Prey-capture strategies in sympatric web-building spiders

Samuel Zschokke, Yann Hénaut, Suresh P. Benjamin, and J. Alvaro García-Ballinas

Abstract: Arthropods in several orders use traps to capture prey. Such trap-building predators expend most of their foraging energy prior to any prey contact. Nevertheless, relative investments in trap construction and actual prey capture may vary among trap builders, and they are likely to face a trade-off between building very effective but energetically costly traps and building less effective traps requiring faster reaction times when attacking prey. We analysed this trade-off in a field experiment by comparing the prey capture behaviour of four different sympatric web-building spiders (Araneae: Araneidae, Nephilidae, Tetragnathidae, Theridiidae) with the retention times of five different prey types in the webs of these spiders. Retention times differed greatly among webs and among prey types. The vertical orb webs retained prey longer than the horizontal orb web and the sheet web, and active prey escaped more quickly than less active prey. Among spiders with orb webs, the spider with the web that retained prey for the shortest time was the fastest to capture prey, thus confirming the expected trade-off between building long-retaining webs and attacking slowly versus building short-retaining webs and attacking more rapidly. The sheet web, however, neither retained prey for an appreciable period of time nor facilitated rapid prey capture. We suggest that this low capture effectiveness of sheet webs is compensated by their lower maintenance costs.

Résumé : L'utilisation de pièges pour capturer des proies est assez répandue chez les arthropodes. Ces prédateurs dépensent la majeure partie de leur énergie de recherche de nourriture dans la construction du piège avant tout contact avec la proie. Cependant la quantité relative d'énergie investie pour la construction du piège et celle investie dans la capture de la proie peuvent varier suivant les prédateurs qui peuvent construire un piège très efficace et coûteux ou un piège moins efficace et moins coûteux, mais qui demande des réactions plus rapides au moment de la capture de la proie. Nous avons analysé ce choix stratégique en comparant les comportements de capture des proies de quatre araignées tisseuses de toiles sympatriques (Araneae : Araneidae, Nephilidae, Tetragnathidae, Theridiidae) en fonction de la durée de la rétention sur la toile de cinq types différents de proies. Les durées de rétention diffèrent grandement suivant les différentes toiles et les types de proies. Les toiles orbitèles verticales retiennent plus longuement les proies que les toiles orbitèles horizontales ou les toiles en nappe. Les proies les plus actives s'échappent plus rapidement de la toile. Chez les araignées tisseuses de toiles orbitèles, celle qui possède la toile avec le temps de rétention le plus court a la réaction de capture la plus rapide; ce résultat confirme l'existence d'un compromis entre les pièges très efficaces mais avec un moindre investissement du côté du comportement de capture et les des pièges moins efficaces mais avec un comportement de capture plus rapide. La toile en nappe ne retient cependant pas les proies longuement et ne permet pas une capture rapide de la proie. Nous suggérons que la faible efficacité de ces toiles en nappe est compensée par leur coût d'entretien faible.

Introduction

Predators use a diverse array of strategies to capture prey (e.g., Schoener 1971; Pianka 2000). One strategy is the use of a trap built by the predator, an approach that has evolved in several groups of predators, among them antlions (Neuroptera: Myrmeleontidae), fungus gnats (Diptera: Mycetophilidae), caddisflies (Trichoptera: Hydropsychidae), and spiders (Araneae). Trap building is largely genetically determined and the trap can therefore be considered an extended phenotype of the predator (Dawkins 1982). Trap builders tend to enjoy

higher prey capture success than other predators (Vermeij 1982) but may have only limited influence on the kind and number of prey caught by the trap (Mayntz et al. 2003). Additionally, building the trap requires a considerable investment that must be made before any prey is encountered and that may be futile when no prey is caught or if the trap is destroyed (Higgins and Buskirk 1992). In the classical categorization of foragers into searchers and pursuers (MacArthur and Levins 1964; Schoener 1969; MacArthur 1972; Pianka 2000), trap builders have been categorized as searchers because they expend most of their

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foraging energy before they have any contact with the prey (e.g., Peakall and Witt 1976; Lucas 1985; Venner et al. 2003). However, even among trap builders the relative energy invested in trap construction and actual prey capture varies (Enders 1975; Statzner and Bretschko 1998). Trap builders face a trade-off between building a very effective, probably costly trap and building a less effective trap that, while less costly, requires the predator to be more alert, to expend more energy, or to take higher risks to overwhelm the prey compared with trap builders with more effective traps. When considering the trap as an extended phenotype, this trade-off between effective and energetically cheap traps can be seen as a trade-off between investments in the extended phenotype (an effective trap) and investments in the behavioural phenotype for faster reaction and unaided overwhelming of the prey.

