

The aggregating behaviour of *Argiope radon*, with special reference to web decorations

Dinesh Rao · Malcolm Webster · Astrid M. Heiling ·
Matthew J. Bruce · Marie E. Herberstein

Received: 22 June 2007 / Accepted: 11 December 2007
© Japan Ethological Society and Springer 2008

Abstract The existence of aggregations in taxa that are normally solitary poses questions regarding the costs and benefits of group living. Most orb-web spiders are solitary and are aggressive to conspecifics, but a few species aggregate in large numbers. These spiders benefit by enhancing the prey interception potential, but also suffer costs of increased predation and parasitism. In this study, we report on the natural history characteristics of the orb-web spider, *Argiope radon*, which not only lives in aggregations but also builds silk decorations. Our results show that *A. radon* aggregates facultatively and that the main benefit of aggregation that we could identify is enhanced mating potential. We also show that decorations built by *A. radon* are highly visible to both model prey and predator, and suggest that solitary individuals with longer and more frequent decorations may offset the foraging advantage of being in aggregations.

Keywords *Argiope radon* · Web decorations · Stabilimenta · Aggregations · Reflectance · Araneidae

Introduction

The existence of aggregations in taxa that are normally solitary poses questions regarding the costs and benefits of

group living. The majority of spiders are solitary organisms that demonstrate aggression towards conspecifics. However, approximately 60 of the 38,000 known species of spiders (Platnick 2007) can be considered as group-living spiders (sensu Whitehouse and Lubin 2005). All spiders can be considered as belonging to a continuum that ranges from solitary, facultatively aggregating, colonial, subsocial, to social spiders. In solitary spiders, territories are guarded aggressively and there is no cooperation between conspecifics (e.g. St. Andrew's cross spider; *Argiope keyserlingi*, pers. obs., Rao D). Facultatively aggregating spiders are known to share anchor strands but each spider builds its own web and breeds independently (e.g. *Nephila pilipes*, Whitehouse and Lubin 2005). Colonial spiders (e.g. *Cyrtophora citricola*, Whitehouse and Lubin 2005) also share web strands, and breed independently, but these aggregations are mostly obligate. The indirect benefit of living in groups is enhanced prey capture by means of the "ricochet effect", wherein a prey that manages to untangle itself from one web runs the risk of falling into another web (Uetz 1989). In subsocial spiders, there is a period of extended maternal care, which results in a group consisting of a mother and her offspring (e.g. *Stegodyphus lineatus*, Whitehouse and Lubin 2005). However, juveniles disperse on reaching maturity. In social spiders, there is cooperative brood care and foraging, and spiders do not have independent webs (e.g. *Anelosimus eximus*, Whitehouse and Lubin 2005).

The benefits of aggregating may include protection from predators, enhanced prey capture, and exploitation of resources not available to single individuals (most notably by spanning trees high in the vegetation; sensu Lubin 1974). Costs of aggregation may include an increased amount of parasitism and kleptoparasitic load (Lloyd and Elgar 1997). Furthermore, shadow competition, where

D. Rao (✉) · M. Webster · A. M. Heiling · M. E. Herberstein
Department of Biological Sciences, Macquarie University,
North Ryde, Sydney, NSW 2109, Australia
e-mail: dinrao@gmail.com

M. J. Bruce
Behavioural Biology and Helmholtz Institute,
Utrecht University, P.O. Box 80086, 3508 TB Utrecht,
The Netherlands

sedentary foragers that are closer to a food source restrict the access of those further away to the food source, may also be a cost. This may be particularly relevant when there is an overlapping of orb-webs and thus a potential prey item is “blocked” from reaching an individual’s web by the web of another individual (Lubin et al. 2001). Most studies of aggregating spiders have focused on the enhanced foraging success as a direct benefit of being in aggregations (Uetz 1989). A further advantage to being in aggregations is with respect to mate searching. Since males mate more than once in this genus (Gaskett et al. 2004; Herberstein et al. 2005a), there is an advantage to males if females are clustered together. In *Argiope aurantia*, there is a decrease in male body condition during the searching phase (Foellmer and Fairbairn 2005), and this cost could be reduced if females aggregate.

