Spider effects on prey: tests for superfluous killing in five web-builders

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Summary

We tested five species of web-building spiders for the exhibition of superfluous killing of prey at high levels of prey encounter. A measure of the mass of prey captured was compared with the average mass of prey consumed by spiders in feeding trials where test individuals were offered unlimited sequential prey encounters and then unlimited feeding on the prey they had procured. For each species tested, mean total capture (i.e. active capture by the spider itself + passive capture by its web) was significantly greater than the mean prey consumption level for that species. Passive (web-trap) capture of excess prey items contributed to the significant levels of superfluous killing in two of the five species. Active capture was responsible for the high levels of superfluous killing in two other test species. In a high proportion of the foraging trials completed on each spider species, the test subjects failed to feed at all on some of the prey items they or their webs had captured. The results indicate that superfluous killing probably occurs when flushes in prey numbers are encountered. One possible adaptive explanation for apparent superfluous killing, that spiders may more easily extract nutrients from many partially consumed prey items than from one fully consumed item, was found to be plausible for only one of the species tested.

Introduction

New impetus for considering the potential of spiders to control insect prey comes from foodweb models indicating that generalist predators can limit prey populations through the establishment of stable population equilibria between predators and associated prey (De Angelis *et al.*, 1975; Tanner, 1975; Post & Travis, 1979). Spiders are generalist feeders (Riechert & Łuczak, 1982) that meet the criteria for equilibrium point control of prey as they are: (1) selfdamped through territorial behaviour and cannibalism (Riechert, 1982), and (2) can both recognize and respond to patterns of prey availability in a positive density-dependent fashion (Riechert, Provencher & Lawrence, in press).

Recent work indicates that the maintenance of spider diversity within a system significantly increases the limiting effect these predators may have on associated prey populations beyond that which a single, prominent species might exert: spider species assemblages limit assemblages of insect species (Provencher & Riechert, 1994; Riechert & Lawrence, 1997). Though an assemblage of predatory species is not a necessary condition of equilibrium point control, the presence of numerous spider species exhibiting varied foraging strategies, phenologies, and sizes significantly augments the limiting influences spiders might have on prey populations over what a single spider species would have.

Other factors that may increase the limiting effect spiders may have on associated insect populations include: (1) their numerical prominence in habitats, and (2) the potential for spiders to capture more prey than they consume. Nyffeler & Benz (1987), reviewing studies conducted worldwide on spider population numbers in natural habitats, estimated that they attain densities of up to 1000 individuals m⁻² with a mean of 130.8 individuals m⁻². The introduction of a mulch cover to agricultural systems overcomes the impoverished spider fauna (Foelix, 1996) typically found in the agroecosystem and produces spider densities and diversities more common to natural habitats (e.g. 30 times those

h C а Fig. 1: The spider species used in e

observed in tilled annual crop systems: Riechert & Bishop, 1990; Riechert, in press).

Superfluous killing

In addition to numerical prominence in habitats, spiders may exhibit attack rates towards prey that far exceed the quantities they actually consume. The phenomenon has variously been referred to in the invertebrate literature as "superfluous killing" (Conover, 1966), "wasteful killing" (Johnson et al., 1975), and "overkill" (Riechert & Lockley, 1984). Superfluous feeding/killing had been used in the marine biology literature for some 30 years: it is attributed to Conover (1966). Thus this term should take precedence over the other descriptors and we use it synonymously with the other terms here. Wise's (1993) criticism of the superfluous killing hypothesis lies largely in the use of the term "wasteful" which implies maladaptive behaviour. He stated that "Riechert and Lockley seem to equate failure to extract all the energy from a prey item with wasteful killing, though this behaviour is not necessarily wasteful, as the spiders are collecting usable calories from the captured prey". In fact, Riechert & Lockley

(1984) referred to superfluous killing in a less specific sense: as the tendency for spiders faced with high prey encounter rates to kill more than they are able to eat. They referred to superfluous killing as both partial consumption of multiple prey items and failure to feed at all on some prey items that they have attacked and killed. Implicit in the definition is the idea that such activities do not have an underlying adaptive function.

