1998. P. A. Selden (ed.). *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh 1997.

Management of web construction in different spider species

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Summary

In many spider species, the web has a more or less geometrical structure. In a particular species, it may vary from one individual to another and also from one construction event to the next. Different sources of variation may affect the size of successive capture traps and their structure. We have studied web variation by comparing several spider species: variation was induced by changes in environmental factors. We have used an economic approach (cost/benefit analysis) to discover how spiders may manage their web construction.

Introduction

The characteristics of webs have been considered as species-specific and may be used to recognize species. But if we look at web parameters (size of the capture area, number of radii, number of spiral turns), we find variability. Size and structure of webs may vary with the needs of the spider (egg maturation, moult: Shermann, 1994) or with the quantity of available silk (Eberhard, 1988). They vary also with environmental factors: abiotic (Ap Rhisiart & Vollrath, 1994) or biotic: i.e. prey (Pasquet *et al.*, 1994) and conspecifics (Lubin, 1980; Buskirk, 1986; Leborgne & Pasquet, 1987).

Web characteristics are directly linked to the efficiency of prey capture (Nentwig, 1982; Vollrath, 1992). This allows us to study web construction behaviour using an economic analysis. Web construction has a cost for the spider; it needs energy and time, but the spider has a reward (quantity and quality of prey caught). If web characteristics can vary, the spider may become more efficient by adjusting its cost/benefits balance of web construction.

This paper summarizes our results from testing the influence of prey and/or conspecifics on web construction and the characteristics of the web. We have tested prey because it is essential for spider development and because we suspected that spiders might modify web parameters according to the presence of certain types of prey. *Agalenatea redii* spins its web at different heights of the vegetation and the web size is negatively correlated with the height of the hub and also the size or the quality of potential prey: small prey are found at the top and larger prey nearer the ground (Pasquet, 1984). This result shows that, in a population, web characteristics vary in relation to environmental factors.

Conspecifics were taken into account because they play an important part in the organisation of the population. Manipulations of three species: *Zygiella x-notata*, *Cyrtophora citricola* (ecribellate spiders) and *Stegodyphus lineatus* (cribellate spider) were carried out in the field or under laboratory conditions. The first species is a solitary spider, the second is a facultative colonial species, and the third one has maternal care. So they differ in their relationships with conspecifics and in the extent of their investment in their progeny.

Influence of conspecifics on web construction and web structure

Zygiella x-notata *(Kremer* et al.*, 1987; Leborgne & Pasquet, 1987)*

Zygiella x-notata webs occupy frames of the windows of the University of Nancy (France). Spiders may be solitary, without any contact with conspecifics, or in aggregations of several individuals. These groups are situated along the vertical part of the window frames and the webs are in the same plane as the frames. Webs are not all the same size: there is an alternation of webs so that a large web is generally surrounded by two smaller ones (mean size of small webs x = 17.9 ± 4.6 cm, n = 12; of large webs x = 22.1 ± 5.6 cm, n = 22) for spiders separated by an average inter-retreat distance of 32.7 ± 20.1 cm (n = 34).

In this "natural" population, we modified the organization by removing either individuals with large webs or those with small webs. If the spider removed had a small web, its remaining neighbours that had larger webs did not change the size when they rebuilt. But if we removed a spider with a large web, its neighbours with smaller webs rebuilt larger webs than previously. This result suggests that in the aggregations of *Zygiella x-notata*, some spiders exert a constraint on others: the result is a reduction of web size.

To confirm this result, an experiment was carried out in the laboratory. Two spiders were simultaneously put in a wooden frame (50 × 50 × 10 cm). In each frame, one spider built a large web (median = 17 cm (14.5–20), n = 29) and the other a small one (median = 14 cm (9.75–18.75), n = 29). When we separated the spiders and put them immediately, individually into a frame, they built a "large" web (median = 18.75 cm (13.5–23.25), n = 20 and median = 18 cm (16–21), n = 20). Therefore, one exerted a constraint on the other and this constraint affected web size. We determined by direct observations that the first web built was the largest. The order of web construction was not correlated to spider size.

Cyrtophora citricola *(colonial spider) (Leborgne* et al.*, 1998)*

Cyrtophora citricola may live in large colonies where each spider spins its own web, or may be solitary. We compared webs of colonial and solitary individuals, and showed that the presence of conspecifics influenced web size. Webs were smaller for colonial spiders than for solitary individuals (diameter 35 ± 2 cm versus 40 ± 1.5 cm; t-test = 1.92, P = 0.031). When we destroyed webs (colonial and solitary), spiders took several days to rebuild their webs, and after three days, webs of solitary spiders were larger than webs of colonial individuals. Therefore, in these colonial spiders, individuals take into account the presence of their neighbours to build their web and the result is a reduction of web size.

