Anim Cogn (1999) 2 : 171–177

ORIGINAL ARTICLE

Astrid M. Heiling · M. E. Herberstein

The role of experience in web-building spiders (Araneidae)

Received: 1 March 1999 / Accepted after revision: 18 August 1999

Abstract A typical feature of vertical orb-webs is the 'top/bottom' asymmetry, where the lower web region is larger than the upper web region. This asymmetry may improve prey capture success, because, sitting in the hub of the web, a spider can reach prey entangled below the hub faster than prey entangled in the area above the hub. While web asymmetry is known to vary intraspecifically, we tested if this variation also exists at the individual level and whether it is the result of experience, using two orb-web spider species, *Argiope keyserlingi* and *Larinioides sclopetarius*. The results reveal that experienced web-building spiders constructed more asymmetric webs than conspecifics deprived of any prior building experience over a period of several months. Experienced individuals invested more silk material into the web region below the hub, which covered a larger area. Moreover, web asymmetry was also influenced by previous prey capture experiences, as spiders increased the lower region of the web if it intercepted the most prey over a period of 6 days. Consequently, spiders may be able to use long-term web-building experience as well as short-term prey capture experience to build better traps. In contrast to previous views of spiders, experience can contribute to intraspecific as well as to individual variations in web design.

Key words Web asymmetry · Behaviour · Orb-web · *Argiope keyserlingi* · *Larinioides sclopetarius*

A. M. Heiling (✉)
Institute of Zoology, University of Vienna,
Althanstrasse 14, A-1090 Vienna, Austria
e-mail: astrid.heiling@univie.ac.at,
Tel.: +43-1-313361283, Fax: +43-1-31336778

M. E. Herberstein
Department of Zoology, University of Melbourne,
3052 Parkville, Victoria, Australia

Introduction

Our understanding of web-building behaviour in spiders has undergone several paradigm shifts. Initially, it was assumed that orb-web construction was limited to genetically controlled design patterns and that meaningful variation only existed at the species level (e.g. Savory 1952; Levi 1978). This was followed by the recognition of significant within-species variation and its effect on prey capture ability. For example, webs of different size, inclination and mesh height will capture different types and sizes of prey at different rates (e.g. Uetz et al. 1978; Chacon and Eberhard 1980; Herberstein and Heiling 1998). Recent work aims to interpret individual variation using a decision-making approach. Placing the process of web construction within a mechanical context identified algorithmic rules, which are based on cues such as gravity, leg length or sensory feedback (e.g. Vollrath 1992; Vollrath et al. 1997; Krink and Vollrath 1999). Moreover, specific adaptive predictions based on foraging theory revealed that individual variation may reflect foraging strategies aimed to maximise food intake (e.g. Sherman 1994; Herberstein et al., in press) or to minimise intraspecific competition (Leborgne and Pasquet 1987).

Another paradigm shift may recognise the importance of individual experience and learning on web-building behaviour in spiders. General models of vertebrate foraging assume some form of adaptive learning in response to variable food resources in order to increase the efficiency of food encounter (e.g. Stephens and Krebs 1986; Kacelnik 1997). The more primitive nervous system in invertebrates is thought to limit the capacity to acquire and retain information gained through experience. However, the proximate requirements essential for associative learning are met by many invertebrates (see Dukas 1998 for a summary). Moreover, research into the molecular biology of learning and memory implies that learning is a fundamental neural process and does not necessarily require complex neural features (Bailey et al. 1996). Consequently, various degrees of complexity in learning have been demonstrated in a variety of invertebrates including bees (e.g. Hammer and Menzel 1998), phytophagous insects (e.g. Papaj and Prokopy 1989) or fruit fly larvae (e.g. Dukas 1998). Nevertheless, the role of experience and learning in web-building behaviour of spiders is still neglected in favour of more mechanistic approaches (Vollrath 1992). In fact, it is commonly assumed that web-building spiders lack long-term memory or even 'perception' of habitat quality (Vollrath and Houston 1986) and that experience plays little, if any role in web-building behaviour (Reed et al. 1970, Vollrath and Houston 1986; Vollrath 1992).

The aim of this study was to test the influence of web-building or prey capture experience on the web-building behaviour of two species of orb-web spiders by examining variations in web design. Specifically, we studied the up/down asymmetry of the orb-web, a phenomenon which is particularly common among the Nephilinae (see Japyassú and Ades 1998 for summary) but also in many other araneoid species (Eberhard 1990; Heiling and Herberstein 1998a). The asymmetric orb is characterised by the tendency to place the hub above the centre of the web, resulting in a larger lower web region which also contains more silk compared with the reduced upper region (Stowe 1986). In contrast, perfectly symmetrical webs contain equally sized upper and lower web regions.