Web-building spiders are the best-known group of trap builders, and the primary function of their webs is indeed trapping (i.e., interception and retention) of insects (Shear 1986b). When a spider web has intercepted a flying insect, the jolt from the impact alerts the spider, which must then make the decision whether to attack based on vibratory clues transmitted by the web. These vibrations provide information on size, location, and activity level of the trapped prey (Suter 1978; Landolfa and Barth 1996). If the information suggests that the prey is acceptable, the spider will proceed to locate and approach it; if the information suggests that the prey is too small, too large, too dangerous, or non-palatable, the spider may choose to ignore it (Riechert and Luczak 1982; Nentwig 1983; Pasquet and Leborgne 1990; Hénaut et al. 2001). When the spider has approached the prey, it makes first contact with its first pair of legs, thus obtaining information about the prey's armour or other defences without exposing itself too much (Uetz 1990). Only after making sure that the prey is harmless and edible, the spider attacks the prey with biting or wrapping. During this entire process, from prey impact to biting or wrapping of the prey, the prey needs to be retained by the web. This retention time is therefore a central aspect of the spider web's functional quality. Shorter retention times give the spider less time to react and approach and examine the prey, thus requiring the spider to be able to move quickly and implying higher risks during prey capture. Since the web-building spiders analysed in the present study rely entirely on their webs to capture prey, their web is the embodiment of their prey-capture strategy.

Web-building spiders build a wide variety of web types, ranging from very simple trip lines that hardly hinder prey movement and serve mainly to alert the spider to the prey's presence to very effective, specialized sticky webs (Shear 1986a). The architecture and stickiness of the web indeed influence the time an insect is retained (Rypstra 1982), but this retention time also depends on prey activity, with more active insects escaping more quickly from orb webs than less active ones (Nentwig 1982). However, the possible interactions between web architecture and prey activity on retention time in the web are not known.

As outlined above, spiders building webs that retain prey for only a short time can be expected to attack more quickly than spiders building webs that retain prey for a longer period. However, there is no empirical support for this hypothesis; in a comparison between two orb-web spiders, Olive (1980) found that even though webs of *Araneus trifolium* (Hentz, 1847) retained dipteran prey longer than webs of *Argiope trifasciata* (Forskål, 1775), the two spider species did not differ in their attack time.

In the present study, we experimentally assessed how long the webs of four different sympatric spiders building webs with different architectures (vertical orb web, vertical semi-orb web, horizontal orb web, and sheet web) retained five different natural prey types (flies, bees, ants, leafhoppers, and mosquitoes). Additionally, we measured each spider's reaction to prey and compared it with the web's retention time to assess the trade-off between building a long-retaining web and initiating slow attacks versus building short-retaining webs and initiating fast attacks. We predicted that spiders with webs retaining prey for only a short time would attack prey more quickly than spiders with webs retaining prey for longer periods, and we predicted that the prey retention time would decrease with increasing prey activity.

Material and methods

Study site

Our study site was located in a coffee plantation on the grounds of the Instituto Nacional de Investigaciones Agrícolas, Forestales y Pecuarias (INIFAP) agricultural experimental station at Rosario Izapa (14°58′N, 92°09′W), located 400 m above sea level, approximately 15 km east of Tapachula (Chiapas, Mexico) and 1 km from the border with Guatemala. The climate is tropical, with typical daily temperatures fluctuating between 23 and 35 °C and a relative humidity of approximately 85%. Heavy rainfalls occur from May to October (~300 mm/month). The experiments were conducted during September and October 2001 (end of rainy season, when spiders and prey are most abundant) between 0900 and 1530, before the daily heavy rainfalls, which generally occur in the evening and during the night. We conducted this study under natural field conditions because prey retention ability of spider webs likely depends on a variety of factors that are difficult to reproduce in the laboratory (e.g., natural climatic conditions, rigidity of web support; see Benjamin et al. 2002 and references therein).

Spiders and their webs

From among the common sympatric spider species, we selected four that build webs with different architectures (vertical orb web, vertical semi-orb web, horizontal orb web, and sheet web) and that belong to different families (Araneidae, Nephilidae *sensu* Kuntner (2006), Tetragnathidae, and Theridiidae; Table 1, Fig. 1). In the descriptions below, ± denotes standard deviation and orb-web nomenclature follows Zschokke (1999).

Verrucosa arenata (Walckenaer, 1841) (Araneidae) builds a rather loose vertical orb web, elongated towards the lower end. The spider rests at the hub ("centre") of the web, with its prosoma ("head") facing up, which is unusual among ecribellate orb-weavers (Levi 1976). *Verrucosa arenata* webs at the study site had an average distance between the hub and the lower edge of the web of 36 ± 11 cm ($n = 9$) and an average distance between the hub and either side or the top of the web of 24 ± 5 cm. The webs of *V. arenata* are

Table 1. Characteristics of the four spider species and their webs (mean ± SD; sample size in parentheses; n/a, not applicable).

| Species | Spider | | | Web | | | |
	Length (mm)	Abdomen width (mm)	Mass (mg)	Kind	Area (cm²)	Height of centre above ground (cm)	Mesh size (mm)
Verrucosa arenata	13.7±1.2 (10)	9.9±1.0 (10)	232±48 (10)	Vertical orb	2275±762 (9)	157±38 (9)	5.2±0.8 (21)
Nephila clavipes	30.6±2.5 (10)	10.2±2.0 (10)	1477±529 (10)	Vertical semi-orb	1985±434 (25)	133±25 (25)	3.5±0.5 (17)
Leucauge venusta	6.1±0.4 (19)	3.2±0.4 (19)	17±6 (19)	Horizontal orb	724±239 (11)	121±45 (11)	2.6±0.6 (20)
Achaearanea tesselata	6.8±0.3 (5)	4.3±0.8 (5)	34±5 (5)	Theridiid sheet	510±177 (6)	171±78 (6)	n/a

