2019. Journal of Arachnology 47:271–275

SHORT COMMUNICATION

Silk decorations in *Argiope* spiders: Consolidation of pattern variation and specific signal function

André Walter: Department of Biomedicine, Aarhus University, 8000 C Aarhus, Denmark; E-mail: andre.walter@biomed.au.dk

Abstract. Silk decorations in webs of orb-weaving spiders are considered visual signals. However, high pattern variation reduces the plausibility of a single signal function, and accordingly, current literature often presents contradicting explanations. The controversial question is whether specific web decoration shapes also serve specific functions or whether various arrangements can serve a single function. I studied inherent characteristics of the variation of silk decoration shapes in *Argiope bruennichi* (Scopoli, 1772), in the field and under invariant laboratory conditions. The results show, that even within a few days and with a small repertoire of patterns, *A. bruennichi* frequently varies the decoration shape. Field and laboratory data both reveal that this variation follows a predictable pattern, significantly differing from random. Spiders show a preference for two-banded decorations, omitting decorating altogether rather than building one-banded decorations. Since the shape matters to the spiders, this supports the idea of a single signal function in spite of the presence of web decoration pattern variability.

Keywords: Visual signals, web decoration, stabilimentum, pattern variability, orb web spiders

Animal signals convey information through different modalities and are used in a variety of contexts. In the case of honest signaling, the transferred information benefits both sender and receiver, with the signaler thereby expecting the receiver to correctly interpret the signal (Guilford & Dawkins 1991). Without maintaining fidelity of the signal, its reliability may deteriorate, as the receiver will show decreased responsiveness. Hence, animal signals often evolve high specificity (Endler 1992). Apart from that, another way to reinforce receiver responsiveness may be the increase of signal strength to enhance the stimulus (Dawkins 1993). Highly conspicuous signals, however, may be associated with greater production costs and may attract the attention of unwanted receivers (Brandley et al. 2013). Variation of signal quality may be necessary to reduce eavesdropping and to avoid receiver learning, resulting in a delicate trade-off between pattern variability and pattern consistency to preserve at least a minimum level of functional specificity (Dawkins 1993; Craig et al. 2001).

Many signals derive from non-signaling biological traits and may be more variable and less reliable in an early evolutionary stage (Dawkins 1993). Revealing the evolutionary origin and progression of the elaboration of a pre-signal is not a straightforward task, as the signal meaning may change several times during the process (ten Cate & Rowe 2007). For example, the provision of nuptial prey gifts in insects and spiders may have evolved from prey capture behavior; the significance of the signal however, either parental investment or mating effort, is still subject of some debate (Vahed 1998). The situation is aggravated in the case of novel animal signals, which do not even indicate the biological process from which they have originated. Silken web decorations in orb web spiders represent such a case (Walter & Elgar 2012). These extra structures are regarded as novel signals and must be further defined as deceptive, with empirical evidence repeatedly revealing a prey attracting effect (Herberstein 2000; Bruce et al. 2001; Cheng & Tso 2007; Blamires et al. 2008). However, web decorations have also been found to attract the attention of unintended receivers, like predators of the spiders, which use decorations as visual cues to find their prey (Bruce et al. 2001; Seah & Li 2001). Discussions about a potential signaling conflict are complicated by alternative functional explanations like 'predator avoidance' (Schoener & Spiller 1992; Blackledge & Wenzel 2001), 'warning signal' (Eisner & Nowicki 1983; Walter & Elgar 2011), or the idea that web decorations may not represent visual signals at all (Walter & Elgar 2016). Finally, the proposed functions do not need to be mutually exclusive, and web decorations may even be multifunctional (Starks 2002).

