Apply Tinbergen's Four Questions to Explain Spider Orb Web Building Behaviour

Introduction

The *Araneidae*, or orb-web spiders, are a family of *Araneae*. The novel innovation of building spiral webs that evolved 180 million years ago led to their radiation to 2,600 species *(Lin et al, 1995)*. Their webs are either ecribellate, meaning they are coated in glue droplets giving them their sticky property, or, less commonly, cribellate *(Foelix, 1996)*. Such physiology is highly intricate, and the behaviour surrounding the construction, manipulation and utilisation of these webs is equally complex. Therefore, the evolution and adaptive advantage of orb web building in *Araneidae* is a popular area of research. One way of investigating the evolution of such behaviours is by identifying what questions need to be answered regarding them. In response to this, ethologist Niko Tinbergen developed four questions in a paper where distinctions are made between different ways of asking 'why?' a behavioural adaptation exists *(Tinbergen, 2005; Manning & Dawkins, 2012)*. This essay will apply these four questions to orb-weaving behaviour in spiders.

Adaptation

The first of Tinbergen's questions is on at an evolutionary scale, asking what fitness advantage the behaviour confers *(Dawkins, 2018)*. Orb-weaving increases fitness due to the utilisation of the finished web, and many different ways that the web can be used has identified. The primary use is for the capture and subsequent consumption of prey, although it also may enhance fitness in other ways, such as the production of a sperm web in reproduction *(Mortimer, 2017)*. The web design essentially improves efficiency of feeding in two ways, by capturing and retaining prey and by extending the spider's sensorium once said prey has been captured.

The capture of prey by orb webs is generally achieved by the interception of mainly flying insect species. Because the total area covered by the web can only reach a certain threshold (dependent on site of the web, time available to build web and amount of silk), prey interception is generally improved by wider spacing between threads. However, this exists in a balance whereby closer spacing improves retention, thus orb-weaver webs are subtly different in structure to each other in different species depending on specialisation to different prey species such as to maximise both capture and retention *(Chacón & Eberhard, 1980)*.

Following initial capture, the process of prey retention can be divided into sub-processes: sticking to prey, absorbing its momentum and holding it until the spider makes contact *(Chacón & Eberhard, 1980)*. Therefore, in order to increase the spider's fitness, the web should increase the efficiency of these sub-processes. The structure of orb webs effectively revolves around different thread types that permit this retention: (i) frame threads, which define the border of the web, (ii) radial threads, which are strong and radiate into the central 'hub' zone, (iii) auxiliary spiral threads, which form concentric semicircles around this hub, and in ecribellate species (iv) the catching spiral threads, which are dotted with glue droplets *(Foelix, 1996)*. The combination of these threads and the specific way in which orb-weavers construct them results in the web absorbing the prey's energy when they collide with the web without breaking as well as being sufficiently stretchy and sticky to retain the prey

(Foelix, 1996). This capture and retention technique therefore suggests orb-weaving behaviour is beneficial.

As stated, the building of webs also extends spiders' sensoria. Web vibrations are used to detect stimuli through their slit sensilla, substrate-borne vibration sensors present on the legs *(Mortimer, 2017)*. In a paper by Landolfa and Barth, the vibrations in the webs of *Nephila clavipes* were studied as well as the spider's sensation of such vibrations to solve the ambiguity of how spiders discriminate and orientate towards stimulus sources. Longitudinal, transverse, lateral, and to a lesser extent torsional vibrations were all produced by prey, with peak amplitudes correlating with their mass, generally in the 5-10 Hz range. The transmission of vibrations was also measured along single radial threads at varying distances from the stimulus, where peak amplitudes spanned a 40 dB range. Landolfa and Barth also used their results to investigate how vibrations are transmitted from stimulated to non-stimulated radial threads through the auxiliary spiral and how this effects the overall spread throughout the web. In the case of *Nephila*, ca. 0.5 dB was lost at each radius-to-auxiliary-spiral junction during longitudinal transmission and 0.8 dB during lateral transmission. It was therefore suggested that the lateral spread of vibrations (as opposed to a single stimulated radial thread) might contain more information regarding the stimulus location relative to the spider in the hub and thus increase accuracy of approach. As well as this lateral spread increasing accuracy of stimulus detection, the time between prey contact and spider arrival to the prey may be increased depending on the vibration propagation velocities in the threads. It was calculated that the maximum time-of-arrival difference from stimulus to the spider was as low as 0.047 ms in longitudinal vibrations. Therefore, as a result of highly accurate stimulus detection and a quick response, the mean elapsed time between fly impact with the web and initial contact with the spider was just 3.6 seconds, where the distance was 10-30 cm *(Landolfa & Barth, 1996)*.