Fig. 1. Assemblage of spider webs along the road next to the study site. Most prominent are *Nephila clavipes* webs (hubs with spider, marked with N). Also visible is an *Achaearanea tesselata* web (A). No *Verrucosa arenata* or *Leucauge venusta* webs are discernible in this picture, even though *L. venusta* webs were regularly observed suspended between *N. clavipes* webs, with their anchor threads attached to frame or anchor threads of *N. clavipes* webs.

sometimes parasitized by the kleptoparasitic spiders *Argyrodes* spp. (Hénaut 2000).

The orb web of *Nephila clavipes* (L., 1767) (Nephilidae) is also vertical and has the shape of a semiorb (Fig. 1). The spider rests at the hub of the web, facing downwards. *Nephila* spp. webs are special because of their very fine mesh compared with their size, and because the auxiliary spiral remains in the finished web (e.g., Zschokke 2002). In the webs at the study site, the distance from the hub to the top of the web averaged 9 ± 2 cm (*n* = 25), the distance from the hub to the lower edge of the web averaged 41 ± 4 cm, and the distance between the hub and either side averaged 24 ± 5 cm. The webs of *N. clavipes* are often heavily parasitized by the kleptoparasitic spiders *Argyrodes* spp. (Hénaut et al. 2005).

Leucauge venusta (Walckenaer, 1842) (Tetragnathidae) builds nearly round and almost horizontal orb webs. The

spider rests beneath the hub of the web, with the prosoma generally facing towards the web's lower end. The webs at the study site had an average diameter of 30 ± 6 cm (*n* = 11), an average height difference of 5 ± 3 cm between bottom and top, and an average inclination of 8° ± 5°. These webs are only rarely parasitized by *Argyrodes* spp. (Hénaut 2000; Hénaut et al. 2005).

The web of *Achaearanea tesselata* (Keyserling, 1884) (Theridiidae) is a sheet web without gumfooted lines or any other viscid elements found in other theridiid webs (Fig. 6C in Benjamin and Zschokke 2003; Agnarsson 2004). It is superficially similar to linyphiid sheet webs and consists of a dense sheet with knockdown threads extending above the sheet (Eberhard 1972; Benjamin and Zschokke 2003). Theridiid sheet weavers, unlike linyphiids, rest in a retreat suspended in the centre of the knockdown trap above the sheet.

Table 2. Mass, length (mean ± SD, sample size in parentheses), and flight characteristics of the five prey types.

Prey type	Species	Classification	Length (mm)	Mass (mg)	Flight characteristics	Source of animals
Fly	*Anastrepha ludens*	Diptera, Tephrididae	9.8±1.3 (20)	14.4±1.9 (20)	Strong	Laboratory
Bee	*Scaptotrigona mexicana*	Hymenoptera, Apidae	5.3±0.3 (20)	12.8±1.4 (20)	Strong	Rearing nests
Ant	*Ectatomma tuberculatum*	Hymenoptera, Formicidae	10.0±0.3 (22)	15.0±2.0 (22)	Non-alate	Field
Leafhopper	Various species	Homoptera, Cicadellidae	4.7±0.4 (20)	4.0±1.3 (20)	Weak	Field
Mosquito	*Anopheles pseudopunctipennis*	Diptera, Culicidae	4.3±0.2 (20)	1.3±0.2 (20)	Weak	Laboratory

Webs of adult and subadult females of the four species were selected in the field every day. Because orb webs are usually rebuilt every night, we were able to exclusively use webs built during the previous night. Spiders were not marked, and it is therefore possible that webs of the same spider were used several times on subsequent days. For the prey retention experiments, a lack of sufficient webs forced us to use the same web for several subsequent trials. However, for each trial we used another, undamaged part of the web. For the prey capture experiments, only webs that had not been used for another experiment on the same day were used.

Prey insects

Prey species were selected from families forming the bulk of the diet of the analysed spiders and represented different types of prey with different sizes and flight characteristics. The majority of prey insects captured by orb- and sheet-web-building spiders in a neighbouring coffee plantation were Hymenopterans (26%, mainly ants), Dipterans (26%, flies and mosquitoes), and Homopterans (15%, leafhoppers) (Ibarra-Nuñez et al. 2001). Dipterans and Hymenopterans were also the most numerous insects captured by sticky traps in this area (Hénaut 2001). Based on these studies, we selected five kinds of native insects representing the natural prey spectrum of these spiders: the fly *Anastrepha ludens* (Loew, 1873), the stingless bee *Scaptotrigona mexicana* Guérin, 1845, the ant *Ectatomma tuberculatum* (Olivier, 1792), leafhoppers, and the mosquito *Anopheles pseudopunctipennis* Theobald, 1901 (Table 2). The order in which the prey were tested in the prey retention experiments was randomized.