The adaptive value of asymmetric webs may be a greater foraging success. Prey is detected earlier and captured more quickly when entangled in the lower web region, because spiders typically sit head down in the hub of the web facing the lower web region (Klärner and Barth 1982; Masters and Moffat 1983; ap Rhisiart and Vollrath 1994; Landolfa and Barth 1996). Consequently, spiders may increase the lower web region because of its greater prey-capture value, but decrease the less successful upper web region.

A number of proximate, largely mechanistic, factors have been suggested to affect web asymmetry. The degree of web asymmetry may be a compromise between prey capture efficiency and structural constraints (Vollrath and Mohren 1985), and an extensive upper web region may be preserved to provide sufficient physical support for the spider in the hub. Similarly, because horizontally orientated orb-webs generally lack asymmetry, gravity may be used as a compass reference for constructing asymmetric webs (Vollrath 1992). Furthermore, spider weight may interfere with spiral placement in the upper web region where a heavy abdomen is lifted over the head, resulting in a reduced upper web region (Herberstein and Heiling, in press).

However, there is evidence to suggest that web asymmetry may be associated with experience accumulated throughout the development of the spider. Juveniles of several species were observed to construct perfectly symmetrical webs, while mature spiders of the same species constructed highly asymmetric webs (Witt and Baum 1960; Heiling and Herberstein 1998a; Japyassú and Ades 1998). Consequently, web asymmetry may be the result of gradual web modifications based on previous web-building experiences. Enlarging only the lower web region may be a more efficient way of increasing the overall web size. Therefore, inexperienced web-builders should construct more symmetrical webs than experienced individuals. Moreover, asymmetry may be the result of gradual changes in web design due to repeated successful prey capture events in the area below the hub where prey is detected and captured more quickly. We may therefore expect spiders to adjust their webs according to the frequency of prey capture events in either web region. Based on these predictions we tested the effect of web-building experience in *Larinioides sclopetarius* and the influence of prey capture experience in *L. sclopetarius* and *Argiope keyserlingi*.

Methods

L. sclopetarius is a common nocturnal orb-web spider, which occurs in clumped dispersion patterns near water and in the vicinity of artificial lights (Burgess and Uetz 1982, Heiling 1999; Heiling and Herberstein 1999). *A. keyserlingi* occurs along the east coast of Australia and is commonly found in urban habitats such as gardens and parks. As abiotic factors such as wind, temperature and relative humidity may influence web design in spiders (Barghusen et al. 1997; Vollrath et al. 1997) both experiments were performed under controlled laboratory conditions.

The web area and the capture thread length of webs were estimated using various formulae which only required a few measurements (Heiling et al. 1998; Herberstein and Tso, in press). Web asymmetry was calculated as follows. First, we divided the web area above the hub by the web area below the hub. However, even if the areas above and below the hub are different, spiders may nevertheless invest similar amounts of silk in both regions by adjusting the spacing between spirals. Therefore, we also calculated asymmetry in terms of silk investment by dividing the capture thread length above the hub by the capture thread length below the hub. Thus an asymmetry value close to 1 indicates that both web regions are similar in size. An asymmetry value approaching zero indicates that the lower web region is much larger than the upper web region. Our measure of web asymmetry reflects a proportion and is thus dimensionless.

Influence of web-building experience on orb-web asymmetry

To test whether web asymmetry in *L. sclopetarius* is influenced by web-building experience, we compared the degree of web asymmetry of spiders which were either experienced or inexperienced web-builders. We collected 30 females in the field and took one cocoon from each individual laid in the laboratory. This ensured a high genetic variability within the sample. However, due to the high mortality rate (>99%), individuals hatched from only ten cocoons survived until adulthood. Cocoons were maintained separately in glass containers (14 cm × 12 cm × 12 cm) and the emerging spiderlings were allocated randomly to two different treatments: experienced and inexperienced groups. Spiders of the inexperienced group were transferred into individual, small cylindrical plastic cups (3 cm diameter × 5 cm height) filled with paper strips. This ensured that the spiders were unable to construct orb-webs, although they were able to pull out silk material, attach it to the paper strips and to move about and forage without a web. Individuals of the experienced group were individually maintained in enclosures (47 cm × 47 cm × 18 cm) where they were able to construct complete orb-webs.