One of the main reasons for struggling to decipher the signal function of silk decorations is the high variability of observable shapes and thus a potential signal inaccuracy. Apart from a few other genera, the most thoroughly investigated silk decorating genus is *Argiope* Audouin, 1826 (Araneae: Araneidae), which shows remarkable intra- and interspecific, as well as intra- and interindividual variation of web decoration forms. The variety of types comprises linear, cruciate, circular and irregular arrangements of zigzag-shaped silk bands in the orb webs of the more than 80 species (Bruce 2006; Walter & Elgar 2012). Cheng et al. (2010) suggested that different construction patterns might serve different signal functions, with cruciate shapes representing effective prey attractants and the linear forms protecting spiders against predators (cf. Schoener & Spiller 1992; Blackledge & Wenzel 2001). On the other hand, if serving the same function, different patterns may vary in their effectiveness. For example, while single-band decorations in *Argiope keyserlingi* Karsch, 1878 (Araneae: Araneidae) do not increase the prey capture success, a higher number of silk bands significantly increases the interception rate (Herberstein 2000). A great proportion of the reported variation of web decoration shapes arises from different levels of decoration completeness (Craig et al. 2001; Walter & Elgar 2016). Accordingly, different types of web decorations often simply vary in the number of constructed zigzag-shaped silk bands. If the construction pattern is linked to the effectiveness of the signal, spiders can be expected to prefer building an optimal shape in an invariant environment. Yet also under more fluctuating natural conditions, spiders may show, perhaps less obviously, a preference for particular silk band arrangements.

To satisfy the need of more basic investigations of silk decoration construction, I here studied the individual short-term variation of web decoration shapes of *Argiope bruennichi* (Scopoli, 1772) in the field and compared it with that under controlled laboratory conditions. The sole question of this approach was: do the spiders show a preference for particular silk decoration shapes or is the decoration pattern the result of stochastic effects? Based on the fact that within the genus *Argiope* there are species-specific web decoration shapes and thus a genetically fixed component of the decorating behavior (Herberstein et al. 2000; Bruce & Herberstein 2005), I hypothesize

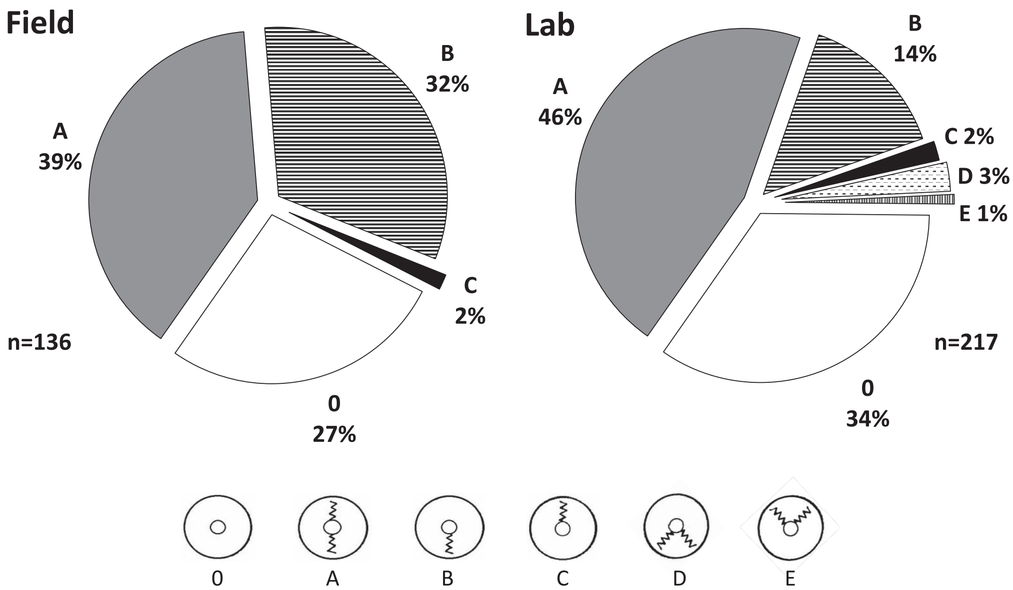

Figure 1.—Web decoration shapes in webs of *A. bruennichi* (I) over a four-day-interval in the field ($n = 136$) and (II) over two weeks in the laboratory ($n = 217$); legend with schematic representation of the basic forms.

that the spiders should follow a stereotype decoration mode, indicating that decorations serve a single function in the web.