Prey retention experiments

We measured how long spider webs (from which the spider had been removed beforehand) retained different prey insects. These retention times were assessed for all possible combinations of kind of spider web and prey type. In each trial, one insect was gently blown with an aspirator into an undamaged part of the web. Only trials in which the insect was stopped by the web, i.e., remained there for at least 2 s, were considered in order to exclude the possible influence of the way in which the experimenter had blown the insect into the web. After impact, the prey was monitored continuously for 5 min or until it escaped. During that time (monitoring time), we measured the amount of time the insect wriggled or moved its legs (movement time) and counted the number of vibrating bouts (i.e., flying bouts in flies, bees, leafhoppers, and mosquitoes and abdomen-vibrating bouts in ants) as well as the number of jumping movements of the leafhoppers. In vertical orb webs we also measured the distance the insect tumbled along the web (downwards displacement

within the web; Eberhard 1989). If the prey was still in the web after 5 min, it was checked again for retention after 30 min. After the trials, the spiders were put back into the webs. For the analysis, we combined the activity measures by calculating the sum of movement time (in seconds), number of jumping movements (each jump considered to be roughly equivalent to a movement lasting 1 s), and two times the number of vibrating bouts (each bout considered to be roughly equivalent to a movement lasting 2 s). This sum was then divided by the monitoring time to obtain a measure of the activity rate. Sample size for each combination of kind of spider web and prey type was 25, with 500 trials in total.

Prey capture experiments

We measured prey capture times by analysing the reactions of the four spider species to experimental prey. In each trial, a fly (*A. ludens*) was gently blown with an aspirator into a randomly chosen undamaged sector of the web. We used only flies for this experiment because some spiders may not notice smaller prey and some spiders may consider ants and bees harmful and may therefore hesitate to approach them. The spider's behaviour was filmed with a digital video camera (Sony TRV900E) at 25 frames per second. We later analysed the filmed sequences frame by frame and measured the reaction time (interval between the fly's impact and the spider's first reaction) as well as the running time (interval between the spider's first reaction and successful prey capture: biting or wrapping the prey, whichever came first). Total capture time was calculated as the sum of reaction time plus running time. Trials in which the fly was not retained by the web or escaped before the spider reached it were discarded. Sample sizes per spider species were between 11 and 18.

Data analysis

To normalize the data, prey retention times and prey capture times were log-transformed, and tumbling rates (mm/min) were $\log x + 1$ transformed. All presented means of these variables were back-transformed. Differences in prey retention, prey tumbling, and prey activity among web types and among prey types were assessed with an ANOVA with the factors spider, prey, spider × prey, and web (spider × prey) and subsequent Ryan–Einot–Gabriel–Welsch post hoc comparisons for spider and prey. To assess the relationships between prey activity on the one hand and prey retention and tumbling on the other hand, we calculated the average retention time, prey tumbling rate, and prey activity rate for each combination of spider and prey. We then used simple regressions to determine the influence of prey activity on prey retention and tumbling. Differences in prey capture

Fig. 2. (*a*) Retention time and (*b*) tumbling rate (means ± SE) of diverse prey in different spider webs (spider removed from web). Note that tumbling rate is relevant only for the vertical orb webs (vertical orb and semi-orb). Sample size is 25 for each spider × prey combination.
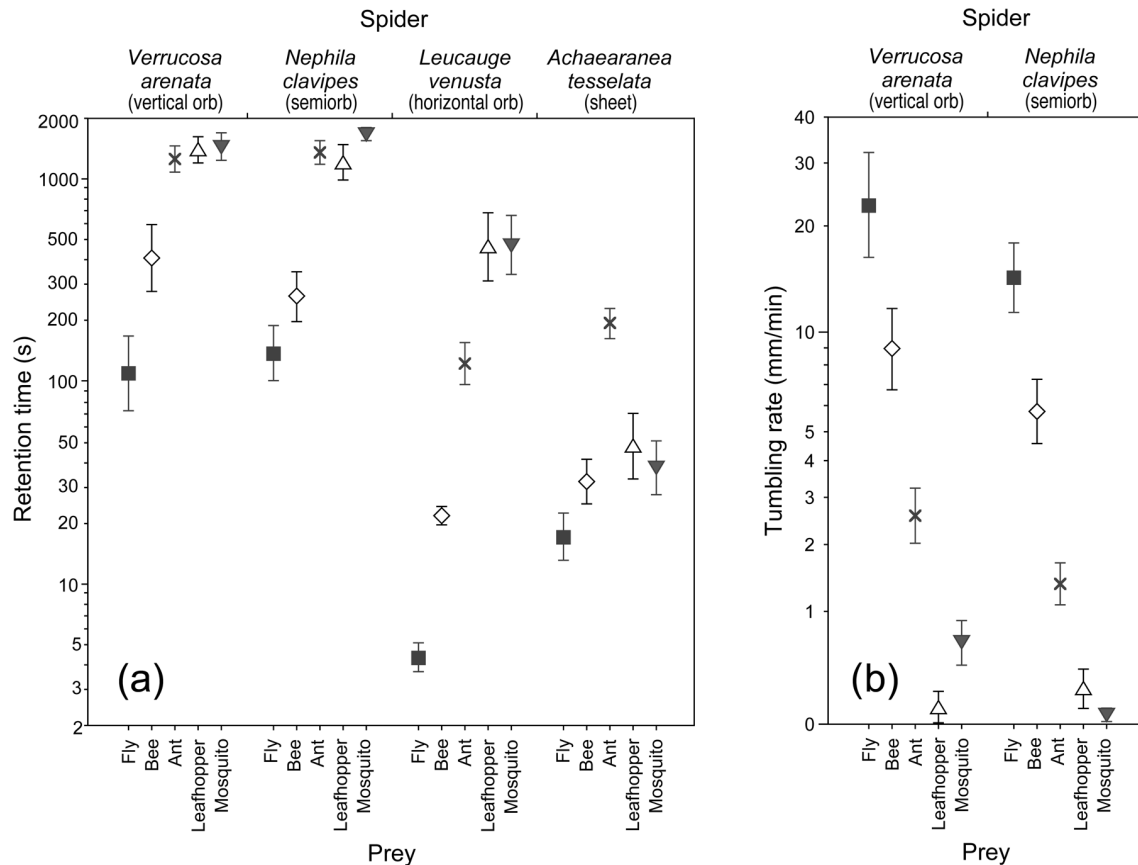
times between spider species were assessed with one-way ANOVAs for reaction time, running time, and total capture time and subsequent Ryan–Einot–Gabriel–Welsch post hoc comparisons. Statistical calculations were done with StatView 5.01 for Macintosh (SAS Institute Inc. 1998) and SAS version 8.02 (SAS Institute Inc. 1999).