Spiders employ a number of different strategies to enhance their foraging success. Since they are primarily sit-and-wait predators, any innovation to the orb-web that optimises prey capture efficiency is beneficial. Some of the common strategies used include dynamic and static distortions of the web-plane, building retreats to minimise visibility and adding web decorations (Craig 2003). Web decorations may be composed from either silk or debris. Despite the long-standing debate concerning the function of these decorations, studies have shown that silk and debris decorations may function by actively attracting and thereby deceiving prey. In the case of silk decorations, the UV reflectance of the decorations may mimic the ultraviolet (UV) signatures of flowers (Herberstein et al. 2000a; Bruce et al. 2005) while debris decorations may achieve the same ends by presenting food supplies to potential prey (Bjorkman-Chiswell et al. 2004).

In this study, we report on the aggregating and decorating behaviour of *Argiope radon* (Levi 1983). *A. radon* is an orb-web spider that is mainly distributed in the Northern Territory and Queensland states of Australia. It was first described by Levi (1983), and the only known study of this species has been with regard to its courting and mating behaviour (Robinson and Robinson 1980). *A. radon* differs from most other *Argiope* species in that it is commonly found in aggregations lining river-banks and sometimes spanning streams (Robinson and Robinson 1980). *Argiope argentata* is another example of an aggregating *Argiope* (Craig 1991). However, like other *Argiope* species, *A. radon* also builds silk decorations. These decorations are frequently diagonal, stretching down from the top left hand side of the web to the bottom right hand side (Fig. 1). On rare occasions, the decorations may pass over the hub in a continuous line.

In this study, we investigate the interaction between decorating and aggregating behaviour. We ask whether aggregations and silk decorations are obligatory or facultative in this species and investigate their effects on prey



Fig. 1 Photograph of an adult female *Argiope radon* with decorations (a)

capture and mating behaviour. We also report on the visibility of the silk decorations from the point of view of their model prey (honeybee) and predators (blue tit). We used blue tits as model predators for three reasons: the visual system of the blue tits is well understood (Hart et al. 2000), blue tits are known to consume spiders, with spiders comprising close to 20% of their diet in one study (Church et al. 1998) and blue tits are known to use UV-specific cues for prey selection (Blondel et al. 1991).

Methods

The study site was located on the banks of the Katherine River in the Northern Territory, Australia. The habitat consists of sandy banks with trees and shrubs such as *Pandanus* sp., scribbly gums (*Eucalyptus rossi*), reeds (*Phragmites* sp.) and Noogoora burr (*Xanthium occidentale*). Populations of *A. radon* were located in the banks of the river, often building their webs in vegetation overhanging the water. We performed two sets of observations for three weeks in August 2005.

Natural history

We carried out a survey of subadult and adult female spiders ($n = 103$) and recorded abiotic variables such as

substrate (i.e. whether the webs were attached to the bank, reeds or trees), location of the spider, compass orientation of the spider, maximum and minimum daily air temperature and relative humidity. We also recorded biotic variables such as the size of the spider (total body length = length of abdomen + cephalothorax), size of the web (vertical and horizontal diameters of the web), presence or absence of decorations and their lengths, height of the hub of the web above water, presence of associated males and number of kleptoparasites (*Agyrodes antipodiana*). We also noted whether the individual was in an aggregation or was solitary. Here, we define an aggregation as those groups of spiders with three or more individuals that share anchor lines or connect their webs together. Solitary spiders are those individuals that do not connect their web to any other individuals and are usually a few metres apart from other spiders. We calculated web area based on the ellipse formula (Herberstein and Tso 2000) as $(\frac{1}{2} \times \text{vertical diameter} \times \text{horizontal diameter} \times \pi)$. Mesh height was calculated as the $[(\text{distance between the first and the last sticky spirals in the lower half of the web}) / (\text{the number of spirals in the lower web half} - 1)]$.

Mating behaviour

A separate survey was conducted during the duration of the study and we recorded instances of mating behaviour. *A. radon* males ($n = 27$) that were found co-habiting female webs or engaged in mating were recorded. In addition, we recorded the location of the female (i.e. whether in aggregation or solitary), and the precise location within the aggregation, i.e. whether in the inner or outer part of the aggregation. Here, we define inner spiders as those that are surrounded on all sides by other spiders, and outer as those spiders that are on the edge of an aggregation. We also recorded the presence or absence of decorations. Since female spiders give out a sex pheromone (Gaskett 2007), we hypothesized that (1) more males would be found in aggregations where the pheromone signal would presumably be stronger, (2) more males would be found in outer female webs since these webs would be easier to access, and (3) males would prefer webs with decorations, since it has been shown in other species that decorations can be an indicator of satiation (Blackledge 1998; Herberstein et al. 2000b; Herberstein and Fleisch 2003), which implies better body condition and consequently higher fecundity.