I examined the inter- and intraindividual web decorating behavior in an *A. bruennichi* population on a homogeneous oat grass-meadow near the village Brachwitz (011°52′24″E, 51°33′05″N Saxony-Anhalt, Germany) in a dry and sunny week in August. I placed dataloggers for humidity (Spirig HumiPick®, model: HK-100.00) and temperature (Spirig CelsiPick®, model: CK-39/+75C) in a height of 30 cm at the center of the 500 m^2 large study site. I further individually marked 34 adult female spiders (mean body length: 13.39 ± 1.02 mm) on the opisthosoma with long-lasting acrylic paint (Edding Lackmarkers 751). All webs were marked with a flag to ensure the recovery of spiders on subsequent days. I examined the orb-webs daily between 10:30 and 11:00, recorded web attachment height (measured from ground level to web hub center) and estimated the capture area of each web using the formula of Tso (1999). Finally, I recorded the shape of the silken web decorations, if present, of all webs. Voucher specimens of *A. bruennichi* are deposited in the Entomological Collection of the Martin-Luther-University Halle-Wittenberg/Department of Zoology (ID 2568).

In addition to the field examinations, I investigated 22 *A. bruennichi* females in the lab. Spiders were lab raised from their emergence from the egg sac according to Walter et al. (2005). For the observation, the adult spiders were kept in wooden web frames (35 × 35 × 7cm) individually. The conditions were controlled at a temperature of 25 ± 1.4°C, 61 ± 13% RH, and a natural light-dark cycle comparable to that of the field study (15hL/9hD). All spiders were fed with one honeybee (*Apis mellifera*) every other day. I daily measured all relevant web and web decoration parameters in accordance with the field study for two weeks.

Out of the one-week observation period, I analyzed a four-day time window since weather conditions were constant only during this time. No rainfall occurred on any day, and midday temperatures ranged between 34.5°C and 39.2°C. The relative humidity at this time varied between 21.4% RH and 36.9% RH. In the observed population of *A. bruennichi,* 73% of all webs ($n = 136$) contained a web decoration. Three basic decoration shapes were found (Fig. 1). Type A, consisting of two arms, one above and one below the web hub, was recorded for 38.97% ($n = 53$) of all cases. Type B, with only a single arm below the hub, was found in 32.35% ($n = 44$) of all webs. Type C, with only a single arm above the hub, was built only twice (=1.47%). I found no significant correlation between the presence of web decorations and web size, although undecorated webs tended to be larger (480.54 ± 27.2 SE cm^2, $n = 37$) than decorated ones (402.21 ± 20.98 SE cm^2, $n = 99$). This difference was statistically not significant (t-test, $t = -1.79$, $P = 0.08$).

During the two-week laboratory observation, not all the females built new webs every day (discernible by identical web parameters to the previous day), leaving a total of 217 out of 308 possible webs for evaluation. Compared to field conditions, the web decorating frequency was slightly lower in the lab (65%, $n = 217$). I found five different decoration shapes under laboratory conditions. Type A was found in 45.62% ($n = 99$), Type B in 14.29% ($n = 31$) of all webs and Type C was only built four times (= 1.84%). In addition to these types, laboratory reared spiders build decorations of Type D, two arms below the web hub, (2.77%, $n = 6$) and Type E, two arms above the web hub, (0.92, $n = 2$). Similar to the field, approximately a third of all webs (34.65%, $n = 75$) had no web decoration (Type '0′) (Fig. 1). Also, no correlation between the presence of web decorations and web size could be detected under laboratory conditions. Undecorated webs were slightly larger (330.44 ± 9.14 SE cm^2, $n = 75$) than decorated ones (314.57 ± 5.7 SE cm^2, $n = 142$). However, this difference was statistically not significant (t-test, $t = 1.55$, $P = 0.12$).