Results

Retention time and tumbling rate

Retention times varied considerably among spider webs and among prey types (Fig. 2*a*). Whereas flies could, on average, escape in less than 5 s from the horizontal orb web of *L. venusta*, ants, leafhoppers, and mosquitoes were retained for more than 20 min by the vertical orb webs of *V. arenata* and *N. clavipes*; in these webs, more than 80% of the leafhoppers and mosquitoes were retained for longer than 30 min. Prey retention times differed significantly among spider webs ($F_{[3,418]} = 135.15$, $P < 0.0001$), with the vertical orb webs retaining prey the longest and the sheet web retaining prey for the shortest time. Prey retention times also varied significantly among prey types ($F_{[4,418]} = 84.57$, $P < 0.0001$), with flies escaping most quickly and ants, leafhoppers, and mosquitoes remaining in the web the longest. In comparison, the interaction between spider and prey and the influence of the individual web were relatively small, but still statistically significant (spider × prey, $F_{[12,418]} = 7.59$, $P < 0.0001$; web, $F_{[62,418]} = 2.66$, $P < 0.0001$).

Tumbling of the prey in the vertical orb webs also varied considerably. Flies in the webs of *V. arenata* tumbled the fastest, at an average rate of more than 20 mm/min, whereas mosquitoes and leafhoppers remained more or less at the same place in the web, with tumbling rates of less than 1 mm/min (Fig. 2*b*). Tumbling rates differed somewhat between webs ($F_{[1,210]} = 8.51$, $P = 0.04$; higher in *V. arenata* webs than in *N. clavipes* webs), but much more among prey types ($F_{[4,210]} = 80.85$, $P < 0.0001$): flies had the highest tumbling rate, ants the second highest, and bees the third highest; leafhoppers and mosquitoes had the lowest tumbling rate. There was no significant interaction between spider and prey ($F_{[4,210]} = 0.97$, $P = 0.43$) and only a weak effect of individual web ($F_{[30,210]} = 1.81$, $P = 0.09$).

Activity rates of the prey also differed to a great extent. Flies and bees were active for nearly the entire monitoring period, whereas leafhoppers and mosquitoes were mostly immobile. Activity rates differed somewhat among webs ($F_{[3,418]} = 43.90$, $P < 0.0001$): they were highest in the sheet web and lowest in the vertical orb webs. Activity rates differed strongly among prey types ($F_{[4,418]} = 306.58$, $P < 0.0001$): flies were most active, bees ranked second, ants ranked third, leafhoppers ranked fourth, and mosquitoes had the lowest activity rates. In comparison, the interaction between spider and prey and the influence of the individual web were relatively small, but still statistically significant (spider × prey, $F_{[12,418]} = 6.38$, $P < 0.0001$; web, $F_{[62,418]} = 5.19$, $P < 0.0001$).

