

## INTERPRETATIONS OF ORB-WEB VARIABILITY: A REVIEW OF PAST AND CURRENT IDEAS

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### Abstract

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The understanding of web-building behaviour in orb-web spiders has undergone several paradigm shifts. In the past, orb-web construction was assumed to be limited to genetically-controlled design patterns, suggesting that meaningful variation only existed at the species level. Subsequently, it was recognised that variation in web design also exists within species and that this variation was linked to the prey capture ability of webs. Another approach to interpreting individual variation is within a decision-making construct. The web-building decisions of spiders may thus be ruled by algorithms or mechanical constraints. Similarly, individual decisions may reflect foraging strategies aimed to maximise food intake. Our own work suggests that experience in web-building and prey capture may also contribute to individual variation of orb-web design. Using several key publications as well as recently collected data we discuss past and current ideas to interpret orb-web variability.

### Orb-webs from a phylogenetic perspective

Orb-webs are constructed by more than 4200 spider species (LEVI, 1982; PLATNICK, 1997) and evolved over a period of about one hundred million years (SELDEN, 1989). They constitute the prey capture device for the Orbiculariae which include two distinct groups of orb-web spiders. The more ancestral Uloboridae, that along with the Deinopoidae form the superfamily Deinopoidea (OPELL, 1998), typically construct horizontally orientated orb-webs consisting of non-adhesive, cribellate silk. In contrast, the more derived araneoid orb-web spiders (Foelix, 1992) construct mostly vertical webs using ecribellate adhesive silk (e.g. OPELL, 1997; 1998). The vertical orientation of orb-webs has a number of advantageous consequences for prey capture: (1) they intercept more prey (CHACÓN, EBERHARD, 1980), (2) retain prey longer

(EBERHARD, 1989), and (3) can absorb greater forces of prey impact (CRAIG, 1987a) which is facilitated by stronger axial fibres in the capture threads (OPELL, 1997). The selective advantage of adhesive threads may be: (1) greater economy, since they are less costly to produce (VOLLRATH, 1992a; OPELL, 1998), (2) lower visibility to insects (less UV-reflective), which enables araneoids to settle in a greater variety of habitats (CRAIG, BERNARD, 1990; CRAIG et al., 1994), and (3) increased extensibility (flexibility) of the webs (KÖHLER, VOLLRATH, 1995; LIN et al., 1995). These synapomorphic characteristics within the araneoid spiders are considered to be key innovations, which led to a variety of orb designs, a greater radiation and an increase in species diversity (95 % all orb-web spider species) as opposed to the Deinopoidea (CODDINGTON, LEVI, 1991; FOELIX, 1992; BOND, OPELL, 1998).

The regular orb is no longer viewed as the evolutionary peak in orb-web evolution but as a basis. Some species of orb-web spiders construct webs, which deviated from the typical orb design (e.g. the sector webs constructed by *Hyptiotes* sp.). Others have lost the ability to construct webs altogether (e.g. *Celaenia* sp.). In general, the diversification of orb-web design has been attributed to changes in spider size. While both small (e.g. Anapidae, Theridiosomatidae) and large orb-web spiders (Araneidae and Tetragnathidae) construct orbs, only small ones build both planar and three-dimensional webs (CRAIG, 1987b). Therefore, the evolution of alternative web-designs may be the consequence of a general phyletic trend of small body size among the Araneoidea (CRAIG, 1987b).

