

PREY CHOICE AND SPIDER FITNESS

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ABSTRACT. Although spiders in general are polyphagous, indiscriminate feeding is not advantageous because prey vary enormously in quality due to toxicity or nutrient deficiency. Active prey selection serves to find the optimal compromise between three “nutritional goals”: maximize energy intake, balance nutrient composition of the body, and minimize toxin consumption. Consumption of toxic prey is reduced by more or less specific induced aversions, probably associated with both prey taste and behavior. Spiders’ ability to avoid toxic prey seems limited because aversions are short-lasting and some toxic prey do not induce an aversion. Such prey may be lethal. Toxic prey in a mixed diet may inhibit feeding on and utilization of good prey. Induced tolerance to toxic prey may be possible, however. Nutritional balance may be obtained through consumption of high-quality prey or through mixing of prey types. It is argued that nutrient balance is more important than maximization of energy intake for fitness.

Foraging decisions influence individual fitness in a variety of ways. Choice of foraging habitat (patch) has been recognized as being of primary importance through its effect on feeding rates, with derived benefits to growth (size) and reproduction (Riechert 1981; Morse & Stephens 1996). Once in a feeding patch, the spider is confronted with an array of potential prey species. Prey selection is the consumption of prey relative to the composition of prey available in the spider’s microhabitat. So defined, selectivity has two aspects (*cf.* Pastorok 1981; Sih & Moore 1990): 1) passive selection or capture success, and 2) active selection (“choice”), i.e., acceptance/rejection of the prey. Both are clearly important for determining the diet composition in the field. The capture success reflects the co-evolutionary balance between prey and predator in a broad sense (Malcolm 1992) and is largely outside the individual spider’s control. Active selection reflects the spider’s decisions (choices) whether positive (acceptance) or negative (rejection). Spiders are selective if they choose differentially between the prey species according to their preferences. Such preferences by individuals may change over short time spans and, contrary to expectations, they are not necessarily related in a simple way to the nutritional value of the prey (see later). Active and passive selection can be distinguished if prey is presented with and without possibilities for escape (Onkonbury & Formanowicz 1997; Lang & Gsödl unpubl. data).

This review is concerned only with active selection or “prey choice,” and in our own experiments we have confined spiders and prey to small containers. Additionally, I have largely neglected the phenomenon of size selectivity and focus on choice between prey species. Finally, my treatment is biased towards wolf spiders (Lycosidae) and money spiders (Linyphiidae). These two families account for most of the species and individuals of spiders found in agricultural fields of Northern and Central Europe (Sunderland 1987; Nyffeler & Benz 1988a, b; Toft 1989), and most of the studies reviewed were completed with the specified goal of analyzing potentially important trophic links of the agroecosystem. The experimental prey types were likewise selected to represent the most important prey groups as revealed by studies of European cereal fields, i.e., Collembola, Diptera and aphids (Nyffeler & Benz 1988a, b; Sunderland et al. 1986, 1987; Alderweireldt 1994).

Food contains three main components: energy, nutrients, and toxins. Viewed in isolation, feeding behavior should aim at the following three “nutritional goals”: maximize energy intake, balance body nutrient composition, and minimize toxin consumption. They cannot all be realized at the same time. Prey choice is expected to achieve the optimal compromise that maximizes the fitness of the spider.

As spiders are generalist predators, we might *a priori* expect that energy gain would be maximized by accepting all kinds of prey,

i.e., by being non-selective. In line with this, the broad polyphagy of spiders is considered to follow from the prevailing sit-and-wait strategy and a temporally varying food supply (Riechert & Luczak 1982; Riechert & Harp 1987). In the notion of polyphagy it is usually understood that most kinds of potential prey are of approximately equal value to the predator and may substitute each other in the predator's diet (*cf.* Slansky & Scriber 1985; Waldbauer & Friedman 1991; Wise 1993). Rejection of toxic, dangerous or difficult prey (Riechert & Luczak 1982; Nentwig 1987) as well as novel (unfamiliar) prey (Turnbull 1960; Riechert & Luczak 1982) has, however, been recognized. Prey selection aimed at obtaining a specific composition of amino acids was indicated by Greenstone (1979); but, generally, nutrient balance is considered to be achieved through a mixed diet (Riechert & Harp 1987; Uetz et al. 1992). In conclusion, though the existence of active choice has been acknowledged, most reviews have considered it to be of limited importance.

The questions raised here are: 1) Does active prey choice improve fitness? 2) What mechanisms influence prey choice? 3) Are the three nutritional goals equally important? 4) Do the answers to these questions confirm the inferior role of active selection for spider nutrition?