Fig. 3. Relationship between activity rate of the prey insect and (*a*) prey retention time and (*b*) prey tumbling rate. Each point represents the mean of the 25 trials for each spider × prey combination. Filled circle, *Verrucosa arenata* (vertical orb web); circle with lower half filled, *Nephila clavipes* (vertical semi-orb web); open circle, *Leucauge venusta* (horizontal orb web); and triangle, *Achaearanea tesselata* (sheet web).
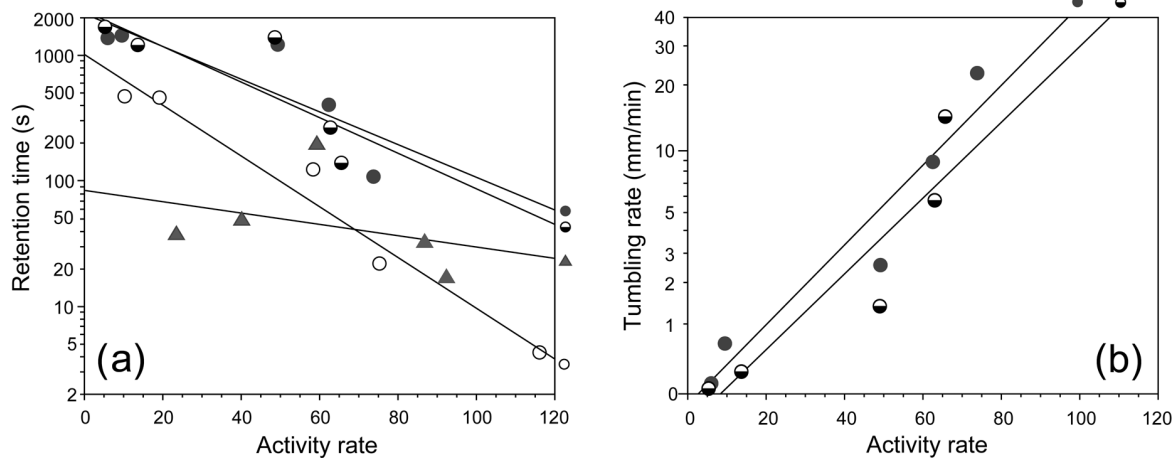

Prey retention times and tumbling rates were largely influenced by the activity rates of the different kinds of prey: more active prey escaped more quickly and tumbled more than less active prey (Fig. 3). Overall, these relationships were highly significant (retention time, $r^2 = 0.566$, $n = 20$, $P < 0.0001$; tumbling rate, $r^2 = 0.855$, $n = 10$, $P < 0.0001$). When calculated separately for each kind of web, the relationship between activity rate and prey retention time was significant for the horizontal orb web (*L. venusta*, $r^2 = 0.965$, $n = 5$, $P = 0.0028$), and for the vertical orb webs there was a tendency for the retention time to decrease with prey activity rate (*V. arenata*, $r^2 = 0.582$, $n = 5$, $P = 0.083$; *N. clavipes*, $r^2 = 0.561$, $n = 5$, $P = 0.090$). For the sheet web, however, prey activity did not seem to influence prey retention ($r^2 = 0.117$, $n = 5$, $P = 0.57$). Prey tumbling was found to increase significantly with prey activity when calculated separately for each spider (*V. arenata*, $r^2 = 0.896$, $n = 5$, $P = 0.0095$; *N. clavipes*, $r^2 = 0.790$, $n = 5$, $P = 0.0278$).

Prey capture

The reaction time of the spider did not differ among species ($F_{[3,55]} = 0.91$, $P = 0.44$; Fig. 4). However, running time was significantly shorter in *L. venusta* than in the other three species ($F_{[3,55]} = 5.67$, $P = 0.0019$). Similarly, total capture time (time elapsed between prey impact and successful capture) was also shorter in *L. venusta* than in the other species ($F_{[3,55]} = 3.76$, $P = 0.016$). The distance between the hub with the spider and the point of prey impact influenced running time (log-transformed) in *V. arenata* (linear regression; $r^2 = 0.301$, $n = 14$, $P = 0.042$) but not in the other species ($P > 0.80$). Similarly, in *A. tesselata* webs there was no difference in running time between flies that were stopped by the sheet and those that were stopped by the knockdown threads above the sheet ($t = 0.880$, $n = 16$, $P = 0.39$).

Among the orb webs, total prey capture time for flies was correlated with prey retention times for this prey type (Fig. 5). In contrast, total prey capture time was highest for the sheet web of *A. tesselata* even though its prey retention time was only intermediate.

Fig. 4. Time taken by the four spider species to capture a fly (means ± SE). Reaction time is the time between prey impact and the first reaction of the spider, running time is the time between the first reaction of the spider and biting or wrapping (whichever came first) of the prey, and total time is the sum of the two. $n = 14$ for *V. arenata* (vertical orb web), $n = 18$ for *N. clavipes* (vertical semi-orb web), $n = 11$ for *L. venusta* (horizontal orb web), and $n = 16$ for *A. tesselata* (sheet web).
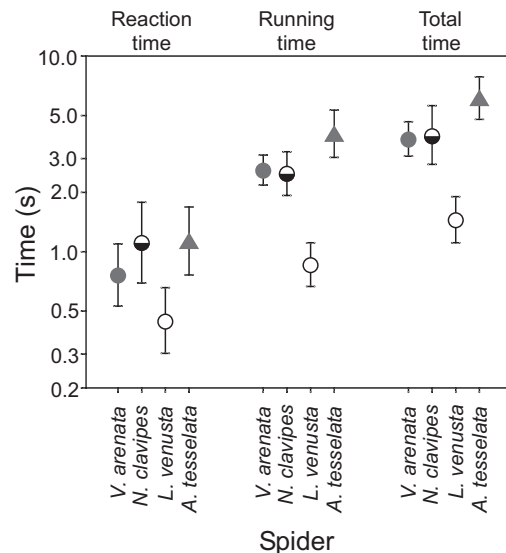