The origin of the orb design is a topic that is still under active discussion. A monophyletic hypothesis suggests that the orb-web is not a derived character, but a plesiomorphic one which has evolved only once. This assumes that the uloborids and araneoids are close relatives, sharing a common, cribellate ancestor. This idea was first supported by THORELL (1886; cited in SHEAR, 1994), and WIEHLE (1927), who did not believe that such complex web building behaviour could have evolved independently twice. Strong support for a common ancestor is provided through anatomical features that are shared by araneoids and uloborids (CODDINGTON, 1990). A convergent hypothesis suggests the independent evolution of orb-webs in the Araneoidea and the Uloboridae. Accordingly, the orb-web evolved after the loss of the cribellum (e.g. EBERHARD, 1982; 1990). Since the cribellum is a primitive character in the Orbiculariae, it is likely that the ecribellate Araneoidea originated independently, many times, by the loss of the cribellum (SHEAR, 1994). The orb-webs within the Araneoidea may be homologous in structure (LEVI, 1978b) and araneoid species may be monophyletic with the orb as a primitive type of web (CODDINGTON, 1986; CRAIG, 1987b). However, even if all orb-web spider species are derived from one ancestor, some design features may have evolved independently (EBERHARD, 1990).

### **Interspecific variation**

The interspecific variability in orb-web design was recognised at an early stage, and orb-webs of different species were described in great detail (e.g. WIEHLE, 1928). Although the design was often viewed in context with its function, variations were attributed to geneti-

cally-controlled design patterns and often, extreme orb designs, such as ladder webs, attracted the most attention. For example, the ladder webs of the araneids *Scoloderus tuberculifer* (O. P.-CAMBRIDGE) (EBERHARD, 1975) and *Scoloderus cordatus* (TACZANOWSKI) (STOWE, 1978) are inverted with an extension above the hub which contrasts with the ladder web of *Herennia ornatissima* (DOLESCHALL), which is extended downwards (ROBINSON, LUBIN, 1979). These webs are thought to be specialised moth traps (EBERHARD, 1975; STOWE, 1978; FORSTER, FORSTER, 1985). In *Hyptiotes*, the triangle spider, the web consists of three sectors (OPELL, 1982; LUBIN, 1986) and in *Miagrammopes* (OPELL, 1990) only a few sticky threads make up the entire web. The bolas spider, *Mastophora*, reduced the web to a single line with a viscid ball at the end, which the spider twirls around. Male moths are attracted to the twirling ball by a pheromone that mimics attractants produced by female moths (EBERHARD, 1977a; 1980). Another curious deviation from the standard orb design is the reduced orb-web of *Wixia ectypa* (WALCKENAER) (STOWE, 1978), the so-called “asterisk web”.

### Orb-web function

The variety of orb designs has inspired numerous studies into their function. In general, the orb-web functions as a multi-purpose device, supporting the spider, transmitting mechanical impulses, and providing a substrate for it to move on. However, the main function of orb-webs is to trap prey. The traditional idea that orb-webs passively sieve prey from the surrounding air stream is no longer accepted. Instead, orb-webs must serve several functions and changes in orb-web design as well as web site selection will influence prey capture success (e.g. MURAKAMI, 1983). Web site selection may greatly affect the number and kind of prey captured. For instance, the nocturnal orb-web spider species *Larinioides sclopetarius* (CLERCK) constructs webs adjacent to artificial light, which also attracts high numbers of prey (HEILING, 1999). Similarly, feeding in conspecific aggregations may enhance capture success, when prey density is low or prey supply is unpredictable (UETZ, 1988; CRAIG, 1991). Web features which further influence prey capture include: web orientation (EBERHARD, 1989), web tension (CRAIG et al., 1985), silk strength (CRAIG, 1987a), web visibility or attractiveness to prey (e.g. CRAIG, BERNARD, 1990; CRAIG, FREEMAN, 1991) and web design (EBERHARD, 1986).

Web design includes the size of the web and the number and arrangement of radials and spirals. In general, a larger web is likely to encounter more prey (CHACÓN, EBERHARD, 1980). The distance between capture spirals (mesh height) may also be related to prey size and type. Orb-webs with a narrow mesh are thought to target small prey, which would otherwise fly through a larger mesh (MURAKAMI, 1983; SANDOVAL, 1994; HERBERSTEIN, HEILING, 1998; SCHNEIDER, VOLLRATH, 1998). However, a densely-meshed web may also be more visible and consequently more likely to be avoided by flying insects (CRAIG, 1986). The absorption of kinetic energy created by prey impact is facilitated by the mechanical properties of spider silk and the design of the web, which distributes the energy from the point of interception (CRAIG, 1986; GOSLINE et al., 1986). Accordingly, orb-webs with a higher number of

radii in relation to their number of capture thread turns can absorb the kinetic energy of large and fast-flying insects (EBERHARD, 1986; CRAIG, 1987a).