Several studies have reported incidences of superfluous killing in invertebrate predators (Johnson et al., 1975; Coyle & Ketner, 1990; Samu & Bíró, 1993). Johnson et al. (1975) noted that when damselfly naiads are offered high densities of prey, they frequently fail to return to and feed upon previously captured and killed prev items. Significant levels of superfluous killing were first observed at prey (Daphnia) densities of 50 to 500 individuals/l of water and increased at higher densities. Samu & Bíró (1993) studied the feeding behaviour of the wolf spider Pardosa hortensis Thorell at varying prey densities in the laboratory. At high prey densities, this wolf spider was observed to partially consume some of the prey items captured and also to entirely ignore other captured prey items. Samu & Bíró considered a partially consumed prey







e orb web of Araneidae (Argiope trifasciata).

item to be superfluously killed if less than onethird of the prey's original mass was consumed. As in the damselfly study (Johnson *et al.*, 1975), the degree of superfluous killing exhibited in this study was positively related to prey density.

Coyle & Ketner (1990) conducted a study in which they investigated the predatory behaviour of funnel-web spiders of the genus Ischnothele. Although their experimental design did not involve a means of testing for density-dependent changes in consumption rates, they did observe that "when provided with a superabundance of prey, Ischnothele exhibited an unlimited functional response" (i.e. no plateau in the functional response curve of capture rate as a function of encounter rate). In an earlier study, Smith & Wellington (1986) had observed similar results with food-deprived orb weavers in a laboratory feeding experiment. Food-deprived individuals exhibited no plateau in the functional response curve within the limits of rates of prev encountered in their experiment. However, sated orb weavers did show a plateau in attack rate (Smith, 1984).

In the experimental study reported here, we quantified the extent of superfluous killing in a spider species representing each of the following web types: hackled-band, scaffold-line, sheet-line, funnel and orb. We also investigated an adaptive explanation for apparent superfluous killing: partial consumption of a number of prey items is energetically favoured over complete consumption of single prey offering equivalent biomasses.

Material and methods

Test subjects

We chose five spider species that offered the different web structures shown in Figure 1: *Dictyna volucripes* Keyserling (Dictynidae: hackled-band web); *Achaearanea tepidariorum* (C. L. Koch) (Theridiidae: scaffold-line web); *Florinda coccinea* (Hentz) (Linyphiidae: sheet-line web); *Agelenopsis aperta* (Gertsch) (Agelenidae: funnel web); and *Argiope trifasciata* (Forskål) (Araneidae: orb web). We collected the *A. aperta* test subjects from a riparian habitat in Cochise County, Arizona. The

other species were taken in Knox County, Tennessee, the scaffold-line web spider from out-buildings and the other species from old field habitats.

Quantitative measure of superfluous killing

We weighed spiders individually after capture and maintained them in the laboratory for a minimum of three days prior to testing. The spiders were individually housed in plastic containers appropriate to the web size for the species and age class of the individual. While in the laboratory, the spiders were fed crickets, mealworms, termites, or fruit flies twice a week, the particular prey offered depending on spider size and web structure. Each spider was re-weighed every week. We tested an individual spider for superfluous killing behaviour after it had established a web in the laboratory and within no fewer than 2 days of the last feeding. In the feeding trials, we offered the same prey types fed during the course of pre-trial maintenance.

Each prey item offered during the trials was weighed prior to its introduction. At the time of testing, we removed the lid from the container housing the spider and waited for 5 minutes before offering the first prey item. A minimum of 5 prey items were then introduced, one at a time, every 3-4 minutes. (These times are only approximate because we extended the time interval where necessary to allow a test spider time to finish subduing a given prey item before making another introduction.) We continued to offer prey items beyond the minimum of 5 encounters to all test subjects that actively captured these prey until each ceased to attack the last prey item offered within 5 minutes of its presentation. We recorded the entire sequence of events during the test interval, including times at which events occurred and the specific prey item that was involved. Twenty-four hours after the test was completed, we recorded the position of all prey items in the web or discarded from it. We then removed and re-weighed all items. If a spider was still feeding on its prey after 24h, we completed the removal and prey weighing at 48 h rather than the normal scheduled time (e.g. some Achaearanea). Twenty-five spiders representing each of the different web types were tested in this experiment. Test subjects included juvenile and adult female spiders but no adult males. Trials in which the test subject failed to