Freshly emerged spiderlings do not build webs for prey capture in nature but live kleptoparasitically on webs of adult females (Heiling and Herberstein 1999). Therefore, spiders of both treatments were provided ad libitum with dead fruit flies (*Drosophila* spp.; mean weight ± SE = 2.65 ± 0.19 mg, $n = 20$) and with water until their third instar. After the third instar (body length approx. 3 mm) they were offered live fruit flies until they reached maturity.

Once the spiders matured, they were maintained in cups for 10 days and fed two dead fruit flies directly into their mouthparts. This procedure helped to reduce the possible influence of short-term foraging experience on web-building behaviour. The spiders were briefly anaesthetised (with CO_2) and weighed to the nearest 0.1 mg. They were placed individually into three-dimensional enclosures (47 cm × 47 cm × 18 cm) and the first five orb-webs constructed by each individual spider were sampled. In the absence of destructive factors such as rain and prey impact, which cause web damage in the field, spiders do not renew their webs regularly (A.M. Heiling, personal observation). Thus, to stimulate daily web construction, we destroyed the webs after feeding two fruit flies into the mouthparts. The lateral support threads of each web were uniformly cut, causing the web to collapse in the middle while still suspended by the frame before being ingested by the spiders.

Influence of prey capture experience on orb-web asymmetry

Juvenile *L. sclopetarius* were collected in the field and transferred into the laboratory where they were maintained in small plastic containers before being used in the experiment. The spiders were provided with water and a diet of live fruit flies *ad libitum* for about 14 days. Juvenile female *A. keyserlingi* were collected in the field and maintained in the laboratory in small plastic cups (13.5 cm × 9 cm × 9 cm) for several weeks. They were provided with water and an ad libitum diet of live blow flies (*Lucilia cuprina*; mean weight ± SE = 0.022 ± 0.004 g, $n = 50$) until they reached maturity.

L. sclopetarius spiders were weighed and transferred into three-dimensional enclosures (47 cm × 47 cm × 18 cm). They were randomly assigned to two different feeding treatments in which each spider received two live fruit flies every day. Spiders of the first treatment were fed in the area above the hub, exactly in the middle of the upper vertical radius. Spiders in the second treatment were fed in the area below the hub, in the middle of the lower vertical radius of the orb-web. The experimental procedures for *A. keyserlingi* were identical. After the spiders had been weighed, they were transferred into three-dimensional enclosures (58.5 cm × 58.5 cm × 15 cm). Spiders in the first treatment were fed one live blow fly every day in the area above the hub, while spiders in the second treatment were fed one blow fly every day in the area below the hub. The first six webs constructed by *L. sclopetarius* and *A. keyserlingi* were measured (see above) and included in the analyses. The webs were destroyed every day after feeding to encourage daily web construction (see above). Only spiders that constructed webs regularly were included in the analyses.

The analyses were performed using SPSS for Windows, Version 6.0 (Norusis 1993) and SYSTAT 5.2 (Wilkinson 1992). Parametric tests were applied on the normally distributed data sets (Kolmogorov-Smirnov Test) with homogeneous variances (Bartlett's test). For both experiments, we used *t*-tests to compare the weights before starting the experiments as well as weight changes during the experiments. For the first experiment, analyses of covariance (ANCOVA) were used to compare web area (median value from five webs) and capture thread length (median value from five webs) of experienced and inexperienced females, using initial weight and weight change as covariates. Similarly, we compared the degree of web asymmetry (median value from five webs) using ANCOVA, with initial weight and weight change as covariates. For the second experiment, we performed repeated measures ANOVA to compare the web area, the capture thread length and the degree of web asymmetry (for web area and capture thread length) between spiders fed above and below the hub for the first six webs.

Table 1 Body weight and web characteristics (*CTL* capture thread length) of web-building experienced and inexperienced adult female *Larinioides sclopetarius*. Asymmetry was calculated by dividing the upper by the lower area and capture thread length, respectively. All data on spider weight are given mean ± SE, data on web parameters are given adjusted mean ± SE

	Experienced spiders ($n = 16$)	Inexperienced spiders ($n = 10$)
Initial weight (mg)	91.25 ± 4.07	80.00 ± 5.38
Weight change (mg)	17.50 ± 3.71	–6.00 ± 5.62
Web area (m^2)	0.027 ± 0.003	0.019 ± 0.004
Web area-asymmetry[a]	0.44 ± 0.023	0.55 ± 0.031
CTL (m)	8.52 ± 0.68	6.61 ± 0.91
CTL-asymmetry[a]	0.26 ± 0.021	0.35 ± 0.028