### **Intraspecific variability in orb-webs**

#### *Ontogenetic shifts in web design*

During the ontogeny of a spider, orb-webs generally undergo an increase in material investment, resulting in larger mature webs compared to small immature webs (e.g. WITT et al., 1972; HEILING, HERBERSTEIN, 1998). Various studies have demonstrated that web area gradually increases with the size and weight of a spider (DENNY, 1976; OLIVE, 1980; HIGGINS, BUSKIRK, 1992; WARD, LUBIN, 1992). This allometric growth of the orb during ontogeny does not necessarily include changes in the structural relationships. For example, the web design of *Argiope aurantia* (LUCAS) (WITT et al., 1972) remains stable throughout the development of spiders. In contrast, other species show quite drastic changes in their web building behaviour. *Peucetia viridans* (HENTZ) (KASTON, 1972) construct webs during immature stages only, while *Mastophora dizzydeani* EBERHARD (EBERHARD, 1980) only builds webs after the final moult. Similarly, most uloborid spiders construct different types of orb-web before and after the first moult, as the cribellum is not functioning during their first developmental stage (EBERHARD, 1977b). All these ontogenetic variations are quite abrupt, without intermediary patterns of web design.

More gradual ontogenetic changes in orb-web design are characteristic in a number of araneid species, particularly with regard to the up/down extension of the orb. In general, young immature spiders tend to construct almost symmetric, less derived, orb-webs (EBERHARD, 1990), which also show higher regularity (WITT et al., 1972). Adults construct asymmetric webs with the area above the hub reduced and the lower area enlarged, a phenomenon which is particularly common among the Nephilinae (see JAPYASSÚ, ADES, 1998 for summary) but also in other araneoid species.

#### *Individual variation in orb-web design*

Individual variation in orb-web design was first recognised in the early sixties, when WITT (1963) identified variation in web design in response to environmental prey conditions in the garden spider *Araneus diadematus* CLERCK. When prey conditions were bad, thread production decreased but both web area and mesh height increased when spiders were starved (WITT, 1963). Since then, numerous studies have shown that variation in web-design also exists on the individual level and these variations were attributed to various biotic and abiotic factors. These include: available space (e.g. LEBORGNE, PASQUET, 1987) the presence of conspecifics (GILLESPIE, 1987; HEILING, HERBERSTEIN, 1999a), spider leg length (VOLLRATH, 1987), weather conditions (CANGIALOSI, UETZ, 1987; AMMITZBO, 1988),

presence of previously-spun lines (GILLESPIE, 1987), amount of available silk (EBERHARD, 1989; ZSCHOKKE, 1997), prey size (SANDOVAL, 1994), spider weight (HERBERSTEIN, HEILING, 1999), gravity (VOLLRATH, 1992b), nutrition (HERBERSTEIN et al., 2000), and experience (HEILING, HERBERSTEIN, 1999b).

### **Approaches of interpreting orb-web variability**

#### *Morphological approach*

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. LEVI, 1978a). Similarly, variation at the intraspecific level was formerly attributed to genetically-controlled morphological characteristics. For instance, ontogenetic changes in orb-web design were attributed to morphological changes during spider development. Accordingly, the 'Bauplan' of the web was interpreted as a projection of the animal's morphology (PETERS, 1937). The resulting image of behavioural inflexibility in orb-web spiders and web building spiders in general remained unchallenged for another 30 years.

