less motivated to prepare for an attack for frequently encountered prey, i.e., those on which they should have gathered the most experience. At an over-supply of prey, optimality models suggest that predators should concentrate their attacks on the preferred prey type (e.g., the "zero-one rule"; Stephens and Krebs 1986). However, this is also not what we found; all flower visitor groups were attacked and there was no single prey type which was clearly preferred. Similar results were obtained by Morse (1979) on the crab spider *M. calycina*. Thus, predators rather behaved as if being under prey shortage by attacking a variety of prey of presumably varying quality. An alternative interpretation would be that predators with an over-supply of a variety of prey do not need to be picky in their diet or sophisticated in their strategy. The abundance of suitable prey would ensure sufficient nourishment for growth and reproduction (Venner and Casas 2005). This should apply particularly to predators with low metabolic rates, such as invertebrate sit-and-wait predators, which can afford to suppress foraging for long times and many prey encounters. Thus, our results indicate that under high prey abundance, benefits of being selective are probably outweighed by the cost to maintain such a strategy. Overabundance of prey would also explain the lack of support for optimal patch choice (Kareiva et al. 1989); even in low-quality patches spiders encountered up to 9 prey per hour, which seems to be more than sufficient given that spiders in our study ate only about one prey item per day. Prey overabundance could furthermore explain the apparently low selection pressure to be cryptic in this crab spider species (Defrize et al. 2010) and the uniform foraging success obtained, irrespective of the degree of color matching with flowers (Brech-

bühl et al. 2010*a*).

In predation ecology emphasis has traditionally been placed on explaining predator-prey encounters, and trophic interactions are usually modeled by functional responses that only take into account encounter rates while assuming that the other steps of the predation sequence (attack probability and capture success) are on average constants, like e.g., Holling's disk equation and its derivatives (Jeschke et al. 2002). By contrast, our results strongly indicate that prey encounters are not the limiting and decisive factor in predator foraging decisions. Recent work suggests that the attack probability of a predator is driven by its satiation level, and accounting for this can dramatically change predictions of prey population dynamics (T. Cornioley, R. P. Rohr, and S. Bacher, *unpublished manuscript*). Thus our results suggest that predation ecology should shift its focus from explaining encounter rates to the factors driving attack probability and capture success in order to understand the impact of predators on prey populations. This may have large implications for the estimates of predation rates and biomass flow through trophic networks in nature.

ACKNOWLEDGMENTS

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