[a] The asymmetry values are proportions and thus dimensionless

Results

Influence of web-building experience on orb-web asymmetry

There was no significant difference between the initial weight of experienced and inexperienced L. sclopetarius ($t_{19} = 1.72$, $P = 0.102$; Table 1). However, there was a significant difference in the change of weight: body weight of experienced spiders increased during the experimental trial but decreased in inexperienced spiders ($t_{17} = 3.5$, $P = 0.003$; Table 1). Web area did not differ between experienced and inexperienced spiders ($F_{1,25} = 2.36$, $P = 0.138$; Table 1) and was not influenced by weight change ($F_{1,25} = 0.28$, $P = 0.603$), but by initial weight ($F_{1,25} = 4.28$, $P = 0.045$). Similarly, there was no difference in the capture thread length ($F_{1,25} = 1.93$, $P = 0.179$; Table 1) which was influenced by both weight change ($F_{1,25} = 7.96$, $P = 0.01$) and initial weight ($F_{1,25} = 11.86$, $P = 0.002$). The level of web-building experience significantly effected the degree of web asymmetry in *L. sclopetarius*. Experienced spiders constructed more asymmetric webs in terms of web area and capture thread length by enlarging the lower web region (web area: $F_{1,25} = 6.054$, $P = 0.022$; capture thread

Table 2 Initial weight and weight change (mg) during the experiment of adult female *Argiope keyserlingi* and immature female *L. sclopetarius* of two different treatments (fed in the area above or below the hub of their orb-web). All data are given mean ± SE

	Initial weight (mg)		Weight change (mg)	
	Fed above hub	Fed below hub	Fed above hub	Fed below hub
A. keyserlingi ($n = 13$)	257.2 ± 13.8	242.2 ± 14.3	49.6 ± 6.3	55.6 ± 7.2
L. sclopetarius ($n = 23$)	38.2 ± 5.2	32.5 ± 4.1	8.2 ± 2.3	10.0 ± 2.8

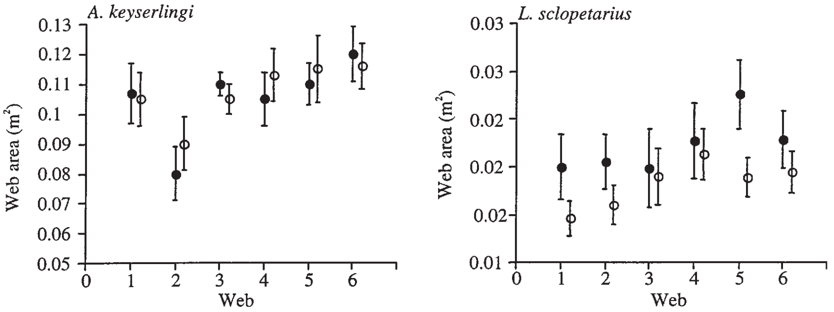

Fig. 1 Changes in mean (± SE) web area over six consecutive webs built by two species of orb-web spiders, adult female *Argiope keyserlingi* (n = 13) and juvenile *Larinioides sclopetarius* (n = 23), which were offered prey in the area below the hub (○) or above the hub (●)

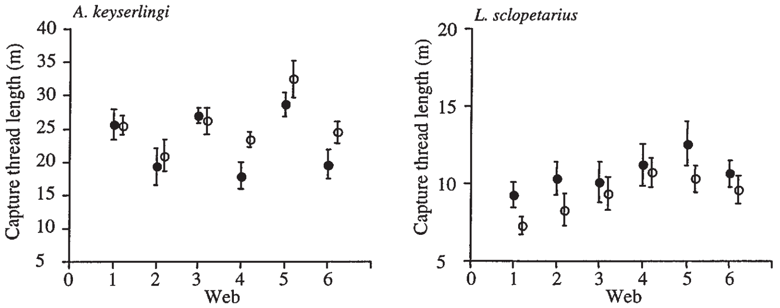

Fig. 2 The mean (± SE) capture thread length of six consecutive webs built by two orb-web spider species. Spiders of both species, adult female *A. keyserlingi* (n = 13) and juvenile *L. sclopetarius* (n = 23), were exclusively fed in the area below the hub (○ or above the hub (●)

Table 3 Results of the repeated measures ANOVA for the effects of web number (1 to 6) and treatment (fed in the upper or in the lower vertical radius of the web) on the web area and capture thread length (*CTL*) in orb-webs of two species, *A. keyserlingi* and *L. sclopetarius*