#### *Mechanistic approach*

The symmetric nature of orb-webs and the regularity in the arrangement of radials and spirals seems to imply that the process of web construction is based on strict physical and mathematical rules. Not surprisingly, one approach to understanding design variability is to place web building behaviour within a mechanistic context to identify algorithmic rules (e.g. VOLLRATH, 1992b; VOLLRATH et al., 1997). Accordingly, the placement of the sticky spirals may be based on leg length, which the spider uses as measuring tool. If leg length is reduced, so is the distance between the capture spirals (VOLLRATH, 1987). In contrast, the construction algorithm for the auxiliary spiral may be based on angles rather than distance (VOLLRATH, 1992b). Moreover, by loading these algorithmic rules into computer models, web building behaviour can be simulated (KRINK, VOLLRATH, 1999).

Web building algorithms may be further modified by incorporating environmental cues, such as gravitational information. As orb-web spiders do not rely on visual cues during web construction, they may use gravity as a compass reference (VOLLRATH, 1992b; ZSCHOKKE, 1993). When *Araneus diadematus* were rotated in a vertical plane during web construction they appeared disoriented and constructed tangled and irregular capture spirals (VOLLRATH, 1992b). Similarly, web asymmetry may also be based on gravitational cues. Vertical orb-webs are often characterised by a top/bottom asymmetry, whereby the lower half of the web is larger than the upper. Orb-webs constructed in the absence of gravity are more symmetric, and the horizontal orb-webs built by uloborids, are also more symmetric (VOLLRATH, 1992b).

The extent of web-asymmetry may further be limited by physical factors such as the body weight of the spider. The position of a spider when it lays the capture spirals below the hub is carapace up or sideways. In contrast, when laying the threads above the hub, the spider has to lift and direct the abdomen with the spinnerets from sideways to above its carapace (VOLLRATH, 1986), which may be energetically more costly and time-consuming for larger or heavier spiders. Thus heavier *Argiope keyserlingi* KARSCH and *Larinioides sclopetarius* also produce more asymmetric webs than lighter individuals (HERBERSTEIN, HEILING, 1999).

### *Optimality approach*

Another approach to understand orb-web variability is to interpret web building behaviour within the theoretical concepts of optimal foraging theory. Spiders benefit by maximising growth and reproductive output whilst minimising time of development and costs associated with foraging (e.g. HODGE, UETZ, 1996). Thus web building behaviour, and specifically web design, can be viewed as a trade-off between the costs and benefits associated with foraging, and individual variation in web design may reflect different trade-offs (HIGGINS, 1995). In one of the earlier studies, SHERMAN (1994) showed that *Larinioides cornutus* (CLERCK) varied its silk investment, and thus web dimensions, with changing energetic gains (from foraging) and energetic expenditures (from egg production). He found that satiated spiders constructed smaller webs containing less silk, presumably redirecting energy to egg production. In contrast, hungry spiders constructed larger webs in order to increase prey interception (see CHACÓN, EBERHARD, 1980) and energy gain, the prerequisite for egg production (SHERMAN, 1994). A similar relationship between foraging success and web design has since been found in other orb-web spiders, including *Argiope keyserlingi* (HERBERSTEIN et al., 2000).

Web asymmetry may also reflect a foraging strategy to optimise prey capture. Spiders are able to detect prey and travel to prey entangled in the lower half of the web more quickly than in the upper one (MASTERS, MOFFAT, 1983; AP RHISIART, VOLLRATH, 1994; LANDOLFA, BARTH, 1996). Thus by increasing the lower and decreasing the upper half of the web, spiders may increase the chance that prey will be intercepted and captured successfully (MASTERS, MOFFAT, 1983; AP RHISIART, VOLLRATH, 1994). Similarly, variation in mesh height may also be interpreted as a specific foraging strategy. By increasing mesh height, spiders may target larger prey, whilst smaller prey may pass between the spirals (SANDOVAL, 1994; SCHNEIDER, VOLLRATH, 1998; HERBERSTEIN, HEILING, 1998).