The shape of web decorations of most individuals varied considerably from day to day, both in the field and under controlled laboratory conditions. In the field, in almost half of all observations (48.04%, $n = 49$) spiders changed the decoration type in newly built webs ($n = 102$ possible alternations). Although decorations were classified into four types only, the individual pattern of decoration construction was highly variable. Only four spiders (11.76%) did not vary the appearance of their web decoration within the four-day observation period. All other spiders ($n = 30$) altered web decoration shapes up to three times in the four-day time window (one change: 41.18%, $n = 14$; two changes: 38.24%, $n = 13$; three changes: 8.82%, $n = 3$). In the lab, all newly built webs were included in the analysis, as conditions were kept constant for the entire two weeks of the observation and did not need to be restricted to the shorter four-day time window of the field study. Here, half of all observations revealed a change of the decoration shape (50.77%, $n = 99$) in newly built webs ($n = 195$ possible alternations). Very similar to the results of the field

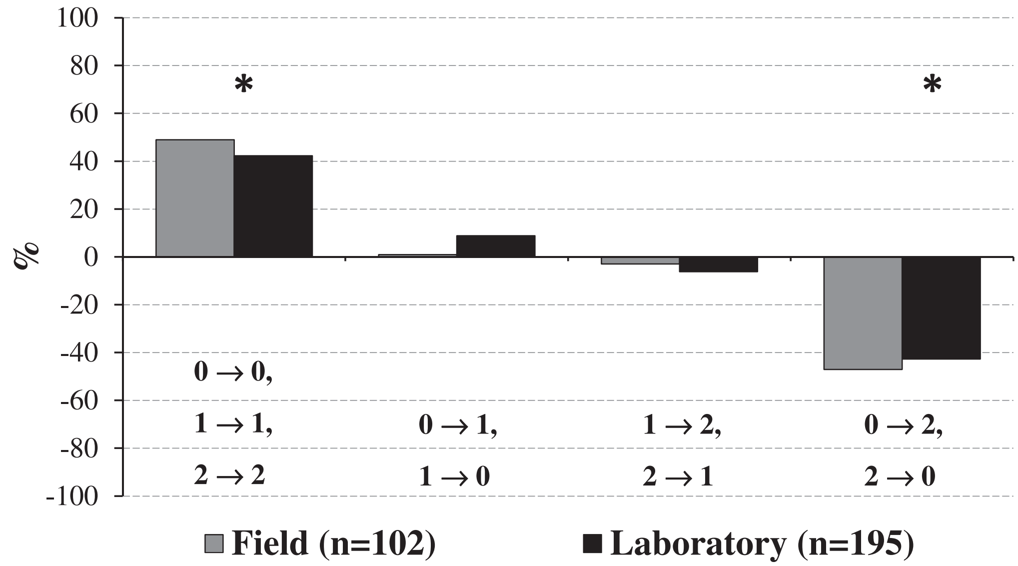

Figure 2.—Frequency of alternation of web decoration shapes of *A. bruennichi* on a web-to-web-basis. Deviation from a random distribution (Zero-line) is displayed. Numbers represent the number of decoration bands.

observations, individual variation of decoration types was high. Within the first four days (for comparison with the field data), only four of the 22 spiders did not vary the silk band arrangement (= 18.18%). Other individuals changed the decoration type on a daily basis up to the maximum of three times (one change: 31.82%, $n = 7$; two changes: 49.91%, $n = 9$; three changes: 9.09%, $n = 2$).

A closer look on the alternation pattern revealed a significant deviation from a random distribution in both the field and the lab data sets. Changes from two bands to no bands and vice versa were significantly less frequent than one would expect by a random distribution. In the same manner, keeping the decoration shape from one web to another (2 to 2 bands and 0 to 0 bands) was significantly more frequent than by chance (Kolomogorov-Smirnov; $P<0.01$, power: 0.72 for field data, power: 0.95 for lab data). However, slighter changes of the decoration type with a margin of one band were not different from random (Fig. 2).