Prey capture monitoring

We monitored a subset of marked spiders ($n = 30$) daily for three weeks and recorded body size, web size,

decoration presence and decoration lengths. Prey capture was estimated by observing each test spider every hour from 0900 to 1500 hours. Monitoring prey capture consisted of noting the presence of any prey greater than 5 mm in the web (spiders generally ignored prey smaller than 5 mm; pers. obs.). Of these, small prey were consumed by the spider before the subsequent observation, and the locations of large prey were noted in order to avoid double counting.

Silk decorations and satiation levels

In an experiment conducted in semi-natural field cages at Macquarie University, we recorded the influence of satiation levels on web decoration length as well as the propensity to form aggregations. We weighed 20 spiders and individually labelled them with bee-tags (manufactured by Cislovane Znacky[®]), and then released them into two enclosures with different feeding regimes (of houseflies, *Musca domestica*), namely (1) fed ad libitum and (2) with no food supply. After four nights, webs were removed and the spiders were allowed to build new webs. Although we did not directly record how often *A. radon* rebuilds its webs, we surmise that since the webs are large and fairly sturdy, they do not rebuild on a daily basis. The decoration lengths of the spiders were measured and we recorded whether they built webs in aggregations or were solitary.

Decoration visibility to potential prey and predators

To determine whether the decorations were cryptic or visible to representatives of *A. radon*'s potential prey (honeybees) and predators (blue tits), we measured the spectral reflectance of decorations as well as that of the dorsal side of the spider abdomen. The spectral reflectance (300–700 nm) was measured using a USB 2000 spectrometer with a PX-2-pulsed xenon light source attached to a PC running OODBase32 software (Ocean Optics, Dunedin, FL, USA). The integration time was set to 7 ms, with each measurement taken at an angle of 45° and averaged ten times by the software. Nine individuals and the silk decorations of eight separate individuals were measured six times each. We calculated median values for the average proportion of light reflected at each 5 nm interval. Based on these values, we calculated the relative receptor excitation values (E), giving the maximum potential excitation for each photoreceptor type involved in honeybee vision (UV, blue and green; Dyer and Chittka 2004) and blue tit vision (UV, blue, green and red; Hart et al. 2000). The illumination spectrum used was the standard daylight irradiance spectrum D65 and the

background spectrum was that of a typical green leaf (see Chittka and Kevan 2005 for methods). Based on the E-values, we calculated the chromatic contrast (colour contrast) and the achromatic contrast (brightness) between spider abdomens and silk decorations from the view of honeybees and blue tits.

All data were tested for normality, and nonparametric tests were used on data that were not normally distributed. The software programs SPSS v.11 and GraphPad Prism were used for the analyses. All values mentioned in the results are mean \pm SE.

Results

Natural history

Argiope radon spiders were more likely to be found in aggregations than as solitary individuals (125 out of 161 spiders; binomial probability test, $p < 0.001$). Spiders built webs that were attached to trees, reeds and the bank of the river. However, there was no difference in the frequency of spiders that built webs on different substrates between the aggregating spiders and the solitary spiders (substrates: river bank, reeds or trees; $\chi^2 = 0.629$, $p = 0.73$). More spiders oriented their orb-webs in the southeast–northwest plane (63 out of 86, binomial probability test: $p < 0.001$). There were no differences between the aggregating spiders and solitary spiders for any of the variables associated with the spider, such as body length, web height, web area and mesh height (Table 1).