		SS	*df*	*F*	*P*
A. keyserlingi (n = 13)					
Web area	Web number	0.0849	5	9.48	0.0001
	Treatment	0.00005	1	0.03	0.87
CTL	Web number	1058.4	5	9.47	0.0001
	Treatment	123.8	1	2.39	0.15
L. sclopetarius (n = 23)					
Web area	Web number	0.0004	5	3.24	0.009
	Treatment	0.0004	1	1.4	0.25
CTL	Web number	150.9	5	6.44	< 0.001
	Treatment	68.75	1	1.36	0.256

Table 4 Results of the repeated measures ANOVA for the effects of web number (1 to 6) and treatment (fed in the upper or in the lower vertical radius of the web) on the asymmetry of the web area and the capture thread length (*CTL*) in orb-webs of two species, *A. keyserlingi* and *L. sclopetarius*

		SS	*df*	*F*	*P*
A. keyserlingi (n = 13)					
Web area-asymmetry	Web number	0.27	5	2.73	0.03
	Treatment	0.39	1	6.84	0.02
CTL-asymmetry	Web number	0.1	5	1.45	0.22
	Treatment	0.3	1	5.5	0.04
L. sclopetarius (n = 23)					
Web area-asymmetry	Web number	0.08	5	0.73	0.60
	Treatment	0.23	1	4.14	0.04
CTL-asymmetry	Web number	0.11	5	0.79	0.56
	Treatment	0.31	1	5	0.04

length : $F_{1,25}$ = 3.972, P = 0.049; Table 1). However the degree of asymmetry was not affected by the initial weight of spiders (web area: $F_{1,25}$ = 1.602, P = 0.219; capture thread length: $F_{1,25}$ = 1.15, P = 0.296) or by the change in weight during the experiment (web area: $F_{1,25}$ = 0.654, P = 0.427; capture thread length: $F_{1,25}$ = 3.564, P = 0.072).

Influence of prey capture experience on orb-web asymmetry

The initial body weight in *L. sclopetarius* was not significantly different between spiders fed above or below the hub (t_{20} = –0.86, P = 0.401) and weight change during the experiment was also similar for both treatments (t_{20} = 0.59, P = 0.564; Table 2). Similarly, initial body weight in *A. keyserlingi* did not differ between spiders fed above or below the hub (t_{11} = 0.75, P = 0.468) and weight change was not affected by the feeding treatment (t_{11} = 0.63, P = 0.537; Table 2).

Web area (Fig. 1) and capture thread length (Fig. 2) were not affected by the feeding treatment in *L. sclopetarius* and *A. keyserlingi* (Table 3). However, the size of the web and the amount of sticky silk incorporated into the web showed some variation, generally increasing from the first to the last web (Table 3; Figs. 1, 2). In contrast, web asymmetry in both species was affected by the feeding treatment (Table 4). The spiders constructed more symmetrical webs when they were fed above the hub (Figs. 3, 4). In contrast, when the spiders were fed in the area below the hub, they increased the size and the amount of silk in the lower web region, which resulted in more asymmetric webs (Figs. 3, 4).

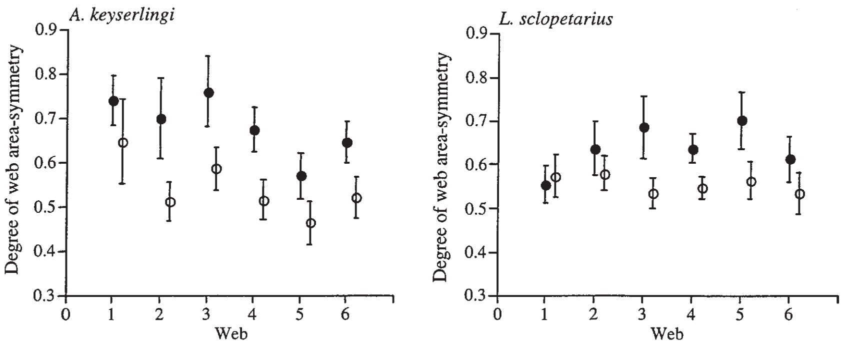

Fig. 3 Degree of web area symmetry (mean ± SE) of six consecutively built webs of adult female *A. keyserlingi* (*n* = 13) and juvenile *L. sclopetarius* (*n* = 23), both species fed in the area below the hub (○) or above the hub (●). The symmetry values are proportions and thus dimensionless