Silken web decorations are considered to represent visual signals (see review in Walter & Elgar 2012). In previous studies on *Argiope* spiders, researchers almost always focused on a particular decoration pattern, thereby implicitly presuming that the shape of this extra silk structure is important for its function, and discounting another collection of papers that highlights the remarkable inter- and intra-individual variation of web decoration patterns (e.g., Edmunds 1986; Nentwig & Heimer 1987; Craig et al. 2001; Cheng et al. 2010; Walter & Elgar 2016). My study on *Argiope bruennichi* aims to offer a consolidation of signal consistency and decoration variability. Although only few decoration types can usually be recorded, it emerges to be rather typical that individual spiders vary the arrangement of their web decoration bands frequently, even within a short observation period of four days. The alternation of the decoration, however, followed a distinct rule on a web-to-web basis, both in the field and under controlled laboratory conditions. The number of silk bands was altered in one-band-steps rather than more distinctly from *none* to complete two-arm decorations and vice versa. In *A. bruennichi*, the one-banded decoration can therefore be regarded as an intermediate form both for increasing the decoration activity as well as for ceasing it. This result further highlights that spiders prefer to build either a complete or no decoration rather than only building parts of it; revealing that the shape indeed is of importance to the spiders, irrespective of what the actual signal function is.

Previous studies identified the problem of web decoration variation for the validity of a single signal function (e.g., Craig et al. 2001). The question is: How can different decoration shapes function in the same adaptive way? Tactical adaptations to local and rapidly changing conditions have been invoked to explain high pattern diversity (Starks 2002), with different decoration shapes serving different signal functions (see also Théry & Casas 2009). If web decorations serve a single signal function, then maybe varying the arrangement of the silk bands is necessary to avoid receiver learning. Ewer (1972) and Eberhard (1973) state that varying decoration patterns might prevent araneophagic predators from associating a particular decoration shape with a food source. In addition, Craig et al. (2001) argue along a similar route, but discuss the avoidance of pattern learning of prey attracted to the web by the decoration signal (see Craig & Bernard 1990; Herberstein 2000; Cheng & Tso 2007). Craig et al. (2001) found that *A. argentata* builds more web decorations when prey abundance is high and conclude that the variance in decoration pattern might prevent prey insects from associating decorations with the risk of being caught. In my field study, the foraging history of *A. bruennichi* and the number of previous predatory attacks towards the spiders was unknown. Thus, I cannot exclude that the intra-individual web decoration variability resulted from those biotic factors. However, under laboratory conditions, the feeding regime was constant and predators were absent, and the very same decoration mode was still observable. Walter & Elgar (2016) also reported a constant decoration variability in *Argiope mascordi* Levi, 1983 under controlled lab conditions. As plausible as the variation of the signal quality appears with respect to the avoidance of receiver learning, it implies that different qualities will also cause variation of the signal's efficacy. If the margin of significant deviation from an "optimal" signal effect is large, the shape of the decoration may be expected to vary rather randomly. However, if selection favors the construction of more effective decoration forms over less effective ones, a pattern preference would emerge, associated with only a limited set of potential alternatives to allow for variation. My results reveal that the latter case holds true for *A. bruennichi*, highlighting that both the variation *and* the shape of web decorations is of significance for their signal function.

The importance of the web decoration shape has been indicated before. For cruciate decorations, an increase of the number of decoration bands increases the prey attracting effect with one-armed decorations being ineffective (cf. Herberstein 2000). Moreover, in *A. mascordi*, Walter & Elgar (2016) found that two and four-banded cruciate decorations are preferred over other patterns. Here, I show that *A. bruennichi* shows a strong preference for (complete) two-banded linear silk decorations and would rather build no decoration than one silk band only. Variation of web decoration completeness also includes the temporary lack of decorations (Hauber 1998). Blackledge (1998) emphasized the metabolic costs of web decorating and that *Argiope* spiders can only invest in web decorations when they are physiologically in good condition. Whatever the signal function might be, a minimum decoration size / minimum number of bands can be expected to be necessary to trigger the response of the receiver. This fact may explain why *A. bruennichi* favors building either a complete or no decoration rather than the one-armed intermediate form that may be ineffective. In the case of web loss, this would mean an unnecessary waste of silk, which could not be recycled then (for silk recycling, see e.g., Craig 2003).