Web Type	Spider mass (mg)		Total mass captured (mg) (A)		Mass actively captured (mg) (B)		Mass consumed (mg) (C)		Comparison of (A) & (B) with mass consumed (C)
	Μ	SE	Μ	SE	Μ	SE	Μ	SE	Sig. @ P <0.05
Hackled-band	2.42	0.21	10.20	0.27	3.15	0.33	8.23	0.28	A,B
Scaffold-line	64.62	4.42	155.77	14.68	143.42	14.68	60.52	15.06	A,B
Sheet-line	5.27	0.63	14.44	0.83	10.89	1.12	8.12	1.02	А
Funnel	157.10	19.15	305.95	32.90	305.95	32.90	206.84	33.61	A,B
Orb	147.79	56.24	1.52	0.03+	1.09	0.25+	0.77	0.27+	А

+ Proportion body mass

Table 1: Pairwise comparison of mean mass consumed versus captured (active and total) for spiders species representing different web types. Student's t means comparisons: $\alpha = 0.05$.

consume any prey were not included in the analyses.

Partial versus total prey consumption

Two sets of trials were completed to determine whether it is advantageous for the species used in this study to partially consume prey when multiple prey are available. In the first set of trials, we offered 25 individuals of each species a single pre-weighed prey item and recorded the time at which feeding was initiated and the time at which it was terminated for each spider. The remains of each prey item were removed and weighed.

Using the mean feeding time obtained from the first set of trials for each species, we interrupted feeding on a single prey item in the next set of trials after one half of the mean feeding time had elapsed. As in the first set of single prey trials, each prey item was weighed prior to its being offered and again at removal.

Results

Quantitative measure of superfluous killing

Before analysing our trial results, we tested for a relationship between spider mass and the mass of prey consumed. We analysed the mass data for the orb weaver, *Argiope trifasciata*, as proportional to body weight because this species did show a significant relationship between its mass and the mass of prey it consumed ($r^2 =$ 0.36, *F* ratio = 8.0, *P* < 0.01). The ratios of mean total mass captured to mean mass consumed under ad libitum conditions are shown for each species in Table 1. For all of the species tested, the spiders captured significantly more prev biomass than they consumed. For three of the species, passive capture by the web trap accounted for some of the excess capture. This was not the case for two of the species: Agelenopsis aperta and Achaearanea tepidariorum actively captured significantly more prey biomass than they consumed. (Note that we did not correct the prey captured data for inedible wastes, as we found in the trials involving single prey that some individuals of each species tested consumed prey items in their entirety, with no measurable inedible material remaining.)

Figure 2 shows the relationship between active versus passive capture for the different web types. It represents the proportion of observations in which the mass actively captured and total mass captured (active + passive capture by the web trap) exceeded 95% confidence intervals (based on the Student t value for $\alpha = 0.05/2$ and n-1 degrees of freedom) around ad libitum prey consumption. Two points are obvious from inspection of Figure 2: (1) the majority of the spiders tested captured far more prey mass than they actually consumed (the relatively low score achieved for the orb weaver is probably an artifact of the high body mass variability of the individuals used in the trials), and (2) different web types have different foraging strategies that formed a continuum from almost no spider involvement in prey capture beyond the construction of a web trap to prey capture that required the active involvement of the spiders.



Fig. 2: Proportion of trials in which the mass captured was greater than 95% confidence limits above mean *ad libitum* mass consumed for the web types shown. Confidence limits from Student's t values and n-1 degrees of freedom for an α of 0.05/2. Each bar depicts cumulative contribution of active capture by the spiders themselves and passive capture by the web trap.



Fig. 3: Evidence for one aspect of superfluous killing in the five web builders studied: proportion of trials in which some captured prey were not fed on at all.