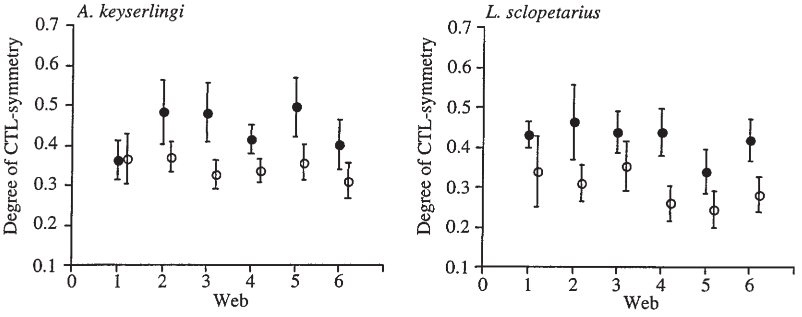

Fig. 4 Degree of capture thread length (CTL) symmetry (mean ± SE) of six consecutive webs built by adult female *A. keyserlingi* (*n* = 13) and juvenile *L. sclopetarius* (*n* = 23) which were offered prey in the area below the hub (○) or above the hub (●). The symmetry values are proportions and thus dimensionless

Discussion

Previous experience of either web construction or prey capture can influence the web-building behaviour of *A. keyserlingi* and *L. sclopetarius* in terms of orb-web asymmetry. Although our experimental procedures rule out any mechanical or physiological influence on the behaviour of spiders, it is not easy to interpret their behavioural variability within current learning concepts.

The influence of prior experience on foraging behaviour has been demonstrated in invertebrates such as marine gastropods (e.g. Hughes and Dunkin 1984a) and ants (e.g. Johnson 1991), where inexperienced individuals were less efficient foragers than more experienced conspecifics. Depriving *L. sclopetarius* of long-term web-building experience resulted in circular webs, which resembled the webs built by inexperienced juvenile spiders (Heiling and Herberstein 1998a). As a consequence, the lack of web-building experience may also have resulted in a reduction in foraging efficiency. Since asymmetric orb-webs, such as those constructed by experienced *L. sclopetarius*, are thought to be more efficient in prey capture (Masters and Moffat 1983, ap Rhisiart and Vollrath 1994); the ability to incorporate experience into web-building suggests that learning can increase foraging efficiency and ultimately the fitness of spiders under natural conditions.

These results are unlikely to be due to differences in any short-term experiences, since spiders of both treatments were kept in small containers for 10 days prior building a web and hand-fed directly into the mouthparts. While our results illustrate that web-building experience gained during ontogeny may greatly influence web design, they do not suggest that spiders require previous experience to be able to construct a complete orb-web. Even when completely deprived of any web-building opportunity, L. sclopetarius spiders were able to construct a complete and functional web. Clearly, web-building behaviour in spiders has a substantial genetic, and thus innate, component.

Using a similar approach, Reed et al. (1970) deprived *Araneus diadematus* of long- and short-term web-building experience. In contrast to our study, they found that prior experience did not influence web-building behaviour. Similarly, the web design did not differ between spiders that were either fed directly into the mouthparts or fed into the web. However, Reed et al. (1970) only looked at the total web area and total silk length, rather than at within-web design variation. Based on these results, they concluded that ‘web-building behaviour does not seem a fruitful ground for investigating plasticity in the spider nervous system’ (Reed et al. 1970).

In contrast to experienced *L. sclopetarius*, inexperienced web-builders lost weight during the experimental procedure. This may be caused by their inability to capture prey entangled in the web, which were consequently not ingested, a phenomenon also observed in inexperienced *A. diadematus* (Reed et al. 1970). Nevertheless the difference in weight gain was unlikely to bias our results, since weight and weight change were controlled for in the statistical analyses.

Predators can learn through prey encounter to become more selective and thus to forage more efficiently (e.g. Hughes and Dunkin 1984b; Palmer 1984). In orb-web spiders, prey encounter can also affect web-building behaviour. In general, spiders that had captured more prey built smaller webs than food-deprived individuals (e.g. Higgins and Buskirk 1992; Sherman 1994; Lubin and Henschel 1996; Herberstein et al., in press), a response which is likely to be based on physiological changes associated with prey ingestion. But even when the level of satiation is kept constant, the spiders can detect subtle differences in rates of prey encounter, suggesting that they are able to use not only physiological information but also other kinds of cues (Herberstein et al., in press).

