Animal Behaviour 103 (2015) 137–146

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

The web repair behaviour of an orb spider

Eleanor R. Tew, Alex Adamson, Thomas Hesselberg*

Department of Zoology, University of Oxford, Oxford, U.K.

ARTICLE INFO

Article history:
Received 1 December 2014
Initial acceptance 6 January 2015
Final acceptance 11 February 2015
Available online 16 March 2015
MS. number: 14-00971R

Keywords:
animal architecture
animal cognition
behavioural plasticity
orb webs
repair effectiveness
tension loss
web damage
wind

The study of construction behaviour and animal architecture has yielded significant insights into many areas of animal behaviour including decision making, optimal foraging and behavioural plasticity. In addition, the fitness consequences of constructing nests, protective structures and traps have been amply demonstrated. However, surprisingly little effort has gone into the study of what happens when these structures become damaged. Here we used the orb spider *Araneus diadematus* to explore repair behaviour of its web, with the aim of understanding environmental and structural influences on the repair process. The primary function of a spider web is to catch prey, so its structural integrity is of critical importance. However, orb webs are fragile structures and often become damaged, leading to the need to either repair or rebuild the web. Environmental conditions such as wind increase the likelihood of damage to the web. Here we first described and analysed the full repair process and quantified how effectively the repair restores structural integrity. Second, we investigated how wind affects repair behaviour and the spiders' anticipation of damage or motivation to repair. We found that spiders followed the same sequence of behaviours to repair damage to their webs and the repair significantly increased the effective web area following damage. Spiders reacted more quickly to damage in windy conditions, suggesting that they are attuned to the greater likelihood of damage in wind. Total repair time was the same in windy and control conditions, but repair was less effective in windy conditions.

Many animals build complex structures, which are used as traps, homes and for protection and courtship displays (Hansell, 2005). Most research effort has thus far focused on studying the initial construction, functions and mechanical properties of animal architecture (Bailey, Morgan, Bertin, Meddle, & Healy, 2014; Harmer, Blackledge, Madin, & Herberstein, 2011; Wcislo, Vargas, Ihle, & Wcislo, 2012), while comparatively little is known about other aspects, such as repair to damaged structures. In the natural world, animal-built structures such as bird nests, wasp nests and termite mounds often become damaged, and therefore animals must either rebuild their structure or engage in repair processes in order to ensure their continued integrity and function (Burger, 1978; Crook, 1964; McMahan, 1977; O'Donnell & Jeanne, 1990). Targeted repair can be more efficient than rebuilding a structure from scratch and therefore the repair process has direct fitness consequences for many animals (Crook, 1964; Downing, 1992; Eberhard, 1972). Additionally, since effective repair requires the same behavioural and motor patterns as the original building behaviour, but usually only utilizes a subset of these and not in the original construction order, the study of repair behaviour has significant potential for testing and furthering our understanding of animal cognition and behavioural plasticity (Crook, 1964; Downing, 1992; Pike & Foster, 2004).

Web-building spiders are excellent model organisms with which to study the mechanisms of repair behaviour and the conditions under which repair is carried out following structural damage. Extensive effort has gone into demonstrating how orb spiders display impressive behavioural flexibility in adapting their web-building behaviour to a wide range of environmental factors including temperature (Vollrath, Downes, & Krackow, 1997), wind (Liao, Chi, & Tso, 2009; Vollrath et al., 1997; Wu, Blamires, Wu, & Tso, 2013) and spatial constraints (Barrentes & Eberhard, 2012; Harmer & Herberstein, 2009; Hesselberg, 2013; Krink & Vollrath, 2000). However, relatively little is known about how they react to web damage (but see Chmiel, Herberstein, & Elgar, 2000). Spider webs are fragile structures that often become damaged, which reduces their overall prey capture efficiency (Chmiel et al., 2000; Wherry & Elwood, 2009). Most orb spiders rebuild their webs every night (Breed, Levine, Peakall, & Witt, 1964) yet spiders consistently expend effort in repairing damage that threatens the integrity of the web (Eberhard, 1972; Peters, 1932; Wiehle, 1927), which suggests that web repair is an important adaptive activity.

* Correspondence: T. Hesselberg, Department of Zoology, University of Oxford, South Parks Road, Oxford OX1 3PS, U.K.

E-mail address: Thomas.Hesselberg@zoo.ox.ac.uk (T. Hesselberg).

http://dx.doi.org/10.1016/j.anbehav.2015.02.016
0003-3472/

This is logical for two reasons: first, damage to a web early in the day could potentially be very detrimental as it would greatly decrease prey capture and therefore feeding opportunities; and second, targeted repair is much quicker than rebuilding an entire web and presumably requires fewer resources.