Decoration building is not an obligate trait in *A. radon*, and there was substantial variation in the number of spiders that built decorations and in the patterns of decorations (Fig. 2). We observed five main patterns: no decorations, two-arm diagonal, two-arm bottom, three-arm, four-arm and single-arm. Of the decorating spiders, the three-arm pattern was the least common pattern observed, whereas the diagonal two-arm pattern was the most common

(Fig. 2). Spiders in aggregations were less likely to build decorations. Of the 36 solitary spiders, 28 built decorations, and of the 125 aggregating spiders, 69 built decorations ($\chi^2 = 5.04$, $p = 0.025$). Decorations of aggregating spiders were also significantly shorter than the decorations of solitary spiders (aggregating: 79.2 ± 8.5 mm; solitary: 89.8 ± 7.3 mm; unpaired t test, $t = -3.66$, $df = 97$, $p < 0.001$). The lengths of decorations were influenced by abiotic measures such as minimum and maximum temperature and humidity (multiple regression: $F_{(3,100)} = 3.83$, $R^2 = 0.15$, $p = 0.0138$); however, the R^2 value explains very little (about 15%) of the variation, with minimum temperature being the only significant parameter ($F = 9.16$, $p = 0.0036$). There was no significant difference in kleptoparasitic load between aggregating spiders and solitary spiders. However, there were a greater proportion of males per female spider in aggregations as opposed to solitary spiders ($\Phi = -0.49$, $p < 0.001$, Table 1).

Mating behaviour

More males were found on female webs that were part of aggregations than on webs of solitary females (Table 1). The exact location of the female spider within a particular aggregation did not play a significant role in male choice (Inner -13 , Outer -9 ; Kolmogorov–Smirnov one sample test, $D_{\max} = 0.34$, $p = 0.98$). However, more males preferred females with decorations than those without decorations (23 out of 27; binomial probability test; $p < 0.001$).

Prey monitoring and decorations

From the field monitoring data, we determined that spiders in aggregations show more variability in building decorations than solitary spiders. The proportion of spiders

Table 1 Comparison between aggregating and solitary spiders for various parameters

| Variable | Aggregation (mean \pm SD) | Solitary (mean \pm SD) | Test | p |
|--------------------------------|-----------------------------|--------------------------|--------------------------|--------|
| Prey per individual | 0.47 \pm 0.37 | 0.44 \pm 0.44 | $t_{38} = 0.2274$ | 0.82 |
| Total body length (mm) | 18.9 \pm 3.1 | 19.0 \pm 3.6 | $F_{(1,100)} = 0.023$ | 0.88 |
| Web height (cm) | 83.3 \pm 21.5 | 81.3 \pm 30.7 | $F_{(1,100)} = 0.142$ | 0.707 |
| Web area (cm ²) | 1117 \pm 470.34 | 1220 \pm 549.36 | $F_{(1,100)} = 0.970$ | 0.327 |
| ln mesh height (mm) | -0.89 ± 0.31 | -0.76 ± 0.43 | $F_{(1,100)} = 2.838$ | 0.095 |
| Kleptoparasites per female web | 2.95 \pm 1.67 | 3.11 \pm 2.84 | $t_{58} = 0.255$ | 0.799 |
| Substrate | NA | NA | $\chi^2 = 0.629$ | 0.73 |
| Length of decoration (mm) | 46.5 \pm 56.3 | 69.6 \pm 51.4 | $F_{(1,100)} = 4.080$ | 0.046 |
| Males per female web | 0.18 \pm 0.34 | 0.02 \pm 0.17 | $\Phi_{(24,36)} = -0.49$ | <0.001 |

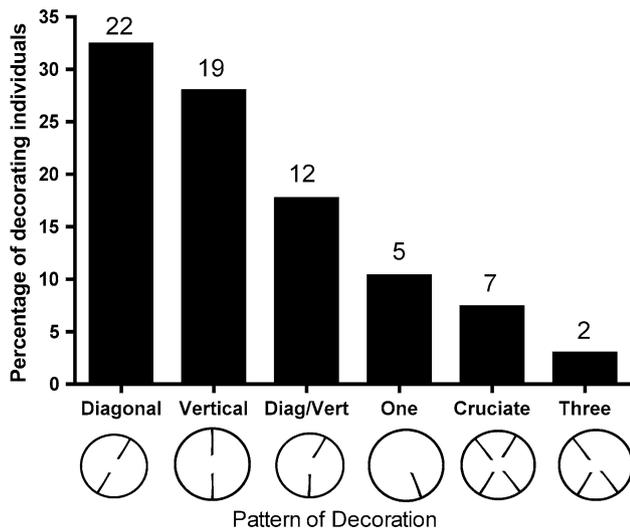


Fig. 2 Variation in the decoration patterns of *Argiope radon*. Numbers on the bars represent number of individuals sampled. The category “Diag/Vert” represents those spiders that had two arm decorations with one arm being diagonal and the other vertical with respect to the web

building decorations over a seven-day period was greater in solitary spiders (mean \pm SE = 0.77 ± 0.04) than in aggregating spiders (mean \pm SE = 0.65 ± 0.04 ; paired t test: $t = 3.78$, $df = 6$, $p = 0.009$). There was no difference in the number of prey caught by solitary or aggregating spiders over a ten-day period (unpaired t test: $t = 0.23$, $df = 38$, $p = 0.82$, Table 1).