The response to feeding events in our experiments may initially appear as associative learning (Smith 1993), where the spider responds to the positive food reward following web construction. However, in contrast to classic conditioning, such as a learnt association of certain odours with food quality (Dukas 1998), our system appears to be more complex. The food reward was delivered regardless of whether the spiders constructed asymmetric webs or not. Instead, the spiders seemed to be able to monitor the capture success of each web region and then increased the portion of the web which captured most prey, presumably to increase foraging efficiency. Additionally, the time delay between food reward and behavioural response (web construction) was also substantial. Webs were constructed in the early hours of the morning (*A. keyserlingi*) or evening (*L. sclopetarius*), but the food was not delivered until several hours after web construction.

The level of top/bottom asymmetry was generally higher in *L. sclopetarius* than in *A. keyserlingi*, which may reflect differences in the structural constraints for both species. *A. keyserlingi* rest in the hub of the web throughout the day (M.E. Herberstein, personal observation). In contrast to juvenile *L. sclopetarius*, which show the same type of behaviour as *A. keyserlingi*, adult female *L. sclopetarius* do not reside at the hub during a foraging bout, but often return to the retreat after web completion (Heiling and Herberstein 1998b). As a consequence, the webs of *A. keyserlingi* may structurally require an extensive upper web region to support the weight of the spider for prolonged periods. Orb-webs that do not contain any upper web region, such as in many *Nephila* species, do however contain an extensive barrier web (Robinson and Robinson 1973) which may provide the needed support at the hub.

The process of orb-web construction is very complex, with a multitude of factors influencing the end design. Our results show that the construction of a functional orb-web does not depend on prior experience. However, even strong innate behaviours such as web-building in spiders can be modified by experience. Long-term experience may act to gradually improve web design, where the resulting asymmetric orb-web increases the capture potential beyond that of the symmetrical web. Cognitive and behavioural adaptations are reflected by optimising web design based on the prey capture success rate in different web regions. As the long-term effects on foraging efficiency improve fitness, asymmetry may be selected for. Accordingly, the prey-capture abilities of the orb-web may act as a selective force through the learning capabilities of the spiders and may thus contribute to orb-web evolution.

Acknowledgements We thank Jutta Schneider, Fritz Vollrath and Mark Elgar for helpful discussions, T. Czeschlik and one anonymous referee for critical review and very constructive comments on the paper. We are grateful to K. Thaler for identifying *L. sclopetarius*. Our study was supported by the Austrian Science Foundation (P12686-BIO to A.M.H. and J1500-BIO to M.E.H.) and the Australian Research Council (A19930103). We are also grateful to Grundig Austria GmbH for generously providing a video camera for research purposes.

References

Ap Rhisiart A, Vollrath F (1994) Design features of the orb web of the spider, *Araneus diadematus*. Behav Ecol 5:280–287

Bailey CH, Bartsch D, Kandel ER (1996) Toward a molecular definition of long-term memory storage. Proc Natl Acad Sci USA 93:13445–13452

Barghusen LE, Claussen DL, Anderson MS, Bailer AJ (1997) The effects of temperature on the web-building behaviour of the common house spider, *Achaearanea tepidariorum*. Funct Ecol 11:4–10

Burgess JW, Uetz GW (1982) Social spacing strategies in spiders. In: Witt PN, Rovner JS (eds) Spider communication – mechanisms and ecological significance. Princeton University Press, Princeton, NJ, pp 317–351

Chacon P, Eberhard WG (1980) Factors affecting numbers and kinds of prey caught in artificial spider webs, with consideration of how orb webs trap prey. Bull Br Arachnol Soc 5:29–38

Dukas R (1998) Ecological relevance of associative learning in fruit fly larvae. Behav Ecol Sociobiol 19:195–200

Eberhard WG (1990) Function and phylogeny of spider webs. Annu Rev Ecol Syst 21:341–372

Hammer M, Menzel R (1998) Multiple sites of associative odor learning as revealed by local brain microinjections of octopamine in honeybees. Learn Mem 5:146–156

Heiling AM (1999) Why do nocturnal orb-web spiders (Araneidae) search for light? Behav Ecol Sociobiol 46:43–49

Heiling AM, Herberstein ME (1998a) The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. J Arachnol 26:91–96

Heiling AM, Herberstein ME (1998b) Activity patterns in different developmental stages and sexes of *Larinioides sclopetarius* (Clerck) (Araneae: Araneidae). In: Selden PA (ed) Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997. The Dorset Press, Dorchester, UK, pp 211–214

Heiling AM, Herberstein ME (1999) The importance of being larger: intraspecific competition for prime web sites in orb-web spiders (Araneae, Araneidae). Behaviour 136:669–677

Heiling AM, Herberstein ME, Spitzer G (1998) Calculation of capture thread length in orb webs: evaluation of new formulae. Ann Entomol Soc Am 91:135–138