The hackled-band and sheet-line weaving species relied largely on the web to capture their prey. We observed, for example, that in the field, the sheet-line weaver, Florinda coccinea, limited active capture to pulling prey items moving off the web edge towards the web centre, and we saw no biting or wrapping of prey by hackled-band weaving spiders, Dictyna volucripes, prior to feeding. On the other hand, more active biting and wrapping of prey was observed in the scaffold and orb-weaving species. The funnel-web spider, Agelenopsis aperta, was at the extreme end of the continuum from passive to active prey capture. It captured prey only through active attack, as evidenced by the fact that all of the prey that individual spiders ignored in the trials readily escaped from their webs. The sheet web of Agelenopsis apparently functions as a prey locating device rather than as a trap.

Further inspection of the data collected during the course of the multiple prey trials demonstrates that partial consumption of multiple prey is not the only potential explanation for the excess prey biomass captured. Over 50% of the individual spiders of each test species failed to feed on all of the prey items they captured (Fig. 3). Captured prey items were sometimes left on the sheet untouched or were discarded from the web along with consumed prey. For example, live silk-wrapped meal worms were often found in the bundles of prey discarded by tested Achaearanea tepidariorum. This spider wraps multiple prey in bundles that it secures to its scaffold-line web prior to initiating feeding. The test spiders killed and subsequently consumed only some of the prey secured in these bundles. Though not killed and eaten, the bundled live prey remained captured by the strong silk threads produced by A. tepidariorum.

Partial versus total prey consumption

It has been suggested that the killing of multiple prey is adaptive because partial consumption of prey permits a higher feeding rate than total consumption and thus shorter handling times. We compared the feeding rates exhibited by test individuals that were permitted to feed to satiation (total consumption trials) to those obtained in interrupted feeding trials (partial consumption). Only the scaffold-line weaver, *Achaearanea tepidariorum*, fed at a significantly higher average rate during partial consumption trials than during total consumption trials (Table 2; Fig. 4). The sheet-line weaver, *Florinda coccinea*, actually fed at a significantly lower rate earlier in the feeding sequence than later. This appears to be true also of rates of feeding by *Argiope trifasciata*. As noted for other analyses in this study, high variation in test spider mass explains the lack of a significant difference between partial and full feeding rates in this orb weaver.

Discussion

We found definitive evidence of wasteful killing in all the web-building species we tested in this laboratory study: over 50% of the individuals of each species tested discarded captured prey items that they failed to feed on. In some species, the excess capture occurred because the web structure trapped prey items without the active involvement of the spiders. In others, active capture was required to secure prey items and the spiders pursued and secured prey items far in excess of those they eventually fed on.

Just as Samu & Bíró (1993) observed both killing without feeding and partial consumption of prey in a wolf spider, *Pardosa hortensis* Thorell, under high prey densities, we observed large discrepancies between the quantities of prey killed and those consumed. Greater feeding efficiency in partial feeding is one possible adaptive explanation for killing multiple prey. In our study, only *A. tepidariorum* exhibited a higher feeding rate during partial consumption

Web Type	F ratio	<i>P > F</i> for Half-time rate > Full-time rate
Hackled-band	0.95	0.34
Scaffold-Line	24.84	0.0001*
Sheet-line	5.01	-0.032*
Funnel	3.29	0.079
Orb	3.83	-0.061

Table 2: *F* statistics results for comparisons of distributions of feeding rates (full v. partial) in the web types indicated. Minus signs before *P* values indicate relationships that are opposite to those hypothesized. * = significant relationships.



Fig. 4: Results of feeding rate trials that tested for greater feeding efficiency in consuming partial rather than entire prey. Dotted line represents equal rates (1:1) of partial and full feeds. Bars above line represent partial feed rates that are higher than rates exhibited in full feed trials; bars below the line represent partial feed rates that are below full feed rates. Significant deviations from 1:1 denoted by *.

of a prey item than it did during full feeding. Even this species, however, captured prey that it failed to feed on at all in the multiple prey trials. Thus, it still exhibited apparent superfluous killing.