The primary function of webs is to stop and retain prey long enough for the spider to capture it (Foelix, 2011). Orb webs are the most recognizable and best-studied type of spider web. These webs have a highly geometric two-dimensional structure consisting of outwards radiating radial threads overlain by a capture spiral and enclosed within a frame that is attached to the surrounding vegetation by anchor threads. The orb web can be viewed as an extended phenotype that acts as an extension of the spider's sensory system (Blamires, 2010; Nakata, 2010). Many spiders sit facing downwards in the centre of their web (Zschokke & Nakata, 2010) with their legs positioned to detect vibrations that are transmitted through the radial threads (Klärner & Barth, 1982; Landolfa & Barth, 1996; Masters & Markl, 1981). They receive information about all mechanical disturbances in the web (e.g. prey capture and male courtship; Foelix, 2011). Paramount to this signal transmission is the maintenance of tension throughout the web. Tension loss has a detrimental effect on a spider's ability to catch prey in two ways. First, loss of tension dramatically decreases the transmission velocity of vibrations (Frohlich & Buskirk, 1982), so spiders are much less sensitive to the presence of prey in the web. Second, loss of tension in a large area reduces prey capture rates within the web (as prey are more able to escape before being detected). Crucially, tension loss is detected by the spider through the radial threads (Klärner & Barth, 1982; Wirth & Barth, 1992), allowing it to assess and, if necessary, repair damage. Given this, it also therefore seems likely that spiders react to damage that causes direct tension loss. In this study we set out to describe the web repair process and use quantitative observations to estimate how effective spiders are at repairing damaged webs, the manner in which they do so and the way in which they detect and respond to damage.

Webs may be damaged in many scenarios in the natural world. For example, large insects or birds may inadvertently damage webs by flying through them (Walter & Elgar, 2011). The probability of damage is greater under certain environmental conditions, especially in windy conditions, where aerodynamic drag on the silk threads increases the risk of damage (Craig, 1989; Lin, Edmonds, & Vollrath, 1995; Zaera, Soler, & Teus, 2014). In response, spiders are known to reduce drag by aligning their webs to incoming wind (Hieber, 1984) or by decreasing the length of silk threads in the webs (Liao et al., 2009; Vollrath et al., 1997); alternatively, they take down their webs, or do not build them at all (Wherry & Elwood, 2009). Following our more general repair observations, we set out to determine how windy conditions affect the repair process.

Environmental conditions are known to affect nest repair behaviour in birds (Burger, 1978) and spiders may similarly become more sensitive or attuned to web damage in windy conditions. This seems especially likely as evidence is mounting that invertebrates too are capable of selectively focusing their attention to specific stimuli in order to increase their fitness (Menzel, Brembs, & Giurfa, 2006). A recent study shows that orb spiders use attention focusing to increase foraging efficiency by adjusting the tension in threads in particularly profitable areas of the web (Nakata, 2010, 2013). Previous studies have shown that orb spiders not only focus their attention to different factors but that this attention focusing is also plastic, as spiders are able to vary the degree of attention they pay to different stimuli under different conditions (Eberhard & Hesselberg, 2012; Watanabe, 2000). Given that spiders appear able to shift their attention focus, it is an intriguing possibility that under strenuous environmental conditions such as wind, orb spiders become more attuned to the possibility of damage, allowing them to react and respond more quickly to the need for repair. In this study, we also tested whether spiders react to the increased likelihood of damage in windy conditions.

Not only is damage more likely in windy conditions, but wind may also impair the ability of spiders to move. Turner, Vollrath, and Hesselberg (2011) showed that spiders run more slowly towards prey in windy conditions, which was thought to be because wind makes movement across the web more difficult. For the same reason, it seems likely that the repair process will either take longer or be less efficient in windy conditions. This study therefore also quantified how such conditions influence the repair process.

In seeking to tease out different environmental and structural influences on web repair behaviour in orb spiders, we performed two sets of experiments. First, we used quantitative observations to (1) describe the repair process in detail, and test the predictions that (2) repairs significantly increase the effective web area compared to the damaged web, and (3) spiders react to damage that causes tension loss, rather than damage per se. Second, we compared repair behaviours in windy and control conditions to test the predictions that (4) spiders are more attuned to the possibility of damage in windy conditions, and therefore respond more quickly than in nonwindy conditions, and (5) although spiders react more quickly, the repair process takes longer overall in windy conditions due to wind impairing the ability of spiders to move.

METHODS

Study Organisms

Juvenile *Araneus diadematus* spiders (average weight $\pm$ SD $= 20.1 \pm 7.1$ mg, $N = 42$) were collected in the field (parkland within Oxford, U.K.) during May 2011 and May 2013 on bright, sunny days, with relatively little wind. In the laboratory each spider was transferred to a separate Perspex frame (measuring 30×30 cm and 5 cm wide) and acclimatized under laboratory conditions for at least a week (23 ± 0.5 °C, 16:8 h light:dark). The frames were stored adjacent to one another, separated by a sheet of Perspex covered in a thin layer of Vaseline (Zschokke & Herberstein, 2005). The spiders were fed one *Drosophila melanogaster* fly every 2–3 days, which was carefully blown into the sticky spiral of the web in order to replicate the natural conditions under which a fly may be caught. Spiders were never fed the day before an experiment but were given one fly following the experiment. Their webs were sprayed with water through a fine diffuser at the same time that they were fed. If, on its allocated day of feeding, a spider had not built a web, a fly was released into the spider's frame (and was therefore available to be caught should a web be built soon afterwards) and the frame was sprayed with water.

Ethical Note

When collected, individual spiders were transported in separate containers and immediately taken to the laboratory and transferred to their individual frames. Each spider was checked 6 days a week, independently of experiments, with a carefully monitored feeding and watering regime. Following the experiments, spiders were released at their original collection site. We adhered to ASAB/ABS's Guidelines for the Treatment of Animals in Behavioural Research and Teaching.

General Experimental Procedure

The evening before an experiment, the spider's web was destroyed using fine dissection scissors or a hot soldering iron. Care