Walter et al. (2008) suggested a direct link between the wrap attack behavior of *Argiope* and its decoration activity via changes in the activity of the aciniform silk glands. Accordingly, high wrap attack frequency is suggested to be associated with high web decorating activity (see also Walter 2018). Based on physiological inertia, the acceleration and deceleration of the gland activity may further explain the gradual change of the decoration shape through a step-wise addition of silk bands rather than by "big leaps". This rationale would not even require the consultation of any visual signal function to explain the occurrence of specific variation patterns. Thus, it would also not disagree with speculations on web decorations not serving as signals at all (see discussion in Walter & Elgar 2016). However, there might be a much larger range of one- and two-band arrangements conceivable than the exclusively vertical alignments observed in *A. bruennichi*.

My conclusions from this study finally highlight the importance of an often-overlooked question in the debate about the signal function of silk decorations, their evolutionary origin. If 'a little' decorating is ineffective, then how has the decoration behavior evolved? The body of evidence reveals a structure with a pattern-independent evolutionary origin that has evolved a pattern-dependent signal function. However, despite more than a hundred years of research, we have stalled with the presentation of significant data on isolated visual effects, but without having a comprehensive explanation of the evolution of the web decorating behavior.

LITERATURE CITED

Blackledge, T.A. 1998. Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). Journal of Zoology (London) 246:21–27.

Blackledge, T.A. & J.W. Wenzel. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. Behaviour 138:155–171.

Blamires, S.J., D.F. Hochuli & M.B. Thompson. 2008. Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web. Biological Journal of the Linnean Society 94:221–229.

Brandley, N.C., D.I. Speiser & S. Johnsen. 2013. Eavesdropping on visual secrets. Evolutionary Ecology 27:1045–1068.

Bruce, M.J. 2006. Silk decorations: controversy and consensus. Journal of Zoology (London) 269:89–97.

Bruce, M.J. & M.E. Herberstein. 2005. Web decoration polymorphism in *Argiope* Audouin, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. Journal of Natural History 39:3833–3844.

Bruce, M.J., M.E. Herberstein & M.A. Elgar. 2001. Signalling conflict between prey and predator attraction. Journal of Evolutionary Ecology 14:786–794.

Cheng, R.-C. & I.-M. Tso. 2007. Signaling by decorating webs: luring prey or deterring predators? Behavioral Ecology 18:1085–1091.

Cheng, R.-C., E.-C. Yang, C.-P. Lin, M.E. Herberstein & I.-M. Tso. 2010. Insect form vision as one potential shaping force of spider web decoration design. Journal of Experimental Biology 213:759–768.

Craig, C.L. 2003. Spider Webs and Silks: Tracing Evolution from Molecules to Genes to Phenotypes. Oxford University Press, New York.

Craig, C.L. & G.D. Bernard. 1990. Insect attraction to ultraviolet reflecting spider webs and web decorations. Ecology 71:616–623.

Craig, C.L., S.G. Wolf, J.L.D. Davis, M.E. Hauber & J.L. Maas. 2001. Signal polymorphism in the web-decorating spider *Argiope argentata* is correlated with reduced survivorship and the presence of stingless bees, its primary prey. Evolution 55:986–993.

Dawkins, M.S. 1993. Are there general principles of signal design? Philosophical Transactions: Biological Sciences 340:251–255.

Eberhard, W.G. 1973. Stabilimenta on the webs of *Uloborus diversus* (Araneae: Uloboridae). Journal of Zoology (London) 171:367–384.