Herberstein ME, Heiling AM (1998) Does mesh height influence prey length in orb-web spiders (Araneidae)? Eur J Entomol 95:367–371

Herberstein ME, Tso IM (in press) Evaluation of formulae to estimate the capture area and mesh height of orb webs. J Arachnol

Herberstein ME, Heiling AM (1999) Asymmetry in spider orb-webs: a result of physical constraints? Anim Behav

Herberstein ME, Craig CL, Elgar MA (in press) Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). Evol Ecol Res

Higgins LE, Buskirk RE (1992) A trap-building predator exhibits different tactics for different aspects of foraging behaviour. Anim Behav 44:485–499

Hughes RN, Dunkin S de B (1984a) Effects of dietary history on selection of prey, and foraging behaviour among patches of prey, by the dogwhelk, *Nucella lapillus* (L.). J Exp Mar Biol Ecol 79:159–172

Hughes RN, Dunkin S de B (1984b) Behavioural components of prey selection by dogwhelks, *Nucella lapillus* (L.), feeding on mussels, *Mytilus edulis* L., in the laboratory. J Exp Mar Biol Ecol 77:45–68

Japyassú HF, Ades C (1998) From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). Behaviour 135: 931–956

Johnson RA (1991) Learning, memory, and foraging efficiency in two species of desert seed-harvester ants. Ecology 72:1408–1419

Kacelnik A (1997) Associative learning and optimal foraging. Adv Ethol 32:81

Klärner D, Barth FG (1982) Vibratory signals and prey capture in orb-weaving spiders (*Zygiella x-notata*, *Nephila clavipes*; Araneidae). J Comp Physiol 148:445–455

Krink T, Vollrath F (1999) A virtual robot to model the use of regenerated legs in a web-building spider. Anim Behav 57:223–232

Landolfa MA, Barth FG (1996) Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. J Comp Physiol 179:493–508

Leborgne R, Pasquet A (1987) Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). Behav Ecol Sociobiol 20:203–208

Levi HW (1978) Orb-webs and phylogeny of orb-weavers. Zool Soc Lond Symp 42:1–15

Lubin Y, Henschel J (1996) The influence of food supply on foraging behaviour in a desert spider. Oecologia 105:64–73

Masters W, Moffat AJM (1983) A functional explanation of top-bottom asymmetry in vertical orb web. Anim Behav 31:1043–1046

Norusis MJ (1993) SPSS for Windows. SPSS Inc., Chicago

Palmer AR (1984) Prey selection by thaidid gastropods: some observational and experimental field tests on foraging models. Oecologia 62:162–172

Papaj DR, Prokopy RJ (1989) Ecological and evolutionary aspects of learning in phytophagous insects. Annu Rev Entomol 34: 315–350

Reed CF, Witt PN, Scarboro MB, Peakall DB (1970) Experience and the orb web. Dev Psychobiol 3:251–265

Robinson MH, Robinson B (1973) Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. Smith Contr Zool 149:1–76

Savory TH (1952) The spider's web. Warne, London

Sherman PM (1994) The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. Anim Behav 48:19–34

Smith BH (1993) Merging mechanism and adaptation: an ethological approach to learning and generalisation. In: Papaj DR, Lewis AC (eds) Insect learning. Chapman & Hall, London, pp 126–173

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton NJ

Stowe MK (1986) Prey specializations in the Araneidae. In: Shear WA (ed) Spiders-webs, behavior and evolution. Stanford University Press, Stanford, Calif, pp 101–131

Uetz GW, Johnson AD, Schemske DW (1978) Web placement, web structure and prey capture in orb-weaving spiders. Bull Br Arachnol Soc 4:141–148

Vollrath F (1992) Analysis and interpretation of orb spider exploration and web-building behavior. Adv Study Behav 21:147–196

Vollrath F, Houston A (1986) Previous experience and site tenacity in the orb spider *Nephila* (Araneae; Araneidae). Oecologia 70:305–308

Vollrath F, Mohren W (1985) Spiral geometry in the garden spider's orb web. Naturwissenschaften 72:666–667

Vollrath F, Downes M, Krachkov S (1997) Design variability in web geometry of an orb-weaving spider. Physiol Behav 62: 735–743

Wilkinson (1992) SYSTAT: statistics, version 5.2 edn. SYSTAT, Evanston

Witt PN, Baum R (1960) Changes in orb webs of spiders during growth (*Araneus diadematus* Clerck and *Neoscona vertebrata* McCook). Behaviour 16:309–318