Decorations and satiation levels

There was a significant increase in the weights of the spiders after feeding (unfed: mean \pm SE = 0.4 ± 0.1 g; fed: mean \pm SE = 0.6 ± 0.2 g; paired t test $t = 9.3$, $df = 17$, $p < 0.001$). In the experiment conducted in field cages, fed spiders built longer decorations than unfed spiders (unfed: 59.0 ± 48.0 mm; fed = 119.8 ± 64.6 mm; paired t test $t = 4.45$, $df = 11$, $p = 0.001$). However, there was no significant difference in the propensity to form aggregations based on satiation levels (unfed: 9 of total 14; fed: 8 of total 16; $\chi^2 = 0.18$, $p = 0.67$).

Decoration visibility

Silk decorations reflected relatively more light than spider abdomens, both in the UV and in the blue wavelengths (Fig. 3). From the point of view of honeybees, receptor excitation values for silk decorations were significantly higher than for spiders in the UV, blue and green wavelengths (Table 2). The differences in visual appearance

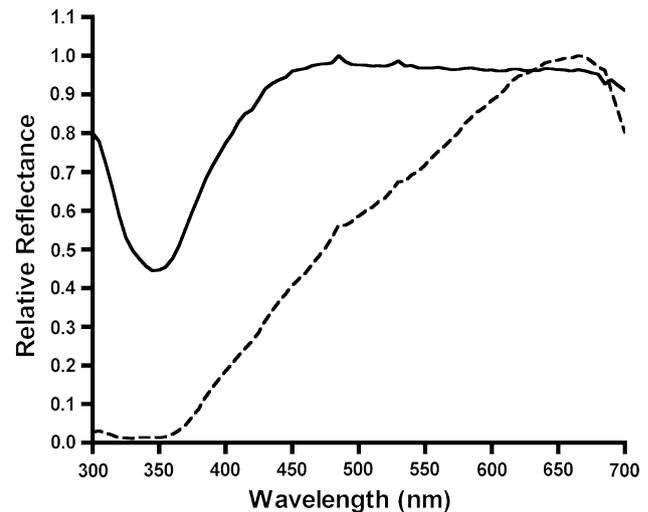


Fig. 3 Relative reflectance of the abdomens of adult female *Argiope radon* (dotted curve, $n = 14$) and web decorations (solid curve, $n = 14$). There was a significant difference between the relative reflectances of the abdomens and those of the decorations

between spider abdomens and silk decorations are indicated by a pronounced chromatic contrast (0.312 ± 0.028 , $n = 14$) and achromatic contrast (0.111 ± 0.024 , $n = 14$). Both chromatic contrast and achromatic contrast are well above the detection threshold of honeybees (0.01; Dyer and Chittka 2004). From the point of view of blue tits, receptor excitation values for silk decorations were significantly higher than for spiders (Table 3). Spiders created a pronounced chromatic contrast against the silk decorations (0.357 ± 0.035 , $n = 14$). Achromatic (double cone) contrast is lower (0.0903 ± 0.0171 , $n = 14$), but well above the detection threshold of birds (0.06; Théry et al. 2005).

Discussion

Our survey of the study area showed that *A. radon* spiders are more likely to be found in aggregations than in the solitary state; however, aggregating is not obligate. The habitat of *A. radon* is limited in terms of potential website location: most spiders prefer to build over the water and in the vegetation overhanging the water. Very few spiders were found away from the river bank. We observed other populations of *A. radon* in a nearby stream where the aggregations spanned the stream, as described by Robinson and Robinson (1980).