Edmunds, J. 1986. The stabilimenta of *Argiope flavipalpis* and *Argiope trifasciata* in West Africa, with a discussion of the function of stabilimenta. Pp. 61–72. *In* Proceedings of the 9th International Congress of Arachnology 1983, Panama. (W.G. Eberhard, Y.D. Lubin, B.C. Robinson, eds.). Smithsonian Institution Press, Washington, DC.

Eisner, T. & S. Nowicki. 1983. Spider web protection through visual advertisement: role of the stabilimentum. Science 219:185–187.

Endler, J.A. 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139:125–153.

Ewer, R. 1972. The devices in the web of the West African spider *Argiope flavipalpis*. Journal of Natural History 6:159–167.

Guilford, T. & M.S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. Animal Behaviour 42:1–14.

Hauber, M.E. 1998. Web decorations and alternative foraging tactics of the spider *Argiope appensa*. Ethology Ecology and Evolution 10:47–54.

Herberstein, M.E. 2000. Foraging behaviour in orb-web spiders (Araneidae): do web decorations increase prey capture success in *Argiope keyserlingi* Karsch, 1878? Australian Journal of Zoology 48:217–223.

Herberstein, M.E., C.L. Craig, J.A. Coddington & M.A. Elgar. 2000. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. Biological Reviews 75:649–669.

Nentwig, W. & S. Heimer. 1987. Ecological aspects of spider webs. Pp. 211–225. *In* Ecophysiology of Spiders. (W. Nentwig, ed.). Springer-Verlag, Heidelberg.

Schoener, T.W. & D.A. Spiller. 1992. Stabilimenta characteristics of the spider *Argiope argentata* on small islands: support of the predator defense hypothesis. Behavioral Ecology and Sociobiology 31:309–318.

Seah, W.K. & D. Li 2001. Stabilimenta attract unwelcome predators to orb-webs. Proceedings of the Royal Society London B 268:1553–1558.

Starks, P.T. 2002. The adaptive significance of stabilimenta in orb-webs: a hierarchical approach. Annales Zoologici Fennici 39:307–315.

ten Cate, C. & C. Rowe. 2007. Biases in signal evolution: learning makes a difference. Trends in Ecology and Evolution 22:380–387.

Théry, M. & J. Casas. 2009. The multiple disguises of spiders: web colour and decorations, body colour and movement. Philosophical Transactions of the Royal Society of London Series B 364:471–480.

Tso, I.-M. 1999. Behavioral response of *Argiope trifasciata* to recent foraging gain: A manipulative study. American Midland Naturalist 141:238–246.

Vahed, K. 1998. The function of nuptial feeding in insects: a review of empirical studies. Biological Reviews 73:43–78.

Walter, A. 2018. Tracing the evolutionary origin of a visual signal: the coincidence of wrap attack and web decorating behaviours in orb web spiders (Araneidae). Evolutionary Ecology DOI: 10.1007/s10682-018-9930-y.

Walter, A. & M.A. Elgar. 2011. Signals for damage control: web decorations in *Argiope keyserlingi* (Araneae, Araneidae). Behavioral Ecology and Sociobiology 65:1909–1915.

Walter, A. & M.A. Elgar. 2012. The evolution of novel animal signals: silk decorations as a model system. Biological Reviews 87:686–700.

Walter, A. & M.A. Elgar. 2016. Signal polymorphism under a constant environment: the odd cross in a web decorating spider. The Science of Nature 103:93.

Walter, A., P. Bliss & R.F.A. Moritz. 2005. The wasp spider *Argiope bruennichi* (Arachnida, Araneidae): Ballooning is not an obligate life history phase. Journal of Arachnology 33:516–522.

Walter, A., M.A. Elgar, P. Bliss & R.F.A. Moritz. 2008. 'Wrap attack' activates web decorating behavior in *Argiope* spiders. Behavioral Ecology 19:799–804.

Manuscript received 22 February 2018, revised 18 January 2019.