



## Cost of complex behaviour and its implications in antipredator defence in orb-web spiders



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### ARTICLE INFO

#### Article history:

Received 3 March 2016

Initial acceptance 21 April 2016

Final acceptance 7 July 2016

MS. number: 16-00186R

#### Keywords:

antipredator defence

building behaviour

*Cyclosa*

*Eriophora*

information processing

Kolmogorov complexity

orb-web

web asymmetry

Complex behaviour may incur a cost. We assumed here that web-building behaviour for two species of orb-web spider, *Cyclosa argenteoalba* and *Eriophora sagana*, was more complex when their webs were asymmetric from top to bottom than when their webs were symmetric. The rationale for this assumption was that, while spiders have to adjust their spiral building behaviour in different web sectors to build asymmetric webs, they do not have to make these adjustments for symmetric webs. To estimate the costs involved in building more asymmetric webs, we measured the time taken for spiders to build orb-webs with various up-down size asymmetries and used this as a measure of the complexity of web-building behaviour. The results showed that the spiders required more time to lay the spiral threads as their webs became more asymmetric even when the length of spiral threads was the same, suggesting a time cost of processing complex information. Furthermore, we found that spiders built more symmetric webs when they perceived a risk of predation, perhaps to reduce the web-building time during which they are more vulnerable. This suggests that the cost of behavioural complexity may mediate the outcome of interspecific interactions and thus may be ecologically important.

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Animal behaviour exhibits profound variability in its complexity, from simple stimulus responses or taxis behaviour, to more complex ones such as experience-based learning and adjustment of behaviour, elaborate courtship, deception, social interaction or behavioural coordination of individuals. Since complex behaviour is often beneficial due to increased foraging efficiency, greater mate acquisition, manipulation of others, resolution of social conflict or the accomplishment of tasks that are not possible by solitary animals, a reasonable question is: why do animals not always exhibit complex behaviour? To answer this question, behavioural complexity, which itself is a part of ecological complexity, should be studied in an ecological context, although it has often been overlooked in ecological studies (Loehle, 2004).

In this study, we used the concept of Kolmogorov complexity which measures complexity as the minimum amount of information required to represent a thing (Li & Vitányi, 2013). It has been used to evaluate the hunting behaviour of ants (Reznikova,

Panteleeva, & Danzanov, 2012), and may also be useful in the comparison of, for example, bird songs. White-backed munia, *Lonchura striata*, and the domesticated strain of this species, the Bengalese finch, have a similar number of acoustic notes, but the songs of Bengalese finches are more complex than those of white-backed munia: a matrix of transition probability among notes had more nonzero cells, implying that more information is required to represent the song of Bengalese finches than that of white-backed munia (Honda & Okanoya, 1999).

One possible reason for the variability in behavioural complexity is that the cost associated with complex behaviour prohibits some animals from behaving in a complex manner. The cost may involve energy expenditure to maintain a large nervous system (Niven & Laughlin, 2008); for example, mammal brain size is often reduced where there is little requirement for cognitive load (Niven, 2005). The time spent on an activity is also costly due to longer exposure to predators and greater energetic expenditure. Several studies have revealed that complex behaviour takes more time to complete than less complex behaviour. For example, specialist herbivores that depend on fewer stimuli from a limited number of host species to select their diet can make faster decisions than generalist herbivores which have to discriminate between a wide array of stimuli from a large number of potential hosts

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(Bernays & Funk, 1999). In a similar way, with bees, there is evidence to indicate that visual searches under complex conditions require more time (Chittka & Spaethe, 2007). The time cost of complex behaviour is considered to have two components: the increased time to complete the complex motor activity and to process the complex information to make decisions.

To examine the time cost of complex behaviour, the building of orb-webs is an ideal subject. An orb-web is a network of threads arranged in a two-dimensional plane. Web building is regarded as a typical example of complex behaviour, and a web is the product of a spider's numerous decisions about where to lay its threads (Vollrath, 1992). The orb-web's architectural structure such as its size, distances between adjacent sticky capture spirals and the shape of its capture area varies between species, between individuals within a species and also within individuals (Heiling & Herberstein, 2000). Some variability in the orb-web structure correlates with its architectural complexity. Orb-web spiders typically rebuild their webs regularly, and the webs built by the same spider often show different levels of architectural complexity (see below). While many studies on insects, including ants, lack quantitative measurement for the level of behavioural complexity (Eberhard & Wcislo, 2011), using the complexity of orb-web structure to represent the complexity of web-building behaviour makes this rather easy. Additionally, although the amount of motor activity is often related to the complexity of behaviour, it is easily quantified for web-building behaviour by measuring the amount of web silk, as this represents a spider's pathway during the laying of radial and spiral threads in web building.