In *Austeracantha minax* (Previously *Gasteracantha minax*, Platnick 2007), an orb-web spider known to live in aggregations, the main factor influencing the formation of aggregations was to facilitate the location of females by males (Lloyd and Elgar 1997). In our study, the number of males per spider was higher in aggregations than in solitary

Table 2 Receptor excitation values from the point of view of honeybees

| Receptor excitation values for honeybees ($n = 14$) | Decorations (mean \pm SE) | Spiders (mean \pm SE) | t | p |
|---|-----------------------------|-------------------------|---------|--------|
| UV | 0.81 \pm 0.025 | 0.351 \pm 0.037 | -11.454 | <0.001 |
| Blue | 0.832 \pm 0.018 | 0.62 \pm 0.02 | -9.183 | <0.001 |
| Green | 0.761 \pm 0.025 | 0.651 \pm 0.016 | -4.627 | <0.001 |

Table 3 Receptor excitation values from the point of view of birds

| Receptor excitation values for birds ($n = 14$) | Decorations (mean \pm SE) | Spiders (mean \pm SE) | t | p |
|---|-----------------------------|-------------------------|--------|--------|
| UV | 0.822 \pm 0.023 | 0.384 \pm 0.041 | -10.02 | <0.001 |
| Blue | 0.827 \pm 0.019 | 0.65 \pm 0.019 | -8.19 | <0.001 |
| Double cone | 0.751 \pm 0.026 | 0.685 \pm 0.014 | -2.68 | 0.019 |

spiders. Furthermore, the number of potential matings was higher in aggregations than in solitary spiders. Female *Argiope* spiders produce pheromones that attract the males (Gaskett et al. 2004; Gaskett 2007), and perhaps the combination of several adult female spiders in a relatively compact space produces a stronger and more reliable signal, thus attracting more males than a solitary female. Since male *Argiope* mate more than once (Robinson and Robinson 1980; Gaskett et al. 2004; Herberstein et al. 2005b), males may also benefit from approaching aggregations by having another potential mate in close proximity.

There were few differences between aggregating spiders and solitary spiders with respect to a variety of variables (Table 1). Our study showed that fewer spiders built decorations while present in aggregations when compared to solitary spiders. Our initial hypothesis was that since both aggregative behaviour as well as decoration building are related to prey capture, a spider that is in an aggregation may reduce decorating behaviour. This hypothesis is partially supported by our field data, where we found that fewer spiders build decorations in aggregations. However, this result does not translate into prey capture differences, since we found that prey capture rates over ten days are similar between solitary and aggregating spiders (Table 1). Furthermore, in the field cage experiment, we did not establish a link between the state of satiation and the propensity of the spider to be either solitary or in an aggregation. However, this experiment only consists of a single trial, and further experiments performed under more controlled conditions may be necessary to obtain conclusive data. The field cage experiment clearly shows that there is a direct link between satiation and the length of the decorations. The positive relation between satiation and

decorations, where we assume that satiated spiders are in better body condition, explains the result where we found more instances of potential mating in spider webs with decorations than those webs without decorations. If there is a link between decorations and male attraction, we presume it would be either (1) pheromone based, since *Argiope* males are very sensitive to the quality of the pheromone (Gaskett et al. 2004), but there is no evidence linking decorations per se to pheromones, or (2) vision based, since it has been shown that *Argiope* eyes are sensitive to UV light (Yamashita and Tateda 1978). However, we also note that a male attraction hypothesis for silk decorations must also account for the fact that juveniles also build decoration, and that males build decorations prior to their mate-searching phase (pers. obs., Rao. D). The link between satiated spiders and silk decorations has been demonstrated by other studies (Blackledge 1998; Herberstein et al. 2000b). Nentwig and Rogg (1988) reported a similar result with more male *Argiope argentata* on webs with decorations, but they did not offer any explanation.

Decoration building in orb-web spiders has been studied numerous times, and many theories have been put forward for its function (for a detailed review see Herberstein et al. 2000a; Bruce 2006). Due to the observed variability in decoration construction, *A. radon* is not an obligate decoration builder. More than 30% of the spiders observed did not build decorations. Very few spiders of the *Argiope* genus build decorations all the time, the notable exception being *Argiope florida* (Justice et al. 2005). Even among individual spiders, there is variability in decoration building (Craig et al. 2001; Seah and Li 2002; Bruce and Herberstein 2005).

Our results on the reflective properties of silk decorations and the contrast they form with the natural

background suggest that they are visible to potential avian predators. Visibility to potential predators may explain why spiders in aggregations build fewer decorations. Furthermore, since there is a marked difference between the chromatic and achromatic contrast of the decorations with respect to the abdomen of the spider, it is unlikely that silk decorations serve to camouflage the spiders. It is more likely that both the decoration and the spider are highly visible to bird predators (see also Bruce et al. 2005). However, in this study, we cannot rule out the function of decorations as camouflage from predators, since the decorations could serve to lower the effectiveness of a direct attack by avian or insect predators.