Influence of prey on web construction and web structure

Zygiella x-notata *(Pasquet* et al.*, 1994)*

Experiments were conducted under laboratory conditions (temperature 20 °C and 12h of light per day; 0600–1800h). Spiders of one group (n = 110) were placed individually into frames and another group (n = 110) had prey (four flies—*Calliphora vomitaria*) introduced at the same time. In the presence of prey, more spiders built webs than in its absence (100% versus 75%) and some individuals built their webs earlier than any of the spiders in the absence of prey. The webs built in the presence of prey were smaller (median web diameter 13 cm (10–18) versus 18.5 cm (14–23), Mann & Whitney test, P < 0.05) than webs built in the absence of prey. Web building is quicker by spiders in the presence of prey than in its absence (median = 62 min (51–78) versus median = 88 min (70–112), Mann & Whitney test, P < 0.05). These results suggest that the spiders receive and integrate information from their environment and adjust their construction to the situation. We also demonstrated that the response to prey may be modulated by the internal state of the spiders. Well-fed spiders did not build earlier, even in the presence of prey, but their webs were smaller than those of individuals without prey.

Stegodyphus lineatus *(Pasquet* et al.*, submitted)*

Stegodyphus lineatus is a desert spider that builds a capture web on bushes. The web is not geometrical like an orb web; nevertheless, it has a structure that can be easily quantified. Studies were conducted in the Negev desert (Israel) during spring in 1994 and 1995. We tested the hypothesis that previous foraging influences web renewal activity and web size. The cost of web building was measured as time and mass loss: to build an average 120 cm^2 web took 5 hours, and spiders lost up to 7% of their body weight during construction. In field experiments, spiders that were given additional prey improved their body size in comparison with individuals whose webs were removed (Wilcoxon test: non-fed spiders, $z = 1.52$, $n = 19$, $P = 0.12$; and spiders supplemented with prey, $z = 2.92$, $n = 19$, $P = 0.003$) and reduced their foraging opportunities in comparison with spiders which did not receive prey. The results showed that the spiders with food supplementation built smaller webs (ANOVA F-test = 4.45, $P = 0.015$) or built fewer webs after three or four supplementary prey items than the non-fed spiders (G-test = 20.52, $P < 0.05$). We showed that web removal did not affect body condition, web-building frequency or web size. This result was confirmed in a laboratory experiment: spiders did not build a web after prey capture and ingestion. *Stegodyphus lineatus* limits immediate foraging risks which outweigh potential long-term time constraints (development, growth, reproduction).

Conclusions

The results of the experiments described above show that spiders react to a range of environmental factors. We have demonstrated that spiders have the capacity to adapt their web to the situation:

• When prey was present, spiders spun earlier, smaller webs than in the absence of prey. After prey consumption, the size of the web of *Zygiella x-notata* decreased, but the spider did not spin earlier. *Stegodyphus lineatus* reduced its investment in web and even stopped building after a few days. For these two species, we noted a decrease in energy costs of web building in the presence of a potential benefit (food).

• In the presence of conspecifics, some *Zygiella x-notata* decreased their web area, showing constraint induced by the presence of conspecifics. This is more general: spiders which live in aggregation or in colonies (like *Cyrtophora citricola*) may adapt their construction according to the presence of conspecifics.

Spiders take into account variations in environmental factors when they build their web. They are able to manage their web construction behaviour: stopping building, decreasing the size of the capture area, changing the structure. These modifications are immediate responses to changes of environmental factors. We may use an economic approach to explain this behaviour based on quantified data. Each behaviour has costs (i.e. energy, time, risks) and benefits (i.e. food intake). If the animal behaves in an optimal manner, the cost/benefit ratio must be maximized. For spiders, the web is a very good element to test the hypothesis: we have data on the cost of the construction of a web for orb-weaving spiders (Peakall & Witt, 1976), even if we take into account that spiders ingest their web at the end of their foraging period (Breed *et al*., 1964).

For the spiders we used in our experiments, web costs (time and energy) vary from one species to another. *Zygiella* uses an orb web which is renewed daily, *Stegodyphus* has a geometrical long-lived web, whilst *Cyrtophora* has a long-lived orb web with a barrier web. We have data on the cost for building each type of web. Web-building takes less than one hour for the first species (Pasquet *et al*., 1994), several hours for the second and one or two nights for the third species (Lubin, 1973). *Stegodyphus* loses up to 7% of its body weight to build a 120 cm^2 web (Pasquet *et al*., submitted). Presence of prey or prey capture and ingestion induce a decrease in web investment in both *Zygiella* (Pasquet *et al*., 1994) and *Stegodyphus*: the first species saves time and perhaps energy and the second one limits its web construction so it saves energy and lessens exposure to parasite or predator attacks (Pasquet *et al*., submitted).

With prey the spider has a direct and immediate result for its investment (number of prey captured and the quantity of prey ingested). Spiders may adjust their behaviour to the cost/benefit ratio of a previous construction. It could have a direct effect on the quantity of prey caught. It seems that it could depend on prey availability in the environment: in a rich environment (high density of prey) spiders are in high density and build smaller webs (Gillespie, 1987). Web reduction does not occur when prey density is low.

To interpret the results with conspecifics in terms of economics is more complex. With *Zygiella x-notata* and *Cyrtophora citricola*, web reduction occurs in high spider density, but there was no difference in prey density between the two zones (Leborgne & Pasquet, 1986; Leborgne *et al*., 1998). So we must find another interpretation of the results. We may hypothesize that a long term benefit is possible for spiders which "accept" staying in a group and which "accept" constraints on their construction with theoretically an immediate reduction of the number of prey captured. The long term benefits could be in reproduction (better access to males for females) or in better protection against predators or parasites.

The conclusion is that these spiders are able to analyse variation in their environmental features and to behave in such a way that they manage costs and benefits.

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