PREY QUALITY

Prey differ enormously in quality as food for spiders, as indicated by the effects on fitness parameters of keeping spiders on single-species diets (Toft 1995, 1996; Sunderland et al. 1996a, b; Toft & Wise 1999a). Based on laboratory experiments with the wolf spider *Schizocosa* sp., the latter authors establish five quality categories: 1) high-quality prey (e.g., the collembolan *Tomocerus bidentatus*) are nutritionally complete; single-species diets allow complete development (possibly full life cycle); 2) intermediate-quality prey (e.g., laboratory fruit flies *Drosophila melanogaster*) give initially high growth rates, but are insufficient for full development and the spiders die before maturity; 3) low-quality prey (e.g., sciarid midges and conspecifics) allow very little growth and development and spiders die in an early instar; 4) poor-quality prey (e.g., several aphid species) allow neither growth nor development, and performance is no bet-

ter than for starved controls; 5) toxic prey (e.g., the collembolan *Folsomia candida*) result in the spiders dying faster than starved controls. Prey species may have roughly the same quality characteristics for all polyphagous predators, as basically similar results have been obtained for lycosids, linyphiids and carabid beetles (Bilde & Toft 1994, 1997a, b).

With single-species diets no selection is possible. Furthermore, prey species may be insufficient as single prey but make positive contributions to fitness as parts of mixed diets.

DIETARY MIXING

Experiments with mixed diets allow us to analyze the extent to which spiders can choose an optimal diet, given varying prey availabilities. Uetz et al. (1992) demonstrated increased survival and growth rate in *Lycosa* spp. on a mixed diet when compared to a single-prey diet. Toft & Wise (1999a) found the same for *Schizocosa* sp., when fruit-flies and the high-quality collembolan *Tomocerus* were mixed. However, other mixed diets have revealed conflicting results. Thus, performance of *Schizocosa* was below that of the starvation control with two diets mixing two toxic Collembola with higher-quality prey. Toft (1995) found improved reproductive success in the linyphiid spider *Erigone atra* when females were given a mixed diet of fruit-flies and the poor-quality aphid *Rhopalosiphum padi*. From these results it is hypothesized that the positive effect of dietary mixing depends on the quality of the prey species being mixed in the following way: mixing of higher-quality prey may or may not be beneficial; mixing of high-quality prey with prey of inferior quality may be beneficial as long as toxic prey is not included; mixed diets including toxic prey may also be toxic even if higher-quality prey is included.

Toft (unpubl. data) tested these generalizations in a comparable experiment with *Pardosa prativaga* and prey mainly from European agricultural fields. This study revealed no positive effects of dietary mixing, but confirmed the low quality of mixed diets consisting of toxic and higher-quality prey. Thus, the most consistent outcome in these experiments was not a positive mixing effect, but that of toxic prey eliminating the possible benefits of higher-quality prey.

These results clearly show that under the experimental conditions, the spiders were unable to select the most profitable diet from the mixture of good and bad prey available. In some cases (*F. candida* and fruit-flies) acceptance of the toxic prey led to a quick death of the spider in spite of high availability of good prey. So far, there is no information available on the impact of toxic prey on spiders in the field, or on whether spiders in the field are better able to avoid consuming these prey.

ACQUIRED AVERSION AGAINST DETERRENT OR TOXIC PREY

What mechanisms do spiders have to reduce or avoid consumption of poor-quality or toxic prey? Clearly, smell or taste may act as deterrents, perhaps as signals of unpalatability or toxicity. Thus, Bilde & Toft (1994) found reduced acceptance by a carabid beetle of fruit flies coated with homogenate of an aphid or fungus gnat. The response is rarely all-or-none, however. Prey species may be classified according to the spiders' response to them: (a) Some potential prey types are never even attacked by spiders; spiders may have an inherent selectivity against them (*cf.* Nentwig 1987). (b) Other prey types are attacked but discarded uneaten. The difference between this group and the first may be only the strength of the signal that informs the spider about the unpalatability of the prey: if perceived at a distance attack is prevented. (c) Many prey types are accepted readily and eaten on several encounters, but eventually rejected: an acquired aversion has developed. These prey must be moderately deterrent at most. (d) Prey that do not induce aversions: palatable prey. Most often these are high- or intermediate quality prey. (e) Prey that do not induce aversions but are nevertheless toxic (e.g., *F. candida*). These prey may be non-deterrent (i.e., palatable) and spiders (at least young individuals) may die even if the prey are only part of a mixed diet. Tolerance may eventually be induced (see below).