As many studies have suggested, there is likely to be a trade-off between predator pressure and prey attraction (Blackledge 1998; Bruce et al. 2001). Stingless bees (a model prey) can easily detect the decorations as well, and may be attracted to the decorations (Craig et al. 2001). Even the colour of the spider may act as a possible prey attractant (Tso et al. 2004; Hoese et al. 2006). In the case of *A. radon*, the UV reflecting properties of its silvery abdomen as well as those of the decorations may function as a prey attraction mechanism. In light of these studies, it is interesting to consider the role of decorations in a spider that is also found in aggregations. Craig's (1991) study on similarly aggregating *A. argentata* spiders showed that while there is no influence of decoration with respect to insect interception in a group as a whole, there was a difference in insect interception between the decorating versus non-decorating spiders within a cluster. Craig (1991) interprets this by suggesting that once the insects approach a cluster of webs, they are more likely to be intercepted by a web with decorations rather than a web without decorations. Such a phenomenon may well occur in *A. radon* as well; however, in this study the aggregations were more elongated due to the habitat constraints of being located on a river bank.

In conclusion, we present baseline natural history data regarding the aggregating and decorating behaviour of *A. radon*. We show that the putative foraging advantage of aggregating may be offset by solitary spiders that build longer and more frequent decorations. We also show that decorations are likely to be visible to both model prey as well as model predators. Further experiments regarding prey capture within aggregations should help to tease apart the interactions between decorations and aggregations.

Acknowledgments We thank the Macquarie University and an Australian Research Council Grant for funding this project. Alexis McIntyre helped us with data collection in the field. We also thank Brian and Stephanie Hill of the Manbulloo Homestead, Katherine for collecting spiders and permitting us to conduct our study on their property. We thank Francisco Sánchez, Greg Holwell and the two

anonymous reviewers for helpful comments on the manuscript and Ed Nieuwenhuys for use of the *A. radon* photograph.

References

- Bjorkman-Chiswell BT, Kulinski MM, Muscat RL, Nguyen KA, Norton BA, Symonds MRE, Westhorpe GE, Elgar MA (2004) Web-building spiders attract prey by storing decaying matter. *Naturwissenschaften* 91(5):245–248
- Blackledge TA (1998) Signal conflict in spider webs driven by predators and prey. *Proc R Soc Lond Biol* 265(1409):1991–1996
- Blondel J, Dervieux A, Maistre M, Perret P (1991) Feeding ecology and life history variation of the blue tit in mediterranean deciduous and sclerophyllous habitats. *Oecologia* 88:9–14
- Bruce MJ (2006) Silk decorations: controversy and consensus. *J Zool* 269(1):89–97
- Bruce MJ, Herberstein ME (2005) Web decoration polymorphism in *Argiope audouin*, 1826 (Araneidae) spiders: ontogenetic and interspecific variation. *J Nat Hist* 39(44):3833–3845
- Bruce MJ, Herberstein ME, Elgar MA (2001) Signaling conflict between prey and predator attraction. *J Evol Biol* 14(5):786–794
- Bruce MJ, Heiling AM, Herberstein ME (2005) Spider signals: are web decorations visible to birds and bees? *Biol Lett* 1(3):299–302
- Chittka L, Kevan PG (2005) Flower colour as advertisement. In: Dafni A, Kevan PG, Husband BC (eds) *Practical pollination biology*. Enviroquest, Cambridge, ON, Canada, pp 157–196
- Church SC, Bennett ATD, Cuthill IC, Partridge JC (1998) Ultraviolet cues affect the foraging behaviour of blue tits. *Proc R Soc Lond B* 265:1509–1514
- Craig CL (1991) Physical constraints on group foraging and social evolution: observations on web-spinning spiders. *Func Ecol* 5:649–654
- Craig CL (2003) *Spiderwebs and silk: tracing evolution from molecules to genes to phenotypes*. Oxford University Press, New York
- Craig CL, Wolf SG, Davis JLD, Hauber ME, Maas JL (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(5):986–993
- Dyer AG, Chittka L (2004) Biological significance of discriminating between similar colours in spectrally variable illumination: bumblebees as a study case. *J Comp Physiol A* 190:105–114
- Foellmer MW, Fairbairn DJ (2005) Selection on male size, leg length and condition during mate search in a sexually highly dimorphic orb-weaving spider. *Oecologia*. 142:653–662
- Gaskett AC (2007) Spider sex pheromones: emission, reception, identification and functions and behavioural interactions. *Biol Rev* 82:1–22
- Gaskett AC, Herberstein ME, Downes BJ, Elgar MA (2004) Life-time male mating preferences in a sexually cannibalistic orb-web spider (Araneae: Araneidae). *Behaviour* 141:1197–1210
- Hart NS, Partridge JC, Cuthill IC, Bennett ATD (2000) Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine birds: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *J Comp Physiol A* 186:375–387
- Herberstein ME, Tso IM (2000) Evaluation of formulae to estimate the capture area and mesh height of orb-webs (Araneidae, Araneae). *J Arachnol* 28(2):180–184
- Herberstein ME, Fleisch AF (2003) Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). *Aust Ecol* 28:622–628