### *Individual experience*

The role of experience and memory in web building behaviour has largely been neglected in favour for more mechanistic explanations (VOLLRATH, 1992b). In an early approach, to test the influence of prior experience on web-building behaviour, REED et al. (1970) confined *Araneus diadematus* in small tubes where they were unable to construct

a web, and tested the effects of this treatment on web design. The test revealed that inexperienced spiders built smaller webs, which was attributed to restricted silk production. REED et al. (1970) found no indication for an influence of prior experience on orb design and concluded that 'web-building behaviour does not seem a fruitful ground for investigating plasticity in the spider nervous system'. We recently provided evidence for the influence of prior experience on the degree of orb-asymmetry (HEILING, HERBERSTEIN, 1999b). Our experiments revealed that *L. sclopetarius* with web-building experience constructed more asymmetric webs compared to inexperienced conspecifics. Moreover, web asymmetry was also influenced by previous prey capture experiences, as spiders increased the region of the web which intercepted most prey. *L. sclopetarius* and *A. keyserlingi* were able to monitor the success rate of different web regions and altered their web design accordingly (HEILING, HERBERSTEIN, 1999b). Thus, previous experience, in either web building or prey capture, may also affect intraspecific variation in orb-web design.

## Conclusion

The surprisingly high degree of variability in orb-web design, particularly within individuals of the same species, has provided a fruitful ground for numerous investigations into factors that may influence this variability. However, to fully understand the complex nature of orb-web design variability, a combination of several different approaches is clearly necessary.

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## References

- AMMITZBO, A., 1988: Fouragering hos *Araneus quadratus* Clerck hunner. M. Sc. thesis. University of Aarhus.
- AP RHISIART, A., VOLLRATH, F., 1993: Design features of the orb web of the spider, *Araneus diadematus*. *Behav. Ecol.*, 5, p. 280-287.
- BOND, J.E., OPELL, B.D., 1998: Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution*, 52, p. 403-414.
- CANGIALOSI, K.R., UETZ, G.W., 1987: Spacing in colonial spiders: effects of environment and experience. *Ethology*, 76, p. 236-246.
- CHACÓN, P., EBERHARD, W.G., 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, 1, p. 29-38.
- CODDINGTON, J.A., 1986: The monophyletic origin of the orb web. In SHEAR, W.A. (ed.): *Spiders: webs, behavior, and evolution*. Stanford University Press, Stanford, p. 319-363.
- CODDINGTON, J.A., 1990: Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae: Araneomorphae; Orbiculariae). *Acta Zool. Fennica*, 190, p. 75-87.
- CODDINGTON, J.A., LEVI, H.W., 1991: Systematics and evolution of spiders (Araneae). *Ann. Rev. Ecol. Syst.*, 22, p. 565-592.