Acquired prey aversions occur when the spider's preference for a prey is reduced following consumption of similar prey, and are probably the main mechanism for limiting consumption of potentially toxic food (Bernays 1993). Several questions arise concerning their specificity and duration. Is an aversion associated with a certain taste of the prey,

with its morphology/behavior or with both? Do spiders learn to associate smell/taste and other prey characteristics in order to be able to avoid poor prey? General answers cannot be given at the moment, but two examples indicate that both taste and behavior can be important for prey recognition. Toft (1997) studied intra- and interspecific aversions of *P. prativaga* against three species of cereal aphids that are similar in behavior and perhaps also in chemical deterrence. Induction of aversion was graded in terms of the number of aphids needed to create it, reflecting a difference in palatability of the aphids to the spider. Also, the duration of the aversion (i.e., the time until the next aphid was accepted) depended on which aphid induced the aversion. However, no matter which aphid induced the aversion, the "aversive" spider showed no differential response in encounters with new aphids. Thus, the motivation to attack was determined by the aversion rather than by the aphid actually confronting the spider, i.e., irrespective of its palatability.

In another experiment with *Schizocosa* sp., the spiders' responses to low-quality fungus gnats were recorded (Toft & Wise 1999b). Spiders were offered prey sequentially and allowed to eat them one at a time. The next prey was offered when the spider had eaten the previous one completely or repeatedly rejected it. In one series only fungus gnats were offered; in a second series only fruit-flies; in a third series fungus gnats and fruit flies were offered alternately. Both prey types were accepted initially, and fruit flies continued to be accepted and eaten completely until satiation in both series. Fungus gnats, however, were often rejected after 4–6 had been consumed, with no difference between the single-prey and two-prey series. In the series given only fungus gnats, most spiders eventually ignored the fungus gnats completely. Presumably, they relied on their experience from the last several captures that only fungus gnats were available and used behavior (flying insect) as the cue to prey recognition. In the mixed treatment, where there was a 50% chance that a flying insect would be a palatable one, the spiders continued to catch fungus gnats, only to release them (mostly alive) when they recognized their identity by taste.

Aversions may modify active prey choice at any of the successive stages of the capture

process (*cf.* Endler 1991). Following recognition of a potential prey, the spider may completely ignore it, or attack-and-retreat if the prey's unpalatability is recognized during attack (but before or at the bite). In the subjugation phase (following bite or wrapping) the prey may be left dead or released alive. In the consumption phase, partial consumption may signify an aversion. Notice that acceptance/rejection is not all-or-none but a graded response, which reflects its conditional nature. Spiders should become more selective when prey availability is high (Riechert 1981; Riechert & Luczak 1982; but see Riechert 1991), or selectivity may depend on an acquired aversion which may develop gradually. As argued by Riechert & Luczak (1982) rejection should occur as early as possible in the predatory sequence. However, acquired aversions indicate that knowledge about the prey depends on experience which takes time to gain, and the information obtained may be uncertain. In the fungus gnat experiment described above (Toft & Wise 1999b), the spiders at first accepted and ate the prey. However, as experience accumulated, they stopped eating (discarded partly eaten prey; released captured prey, very often alive), and eventually stopped attacking the prey (retreating, ignoring the prey). Whether refusing to eat subsequently leads to ignoring of the prey probably depends on the certainty with which the spider is able to identify the prey at a distance. The example indicates that this ability depends not only on the spiders' "knowledge" of (experience with) the prey characteristics, but also on the spider's experiences (expectations) with respect to what prey is available.

An aversion reduces the amount of a poor-quality prey that a spider consumes. However, some poor-quality prey may contribute positively in mixed diets. Thus, complete exclusion from the diet is only advantageous if the prey is always detrimental. A limited duration of an aversion may thus serve to secure a constantly low intake rate, which balances nutrient benefits and toxic damage to the positive side, thus creating a synergistic effect. Toft (1997) measured the duration of aphid aversions in a wolf spider to be mostly < 24 hours. Since only about two aphids were needed to create the aversion in the first place, and probably fewer are needed to reestablish

one, the daily rate of feeding on aphids will be kept quite low. In quantitative estimates with *P. prativaga*, consumption of aphids were only $\frac{1}{10}$ or less of the spider's food demand as determined with fruit flies (Toft 1995).

For some prey types, however, aversions do not protect the spider against toxic overload. Duration of the aversion against the collembolan *F. candida* (animals from USA) was of the same order of magnitude as for aphids, up to *ca.* 24 hours. This was too short to prevent chronic inhibition of feeding and growth in *Schizocosa* (Toft & Wise 1999b). In similar tests with *P. prativaga* and (presumably) the same collembolan species from Europe, an aversion could not be induced (D. Mayntz unpubl. data). With constant availability this Collembola is lethal to *P. prativaga*. However, surviving hatchlings raised on fruit flies with a limited supplementation of *F. candida* eventually developed a partial resistance to *F. candida*. After 5–6 weeks of inhibited growth the young spiders showed compensatory growth and caught up with the fruit fly controls in a few weeks' time (Toft unpubl. data). Such induced resistance to toxic prey may explain why large juvenile *Schizocosa* were not inhibited by *F. candida*, even though small juveniles were (Toft & Wise 1999b). Nentwig (1985) described digestive modifications in a spider following prolonged feeding on KCN-treated prey.