- Herberstein ME, Craig CL, Coddington JA, Elgar MA (2000a) The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biol Rev* 75(4):649–669
- Herberstein ME, Craig CL, Elgar MA (2000b) Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evol Ecol Res* 2:69–80
- Herberstein ME, Barry KL, Turoczy MA, Wills E, Youssef C, Elgar MA (2005a) Post-copulation mate guarding in the sexually cannibalistic St Andrew's cross spider (Araneae: Araneidae). *Ethol Ecol Evol* 17:17–26
- Herberstein ME, Gaskett AC, Schneider JM, Vella NGF, Elgar MA (2005b) Limits to male copulation frequency: sexual cannibalism and sterility in St Andrew's cross spiders (Araneae, Araneidae). *Ethology* 111:1050–1061
- Hoesle FJ, Law EAJ, Rao D, Herberstein ME (2006) Distinctive yellow bands on a sit-and-wait predator: prey attractant or camouflage? *Behaviour* 143:763–781
- Justice MJ, Justice TC, Vespi RL (2005) Web orientation, stabilimentum structure and predatory behavior of *Argiope florida* Chamberlin & Ivie 1944 (Araneae, Araneidae, Argiopinae). *J Arachnol* 33(1):82–92
- Levi HW (1983) The Orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the Western Pacific region (Araneae: Araneidae, Argiopinae). *Bull Mus Comp Zool* 150(5):247–338
- Lloyd NJ, Elgar MA (1997) Costs and benefits of facultative aggregating behaviour in the orb-spinning spider *Gasteracantha minax* Thorell (Araneae: Araneidae). *Aust J Ecol* 22(3):256–261
- Lubin YD (1974) Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). *Zool J Linn Soc* 54:321–339
- Lubin Y, Henschel JR, Baker MB (2001) Costs of aggregation: shadow competition in a sit-and-wait predator. *Oikos* 95(1):59–68
- Nentwig W, Rogg H (1988) The cross decoration of *Argiope argentata* (Araneae: Araneidae): nonfunctional or a nonspecific stress reaction. *Zool Anz* 221:248–266
- Platnick NI (2007) The world spider catalog, version 8. American Museum of Natural History, New York (see <http://research.amnh.org/entomology/spiders/catalog/index.html>, accessed 3 Jan 2007)
- Robinson MH, Robinson B (1980) Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pac Ins Mon* 36:1–218
- Seah WK, Li DQ (2002) Stabilimentum variations in *Argiope versicolor* (Araneae: Araneidae) from Singapore. *J Zool Lond* 258:531–540
- Théry M, Debut M, Gomez D, Casas J (2005) Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behav Ecol* 16(1):25–29
- Tso IM, Lin CW, Yang EC (2004) Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes. *J Exp Biol* 207(15):2631–2637
- Uetz GW (1989) The 'ricochet' effect and prey capture in colonial spiders. *Oecologia* 81:154–159
- Whitehouse MEA, Lubin Y (2005) The functions of societies and the evolution of group living: spider societies as a test case. *Biol Rev* 80(3):347–361
- Yamashita S, Tateda H (1978) Spectral sensitivities of the anterior median eyes of the orb web spiders, *Argiope bruennichii* and *A. amoena*. *J Exp Biol* 74:47–57