- CRAIG, C.L., 1986: Orb-web visibility: the influence of insect flight behaviour and visual physiology on the evolution of web designs within the Arachneidea. *Anim. Behav.*, *34*, p. 54-68.
- CRAIG, C.L., 1987a: The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am. Nat.*, *129*, p. 47-68.
- CRAIG, C.L., 1987b: The ecological and evolutionary interdependence between web architecture and web silk spun by orb web weaving spiders. *Biol. J. Linn. Soc.*, *30*, p. 135-162.
- CRAIG, C.L., 1991: Physical constraints on group foraging and social evolution: observations on web-spinning spiders. *Funct. Ecol.*, *5*, p. 649-654.
- CRAIG, C.L., BERNARD, G.D., 1990: Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology*, *71*, p. 616-624.
- CRAIG, C.L., FREEMAN, C.R., 1991: Effects of predator visibility on prey encounter: a case study on aerial web weaving spiders. *Behav. Ecol. Sociobiol.*, *29*, p. 249-254.
- CRAIG, C.L., OKUBO, A., ANDREASEN, V., 1985: Effect of spider orb-web and insect oscillation on prey interception. *J. Theor. Biol.*, *115*, p. 201-211.
- CRAIG, C.L., BERNARD, G.D., CODDINGTON, J.A., 1994: Evolutionary shifts in the spectral properties of spider silks. *Evolution*, *48*, p. 287-296.
- DENNY, M., 1976: The physical properties of spider's silk and their role in the design of orb-webs. *J. Exp. Biol.*, *65*, p. 483-506.
- EBERHARD, W.G., 1975: The inverted ladder orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. Araneae: Araneidae. *J. Nat. Hist.*, *9*, p. 93-106.
- EBERHARD, W.G., 1977a: Aggressive chemical mimicry by a bolas spider. *Science*, *198*, p. 1173-1175.
- EBERHARD, W. G., 1977b: The webs of newly emerged *Uloborus diversus* and of a male *Uloborus* sp. (Araneae: Uloboridae). *J. Arachnol.*, *4*, p. 201-206.
- EBERHARD, W.G., 1980: The natural history and behaviour of the bolas spider *Mastophora dizzydeani* sp. n. (Araneidae). *Psyche*, *87*, p. 143-169.
- EBERHARD, W.G., 1982: Behavioral characters for the higher classification of orb-weaving spiders. *Evolution*, *36*, p. 1067-1095.
- EBERHARD, W.G., 1986: Effects of orb-web geometry on prey interception and retention. In SHEAR, W.A. (ed.): Spiders: webs, behavior, and evolution. Stanford University Press, Stanford, p. 70-100.
- EBERHARD, W.G., 1989: Effects of orb web orientation and spider size on prey retention. *Bull. Br. arachnol. Soc.*, *8*, p. 45-48.
- EBERHARD, W.G., 1990: Function and phylogeny of spider webs. *Ann. Rev. Ecol. Syst.*, *21*, p. 341-372.
- FOELIX, R.F., 1992: *Biologie der Spinnen*. Thieme-Verlag, Stuttgart, 331 pp.
- FORSTER, L.M., FORSTER, R.R., 1985: A derivative of the orb web and its evolutionary significance. *New Zeal. J. Zool.*, *12*, p. 455-465.
- GILLESPIE, R.G., 1987: The role of prey availability in aggregative behaviour of the orb weaving spider *Tetragnatha elongata*. *Anim. Behav.*, *35*, p. 675-681.
- GOSLINE, J.M., DEMONT, M.E., DENNY, M.W., 1986: The structure and properties of spider silk. *Endeavour*, *10*, p. 37-43.
- HEILING, A.M., 1999: Why do nocturnal orb-web spiders (Araneidae) search for light? *Behav. Ecol. Sociobiol.*, *46*, p. 43-49.
- HEILING, A.M., HERBERSTEIN, M.E., 1998: The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. *J. Arachnol.*, *26*, p. 91-96.
- HEILING, A.M., HERBERSTEIN, M.E., 1999a: The importance of being larger: intraspecific competition for prime web sites in orb web spiders (Araneae, Araneidae). *Behaviour*, *136*, p. 624-632.
- HEILING, A.M., HERBERSTEIN, M.E., 1999b: Asymmetry in spider orb-webs: a result of experience? *Anim. Cogn.*, *2*, p. 171-177.
- HERBERSTEIN, M.E., HEILING, A.M., 1998: Mesh height and prey length in orb webs. *Eur. J. Entomol.*, *95*, p. 367-371.
- HERBERSTEIN, M.E., HEILING, A.M., 1999: Asymmetry in spider orb-webs: a result of physical constraints? *Anim. Behav.*, *58*, p. 1241-1246.
- HERBERSTEIN, M.E., CRAIG, C.L., ELGAR, M.A., 2000: Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evol. Ecol. Res.*, *2*, p. 69-80.