Discussion

Retention time

Prey retention times varied by more than two orders of magnitude among the different spider webs and prey types. Among the tested webs, the vertical orb webs of *V. arenata* and *N. clavipes* retained prey the longest; the horizontal orb web of *L. venusta* retained the mostly inactive mosquitoes and leafhoppers for a similarly long period, but not flies and bees; and the sheet web of *A. tesselata* retained most prey types for only relatively short periods. The difference in prey retention between the vertical and the horizontal orb

Fig. 5. Relationship among different spider webs between the time the webs (without spider) retained a fly and the total time the spider needed to capture a fly: ●, orb webs; ▲, sheet web; error bars indicate SE. Among the orb webs, this relationship was statistically significant (r_p = 0.9998, n = 3, P = 0.013).
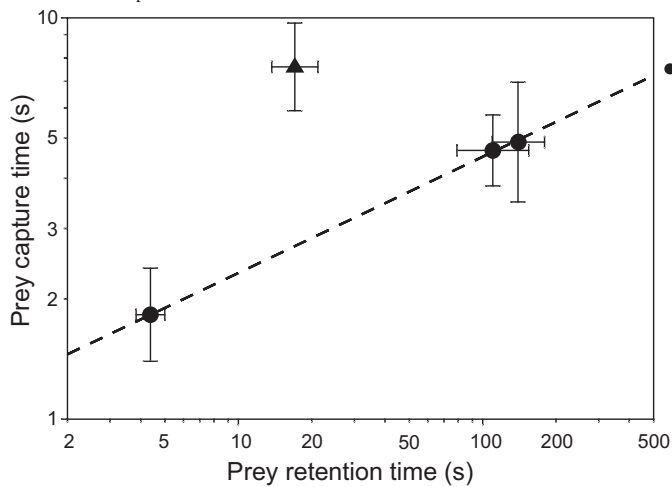
webs is likely due to web orientation. Most prey make some effort to free themselves and sometimes manage a temporary escape, which causes them to fall from their current position in the web. In vertical orb webs, they are often caught again by sticky threads further down in the web (tumbling), whereas they drop completely out of horizontal orb webs (Chacón and Eberhard 1980; Eberhard 1989). This difference can explain why the more active prey types (flies, bees and, to a lesser extent, ants) were retained much longer in vertical than in horizontal orb webs, whereas the less active prey types (leafhoppers and mosquitoes) were retained for similar periods in the horizontal and the vertical orb webs.

The potential prey spectrum probably differs between horizontal and vertical orb webs in the same way. Vertical webs are more likely to intercept horizontally flying prey, whereas horizontal webs are more likely to intercept prey flying vertically (Chacón and Eberhard 1980; Eberhard 1989). Since horizontally flying insects are often strong flyers, such as flies and bees, the strength of the vertical orb web matches that of its potential prey, whereas the strength of the horizontal orb web is sufficient to stop and retain only slowly flying prey such as mosquitoes and jumping insects such as leafhoppers (Zschokke and Vollrath 2000).

The sheet web of *A. tesselata*, which contains no sticky silk, works somewhat differently than orb webs. In this web, prey are not held in one particular place by sticky silk and can walk around on the sheet and on the knockdown threads. However, when they try to fly away, knockdown threads usually stop them again. This difference in functionality between the *A. tesselata* sheet web and the orb webs may explain the relatively small variation in retention time among prey types in the sheet web. Among the different prey types in the *A. tesselata* sheet web, ants were retained the longest. However, in some trials, the ant did not seem to try to escape from the web, probably because ants sometimes forage as kleptoparasites in sheet webs (Y. Hénaut, unpublished data).

With the exception of ants in *A. tesselata* webs, which did

not always try to leave the web, all webs showed essentially the same ranking when prey types were ordered according to their retention time, which is also reflected in the relatively low interaction between spider and prey in the ANOVA. This suggests that none of the webs studied is specialized to retain any of the tested prey types.

As expected, the most active prey types had the shortest retention times and the highest tumbling rates. However, even though sticky silk density is much higher in *N. clavipes* webs than in *V. arenata* webs, prey retention times did not differ between these two kinds of web and tumbling rates differed only slightly between them. To free themselves, prey often grabbed a non-sticky thread and then tried to loosen their contact to the sticky silk. All non-sticky silk in the web can thus increase escape probability and tumbling rate. In *N. clavipes* webs, the non-sticky auxiliary spiral may thus counteract the effects of the smaller mesh size. Similarly, the (non-sticky) draglines of the kleptoparasitic spiders *Argyrodes* spp. may also help prey to escape from these webs.

Overall, our results show that the retention time of the various prey types in orb webs is linked to their activity, with the least active ones being retained the longest, thus confirming an earlier laboratory study (Nentwig 1982). However, prey retention in sheet webs did not seem to be correlated with prey activity.