The time cost associated with complex behaviour leads us to expect that behavioural complexity may vary according to conditions. Humans provided with little incentive appear to use simpler decision rules associated with less time cost but while doing so, they obtain a higher error rate. However, when given a higher incentive, they appear to use more complex decision rules to avoid a decisional error (Kocher & Sutter, 2006). One possible ecological condition that requires animals to behave quickly is predation. We expect that under the risk of predation, animals would refrain from spending a lot of time and exhibit simple behaviour, not only for how the animal escapes from its predators but also for other activities, including foraging. Loss of behavioural complexity in foraging might lower the risk of predation at the cost of reduced foraging efficiency.

Web-building behaviour is also a suitable subject for examining the effect of ecological conditions (such as risk of predation) on time-consuming complex foraging behaviour. The primary function of the orb-web is to trap prey. Furthermore, spiders typically rebuild their webs, and upon rebuilding they adjust the orb-web's architectural structure according to various ecological conditions, including the risk of predation. Several studies have revealed that spiders, following exposure to predator cues, build smaller webs to reduce the building time during which they are considered more vulnerable (Li & Lee, 2004; Nakata, 2008, 2009). Thus, we can predict that, in addition to building small webs, spiders would also simplify their web-building behaviour to reduce the building time when under high predation risk. We also predict that the reduction in time spent building simplified webs would be comparable to the reduction in time spent building small webs.

In this study, we used up-down size asymmetry of orb-webs as a measure of the complexity of web-building behaviour. The web hub where radii converge is not always located at the geometric centre of the web capture area, and instead is displaced upwards in most species and downwards in some atypical species (Nakata & Zschokke, 2010; Witt & Reed, 1965). In other words, the web radius, i.e. the distance from the hub to the outermost spiral, differs

between the upper and the lower parts of the web. Some other spiders build symmetric webs that have similar upper and lower radii, and there is variation between and within species in up-down size asymmetry of orb-webs (Nakata, 2010). To build an asymmetric web, spiders have to build spirals in one of two ways depending on the direction. (1) They can change the distance between adjacent spirals according to the part of the web they are currently on (Fig. 1a). To build typical webs with a larger lower part, spiders may widen the interspiral distance when traversing the lower part of the web and narrow it in the upper part of the web and/or they may adjust the curvature of spiral threads in different web sectors. (2) They may add extra spirals in the larger part of the web by making several U-turns, thus changing the direction of circling in this part of the web (Fig. 1b). In a preliminary analysis, we found that the U-turn itself had no relationship with web-building time.

Web asymmetry is considered an adaptation to increase spider's prey capture success (Zschokke & Nakata, 2010). Spiders should spend minimal time moving to the location of prey trapped in the web to prevent it from escaping (Masters & Moffat, 1983; Zschokke & Nakata, 2010). The time required for spiders to reach prey at a given distance from the web hub differs between upward and downward directions due to the spider's orientation on the web and the effect of gravity on its walking speed and on the prey tumbling down the web (ap Rhihiart & Vollrath, 1994; Nakata & Zschokke, 2010). To minimize the average time to reach prey, spiders adjust the size of the upper and lower halves of their webs according to the difference in the time this takes (Zschokke & Nakata, 2010). Additionally, spiral spacing asymmetry has been considered a result of correlation with radial spacing asymmetries: the angle between adjacent radial threads also typically differs between the upper and lower halves of webs, and to realize a constant mesh shape, spiders may adjust the spiral spacing. Alternatively, spiral spacing asymmetry may function to stop prey tumbling on the web by narrowing the spiral spacing at the lowermost part of the web (Eberhard, 2014; Zschokke & Nakata, 2015).

We assumed that asymmetric webs provide foraging advantages to spiders and are architecturally more complex than symmetric webs. Accordingly, asymmetric webs are likely to be the products of more 'complex' behaviour than symmetric webs. This assumption is based on the last stage of web building, which involves spiders laying capture spiral threads from the web periphery to the centre (Foelix, 1996). As explained above, spiders have to adjust spiral building behaviour according to direction to build asymmetric webs. However, to build symmetric webs, spiders do not have to make such adjustments; they lay spiral threads at constant intervals irrespective of the direction (Fig. 1c). In other words, more information processing is required to build asymmetric webs than to build symmetric webs. Thus, web building is more complex for asymmetric than symmetric webs in the sense of Kolmogorov complexity.

We aimed to test two hypotheses using the up-down asymmetry of a spider's orb-web. First, web-building complexity is associated with the time cost for complex behaviour. Specifically, we expected that the time required for the construction of the spiral threads of unit length would be longer for asymmetric than for symmetric orb-webs. Second, animals under risk of predation avoid time-consuming complex behaviour. Previous studies have demonstrated that spiders build smaller web, perhaps to reduce web-building time, when or after being exposed to predator cues (Li & Lee, 2004; Nakata, 2008, 2009). In this study, we expected that spiders exposed to predator cues would build more symmetric webs that demand less time to build compared to control spiders, which were not exposed to predator cues.

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