Turnbull (1960) and Riechert & Luczak (1982) noted neophobia, *i.e.*, reluctance to accept unfamiliar prey that were later readily accepted, in two web-spinning spiders. We have not observed this in wolf spiders, but it may be more prevalent in web-spinners in which the web may intercept large and dangerous prey.

NUTRITIONAL QUALITY OF PREY

Greenstone's (1979) work on prey selection in *Pardosa ramulosa*, indicating nutritional self-selection (*cf.* Waldbauer & Friedman 1991) for essential amino acids, is still unique. The huge divergence in food quality of potential prey species demonstrated above should leave us more open to accept this possibility. If prey are deterrent or toxic, this fact may completely override any differences in nutritional composition. However, the improved hatching success of *Erigone atra* eggs from females given a mixed fruit fly-aphid diet in-

dicates that even low consumption of the poor-quality aphid gave a significant nutrient supplement to the fruit flies (Toft 1995). Also, palatable prey may differ in nutrient quality. Several authors have stated that fruit flies are nutritionally insufficient for complete development of spiders (Miyashita 1968; Riechert & Harp 1987). Recent studies show that nutrient additions to the standard fruit fly medium create flies of enhanced quality to spiders (Kristensen & Toft unpubl. data; Mayntz & Toft unpubl. data). Wolf spider hatchlings fed flies raised on standard and nutrient-improved media, respectively, show differences in survival and growth rates after six weeks. Thus, spiders may enhance their fitness by selecting the most nutritious prey species and even the most nutritious individuals of each species, if that is possible. It can be hypothesized that nutritional selectivity increases with degree of nutritional imbalance, which is most likely to develop when a limited range of prey species is available, as is the case in most feeding experiments. Greenstone's (1979) results were obtained in a situation where diversity of potential prey was limited to three species.

Toft (1996) proposed a graphical model predicting the relationship between a predator's tolerance (i.e., maximal consumption capacity) to various types of prey and its performance if the diet is restricted to one prey type. If prey are deterrent or toxic and consumption capacity is therefore low, the predator is unable to reach satiation on this prey and fitness will be low. If prey is non-toxic and palatable, the predator may reach satiation on this prey type. If it is also of optimal nutrient composition, fitness (growth or reproduction) is maximal on a feeding rate equivalent to the maximal rate at which food can be converted into spider tissue (or eggs). If the prey is deficient in essential nutrients, the spider may to some degree compensate by increasing consumption at the expense of food utilization. Thus, the model predicts an increased consumption rate of nutritionally deficient prey associated with a lowered benefit.

A test of these predictions was provided by Marcussen et al. (in press) in experiments with the linyphiid spider *Erigone atra*. A collembolan (*Folsomia fimetaria*) was clearly toxic. Both consumption and reproduction were low, and supplementing a fruit fly diet

with this collembolan reduced reproduction compared to the pure fruit fly diet. Another collembolan (*Isotoma anglicana*) was found to be of very high quality, significantly better than fruit flies, in terms of both number of egg-sacs and eggs/sac produced by the females. However, quantification of daily consumption rates showed that the spiders consumed $> 1.5\times$ more fruit fly mass than *I. anglicana* mass. Thus, the spiders attained the maximal reproductive rate by a moderate consumption rate of nutritionally high-quality prey. A result that can be interpreted in the same vein is the finding that limited and unlimited rations of fruit flies gave the same reproductive output in *E. atra* (Toft 1995). Presumably the limited feeding rate was nutritionally superior due to more efficient nutrient extraction of each prey item (Toft 1996).

An interesting consequence of these results is that fitness maximization is achieved by optimal balancing of nutrients rather than by maximization of energy consumption.

CONCLUSIONS

This review has demonstrated that two conditions for the evolution of prey selectivity of spiders, viz. the differences in food quality of various prey and the consequences of prey quality for spider fitness, are met. In several experiments, however, poor performance of the spiders proved that what the spiders chose was not the optimal selection from the available prey mixture. Benefits of prey mixing were found, but so far there has been no experimental demonstration that spiders can choose the optimal diet when a mixture of prey of various qualities is available. Also, nutritional self-selection still needs to be experimentally established. Selectivity is evident in the spiders' responses to some (but not all) low- and poor-quality prey types, which are accepted at a rate much below availability. Acquired aversions are probably the main behavioral mechanism for reducing consumption of toxins and are the most prominent expression of selective prey choice. A short aversion memory may serve to balance toxic damage with the nutritional benefit of a diverse diet.

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