Prey capture

Prey capture times varied among spider species. However, contrary to predictions, no difference in reaction time was found among spider species, and only a weak correlation was found between running time and the distance between the hub and the point of impact, in contrast to an earlier laboratory study that showed such a correlation for *Araneus diadematus* Clerck, 1757 (ap Rhisiart and Vollrath 1994).

Leucauge venusta captured the fly used as experimental prey more quickly than the other three spider species tested in our experiments. Anecdotal observations during our field experiment also suggested that *L. venusta* generally reacted more often and more quickly, especially to small and inactive prey, than the other two orb-web spiders. *Leucauge venusta* also spent less time checking the location and presence of its prey during its approach than did the other two orb-web species, which explains its much shorter capture time and can also help to explain why *L. venusta* webs are attacked less by kleptoparasitic spiders (*Argyrodes* spp.) than webs of the other two orb-web species (Hénaut 2000; Hénaut et al. 2005). On the other hand, the spider may face greater risks when approaching potentially dangerous prey without due caution and probably makes more capture attempts towards nonexistent or already escaped prey. Each capture attempt costs energy and causes some web damage. This damage sometimes requires *L. venusta* to rebuild its web during the day, a behaviour generally avoided by most web-building spiders (Eberhard 1976; Ramousse et al. 1981; Benjamin and Zschokke 2002*a*), probably to avoid predation by predators that rely on visual cues (Curtis and Carrel 2000).

Comparison among webs

As predicted, the spider with the web that retained prey

for the shortest time — *L. venusta* — was the fastest to capture prey. Thus, for the analysed orb webs, our results confirm the expected trade-off between building a long-retaining web and initiating slow attacks (*V. arenata* and *N. clavipes*) versus building a short-retaining web and initiating fast attacks (*L. venusta*). However, the other spider species building a short-retaining web — *A. tesselata* — was slow to capture its prey, probably because its web lacks sticky silk, thus forcing the spider to make several attempts to overwhelm the prey, which often kept walking away on the web. Our results thus suggest that the sheet web of *A. tesselata* is less effective in capturing intercepted prey than the orb webs studied.

In all kinds of webs, average prey capture times were shorter than average prey retention times, suggesting that all kinds of webs are effective. However, to be highly effective, prey capture times need *always* (and not just on average) be shorter than prey retention times, and average prey capture times therefore have to be much shorter than average prey retention times. If this were not the case, a considerable proportion of the prey could escape (if the average prey capture times were the same as the average prey retention times, the spider could capture only 50% of the prey). In addition, large prey, which are essential for the spider's fitness (Venner and Casas 2005), may escape even more quickly than the fly used in our study (Nentwig 1982), and the spider therefore needs to be faster to catch these prey than to catch flies.

The number of prey actually captured by the spider depends not only on the retention quality of the web and the spider's reaction but also on the number of prey intercepted by the web. Prey interception rate is known to increase with web size (Rypstra 1982; Venner and Casas 2005). Among the webs analysed, the sheet web was the smallest (Table 1), which implies that the difference in effectiveness between sheet webs and orb webs is probably even larger than suggested by our comparison based on prey retention alone.

However, when comparing the overall efficiency of spider webs, the spider's investment in the web must also be considered. The average total length of sticky spiral, which is a good estimate of total investment in orb webs (Eberhard 1986; Zschokke and Vollrath 1995a; Venner et al. 2001), was about 56 m in *N. clavipes* webs, 44 m in *V. arenata* webs, and 28 m in *L. venusta* webs (values calculated based on mean areas and mesh sizes, Table 1). However, web renewal rates differ between species. *Nephila clavipes* typically renews about two thirds of its web every night (Peters 1953; Nentwig and Spiegel 1986; authors' unpublished observations), *V. arenata* renews the whole web every night (authors' unpublished observations), and *L. venusta* renews its web every night and sometimes also a second time during the day (see above; Eberhard 1988). Daily investments based on total sticky spiral length are therefore similar among the three orb-web spider species. The comparison with *A. tesselata* webs is more difficult owing to the entirely different web structure but can be made based on the time spiders invest daily in their webs. Theridiid sheet-weavers such as *A. tesselata* require several hours to build their web and, unlike orb-weavers, do not eat their previous web to recycle silk proteins, thus suggesting a rather large investment per web (Eberhard 1972; Janetos 1982; Benjamin and Zschokke 2002b). The daily investment of *A. tesselata* has

not been measured, but another theridiid spider, *Achaearanea tepidariorum* C.L. Koch, 1841, which builds a somewhat different kind of web, is known to invest 2–3 h to build a new web, and afterwards about 20 min per day for web maintenance (Benjamin and Zschokke 2003). Orb-web spiders have larger daily investments of between 40 and 90 min per day (estimates based on our observations and comparisons with other orb-weavers with known activity patterns; Zschokke and Vollrath 1995b). We conclude that sheet webs are less effective at catching prey than orb webs, but sheet-web species compensate for this lower effectiveness by a lower daily investment and probably also by their better protection against predators such as sphecid wasps (Blackledge et al. 2003).

Acknowledgements

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