- HIGGINS, L., 1995: Direct evidence for trade-offs between foraging and growth in a juvenile spider. *J. Arachnol.*, 23, p. 37-43.
- HIGGINS, L.E., BUSKIRK, R.E., 1992: A trap-building predator exhibits different tactics for different aspects of foraging behaviour. *Anim. Behav.*, 44, p. 485-499.
- HODGE, M.A., UETZ, G.W., 1996: Foraging advantages of mixed-species association between solitary and colonial orb-weaving spiders. *Oecologia*, 107, 4, p. 578-587.
- JAPYASSÚ, H.F., ADES, C., 1998: From complete orb to semi-orb webs: developmental transitions in the web of *Nephilengys cruentata* (Araneae: Tetragnathidae). *Behaviour*, 135, p. 931-956.
- KASTON, B.J., 1972: Web making by young *Peuceitia viridans* (Hentz) (Araneae: Oxyopidae). *Notes of the Arachnologists of the Southwest*, 3, p. 6-7.
- KÖHLER, T., VOLLRATH, F., 1995: Thread biomechanics in the orb-weaving spiders *Araneus diadematus* (Araneae, Araneidae) and *Uloborus walckenaerius* (Araneae, Uloboridae). *J. Exp. Zool.*, 271, p. 1-17.
- KRINK, T., VOLLRATH, F., 1999: A virtual robot to model the use of regenerated legs in a web-building spider. *Anim. Behav.*, 57, p. 223-232.
- LANDOLFA, M.A., BARTH, F.G., 1996: Vibrations in the orb web of the spider *Nephila clavipes*: cues for discrimination and orientation. *J. Comp. Physiol. A*, 179, p. 493-508.
- LEBORGNE, R., PASQUET, A., 1987: Influence of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). *Behav. Ecol. Sociobiol.*, 20, p. 203-208.
- LEVI, H.W., 1978a: Orb-weaving spiders and their webs. *Am. Scient.*, 66, p. 734-742.
- LEVI, H.W., 1978b: Orb-webs and phylogeny of orb-weavers. *Symp. Zool. Soc. Lond.*, 42, p. 1-15.
- LEVI, H.W., 1982: Arthropods. *Synopsis and Classification of Living Organisms*. In PARKER, S.P. (ed.): Vol. 2. McGraw-Hill, New York, p. 71-110.
- LIN, L.H., EDMONDS, D.T., VOLLRATH, F., 1995: Structural engineering of an orb-spider's web. *Nature*, 373, p. 146-148.
- LUBIN, Y.D., 1986: Web building and prey capture in the uloboridae. In SHEAR, W.A. (ed.): *Spiders: webs, behavior, and evolution*. Stanford University Press, Stanford, p. 132-171.
- MASTERS, W., MOFFAT, A.J.M., 1983: A functional explanation of top-bottom asymmetry in vertical orb web. *Anim. Behav.*, 31, p. 1043-1046.
- MURAKAMI, Y., 1983: Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). *Oecologia*, 57, p. 72-77.
- OLIVE, C.W., 1980: Foraging specializations in orb-weaving spiders. *Ecology*, 61, p. 1133-1144.
- OPELL, B.D., 1982: Post-hatching development and web production of *Hyptiotes cavatus* (Hentz) (Araneae: Uloboridae). *J. Arachnol.*, 10, p. 185-191.
- OPELL, B.D., 1990: The material investment and prey capture potential of reduced spider webs. *Behav. Ecol. Sociobiol.*, 26, p. 375-381.
- OPELL, B.D., 1997: A comparison of capture thread and architectural features of deinopoid and araneoid orb-webs. *J. Arachnol.*, 25, p. 295-306.
- OPELL, B.D., 1998: Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. *Funct. Ecol.*, 12, p. 613-624.
- PETERS, H., 1937: Studien am Netz der Kreuzspinne (*Aranea diadema*). 1. Die Grundstruktur des Netzes und Beziehungen zum Bauplan des Spinnkörpers. *Z. Morphol. Ökol. Tiere*, 32, p. 613-649.
- PLATNICK, N.I., 1997: *Advances in Spider Taxonomy 1992-1995*. New York Entomological Society, American Museum of Natural History, New York, pp.976.
- REED, C.F., WITT, P.N., SCARBORO, M.B., PEAKALL, D.B., 1970: Experience and the orb web. *Develop. Psychobiol.*, 3, p. 251-265.
- ROBINSON, M.H., LUBIN, Y.D., 1979: Specialists and generalists: The ecology and behaviour of some web-building spiders from Papua New Guinea. 1. *Herennia ornatissima*, *Argiope ocyaloides* and *Arachnura melanura* (Araneae: Araneidae). *Pacific Insects*, 21, p. 97-132.
- SANDOVAL, C.P., 1994: Plasticity in web design in the spider *Parawixia bistriata*. a response to variable prey type. *Funct. Ecol.*, 8, p. 701-707.
- SCHNEIDER, J.M., VOLLRATH, F., 1998: The effect of prey type on the geometry of the capture web of *Araneus diadematus*. *Naturwissenschaften*, 85, 5, p.: 391-394.
- SELDEN, P.A., 1989: Orb-web weaving spiders in the early Cretaceous. *Nature*, 340, p. 711-713.
- SHEAR, W.A., 1994: Untangling the evolution of the web. *Am. Scient.*, 82, p. 256-266.