While our study, and others reported in this paper, demonstrate the exhibition of superfluous killing in laboratory experiments, we have completed the same feeding trials on the five webbuilding species in the field with similar results (unpublished data). The phenomenon appears to be a general one. If superfluous killing has some cost associated with it, then one would expect that mechanisms would evolve that would limit its occurrence. Even spiders whose webs function as traps, for instance, might limit the passive capture of excess prey by taking down capture threads after some threshold level of prey mass or numbers is secured. Two questions need to be addressed in future work: (1) is there opportunity for superfluous killing in nature? and (2) is there a cost to superfluous killing?

Opportunity

One possible explanation for a lack of behavioural mechanisms that prevent superfluous killing is that the opportunity for killing large numbers or quantities of prey is rare in natural systems. Superfluous killing is expected to occur in nature when flushes of insects are encountered by spiders. By flushes, we refer to spikes in prey abundance curves that may be contributed by the hatch of nymphs following rain, or by the swarming of insects to a blooming shrub. Evidence of high levels of temporal and spatial variability in insect numbers and densities would indicate systems in which superfluous killing might be important sources of insect mortality. Long term assessment of prey encounter rates are needed to identify such sytems. Data on the degree to which spider populations in various habitats exhibit superfluous killing should be collected in conjunction with the insect censuses. Of particular importance is the difference in attack rates exhibited by spiders that encounter constantly high levels of prey versus those that are normally prey-limited, but that experience flushes-periods of high prev abundance.

Cost

Field investigations are also needed to answer the question of cost. Actually attacking and subduing prey that are not consumed incurs some costs. There is always, for instance, energy expended in the handling of prey during an active capture effort. There may also be exposure to predators and to unfavourable temperatures and humidities. There may even be risk of injury involved in the active capture of a prey item that kicks (orthopterans), bites (e.g. other spiders, coleopterans, dipterans, orthopterans and hemipterans), or stings (hymenopterans). Such costs have been detailed only for the funnel-web spider, Agelenopsis aperta (Riechert, 1988, 1991). There is another potential cost that has not been directly assessed for A. aperta. This cost would be incurred both by spiders who actively capture prey and by those whose webs serve as web traps (passive prey capture). That is, if by taking more prey than a spider can utilize at the time, the individual is removing prey that it might encounter later (the same prey or potential offspring these killed

prey might have produced). This effect is frequency dependent in the sense that as the frequency of the "superfluous killer" phenotype increases in a population, the potential for paying a cost in lost encounters should increase. This is because, in removing potential prey from the environment, individual spiders are influencing the levels of prey available to other spiders, as well as to themselves.

Phylogenetic constraints

If further study leads to the conclusion that there is the opportunity for superfluous killing in natural systems and that it is exhibited despite definitive costs to fitness, the exhibition of the behaviour might be explained as being a consequence of design constraints. External digestion in spiders is a presumed adaptation to the taking of large meals when prey are available: bulky waste products are not ingested, thereby making room for more nutrients. Because a prey item cannot be consumed until the digestion process has converted it into a nutrient broth, spiders may remain hungry and motivated to continue prey capture activities until they have the opportunity to become sated on the predigested prey. The situation matches the old adage "Don't buy groceries on an empty stomach". Note also that Johnson and his colleagues (1975) attributed the phenomenon of superfluous killing in dragonfly naiads to the occurrence of satiation of the foregut prior to the hindgut, the latter providing the motivation for foraging.

It is unclear whether the spider situation is truly analogous to food shopping in humans and to the two-gut system reported for dragonfly naiads. Foelix (1996) indicated that within a few seconds of secreting digestive enzymes into prey items, spiders can initiate absorption of predigested material. If this is so, it suggests that there need not be a significant lag between capture and satiation feeding.

Significance

Regardless of the mechanisms underlying the phenomenon in spiders, the killing of multiple prey in quantities well beyond what individual spiders consume appears probable in agroecosystems where patches of high prey densities will be encountered. Models that are developed to predict the effects of spider populations on the population growth of targeted prey types should incorporate superfluous killing effects.

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