- SHERMAN, P.M., 1994: The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.*, *48*, p. 19-34.
- STOWE, M.K., 1978: Observations of two nocturnal orb-weavers that build specialised webs: *Scoloderus cordatus* and *Wixia ectypa* (Araneae: Araneidae). *J. Arachnol.*, *6*, p. 141-146.
- UETZ, G.W., 1988: Group foraging in colonial web-building spiders. *Behav. Ecol. Sociobiol.*, *22*, p. 265-270.
- VOLLRATH, F., 1986: Gravity as an orientation guide during web-construction in the orb spider *Araneus diadematus* (Araneae, Araneidae). *J. Comp. Physiol. A*, *159*, p. 275-280.
- VOLLRATH, F., 1987: Altered geometry of webs in spiders with regenerated legs. *Nature*, *328*, p. 247-248.
- VOLLRATH, F., 1992a: Spider webs and silks. *Scientific American*, *266*, p. 70-76.
- VOLLRATH, F., 1992b: Analysis and interpretation of orb spider exploration and web-building behavior. *Adv. Study Behav.*, *21*, p. 147-197.
- VOLLRATH, F., DOWNES, M., KRACHKOV, S., 1997: Design variability in web geometry of an orb-weaving spider. *Physiol. Behav.*, *62*, p. 735-743.
- WARD, D., LUBIN, Y., 1992: Temporal and spatial segregation of web-building in a community of orb-weaving spiders. *J. Arachnol.*, *20*, p. 73-87.
- WIEHLE, H., 1927: Beiträge zur Kenntnis des Radnetzbaues der Epeiriden, Tetragnathiden und Uloboriden. *Z. Morphol. Ökol. Tiere.*, *8*, p. 486-537.
- WIEHLE, H., 1928: Beiträge zur Biologie der Araneen, insbesondere zur Kenntnis des Radnetzbaues. *Z. Morph. Ökol. Tiere.*, *11*, p. 115-151.
- WITT, P.N., 1963: Environment in relation to behaviour of spiders. *Arch. Envir. Health.*, *7*, p. 4-12.
- WITT, P.N., RAWLINGS, J.O., REED, C.F., 1972: Ontogeny of web-building behaviour in two orb-weaving spiders. *Am. Zool.*, *12*, p. 445-452.
- ZSCHOKKE, S., 1993: The influence of the auxiliary spiral in the capture spiral in *Araneus diadematus* Clerck (Araneidae). *Bull. Br. arachnol. Soc.*, *9*, p. 169-173.
- ZSCHOKKE, S., 1997: Factors influencing the size of the orb web in *Araneus diadematus*. In ŽABKA, M. (ed.): *Proceedings of the 16th European Colloquium of Arachnology, Siedlce, 1996*, p. 329-334.