Orb-weaving behaviour can therefore be observed in spiders due to the fitness advantage gained from it regarding the carnivorous feeding of such species, both in terms of initial retention as well as enhancing the sensorium which is used in response to capture.

<u>Phylogeny</u>

The second of Tinbergen's questions is similarly on an ultimate scale and asks how the behaviour historically evolved, and therefore what traits it is derived from *(Dawkins, 2018)*. Orb-weaving behaviour is thought to have evolved a single time thus giving it a monophyletic origin. By looking at molecular data as well as traditional morphological and behavioural characters, it has been hypothesised that the orb-weaver clade, Orbiculariae, are derived from spiders that built substrate-bound webs. This monophyletic origin implies two major evolutionary changes in spinning behaviour between the ancestral and current state of orb webs. The first is that extreme behavioural stereotypy must have evolved in the basal species such that highly regularly spaced radial threads and adhesive capture spirals could be spun in a regular manner. Secondly, a transformation whereby the webs could be suspended on a frame of discrete structural threads must have evolved thus freeing the ancestral ground webs from the constraints imposed by building on substrates *(Blackledge et al, 2009)*.

The orb web monophyly hypothesis also suggests that present day orb webs evolved from dry cribellate webs. These are webs whereby the threads are produced by spiders by spinning a core axial fibre and then combing finer fibrils onto it, which then adhere through van der Waals forces. An evolutionary shift must have took place favouring cribellate silk, where aqueous viscid silk is spun by laying down the axial core fibre at the same time as a layer of glue droplets, leading to a much quicker rate of spinning webs as well as greater adhesion per surface area in completed webs *(Blackledge et al, 2009)*.

Orb-weaving behaviour is therefore monophyletically derived from an ancestral state of building cribellate webs on substrate surfaces. An evolutionary shift resulted in the phylogenetic successors building webs more efficiently thus enhancing fitness of spiders.

Mechanism

Tinbergen's third question asks why an adaptation exists on a proximate scale, specifically referring to how an animal's body works to produce such behaviour. This regards the morphology and physiology of the organism at hand *(Dawkins, 2018)*.

In a paper by Zschokke and Vollrath, the web building of two orb-weaver species (18 webs from 4 individuals of the cribellate *Uloborus walckenaerius* and 30 webs of 6 individuals of the ecribellate *Araneus diadematus*) were observed to understand how the movement patterns work on a spatial and temporal scale, thus indicating the difference in the spider's 'path' and the 'track' of the web itself *(Zschokke & Vollrath, 1995)*.

Spatially, slight differences were observed in the paths. Both species construct radial threads by finding a gap between two radii, which they locate by walking around the frame thread at a slow pace. They then climb along one of the radii (the exit-radius) towards the frame thread and then, tightening their dragline, attach it to the frame thread and walk back to the hub whilst simultaneously laying down a new radius. *Araneus* always used the higher of the two radii on the edge of the gap as the exit-radius, whilst 80% of *Uloborus* used the one on the opposite side of the gap. Auxiliary spiral construction was similar in both species, although *Uloborus* incorporated on average 2.4 reverses (or U-turns) per web, whereas *Araneus* did not. In capture spiral construction, the paths differed significantly. On primary building of the outermost turn, *Uloborus* generally walked along the frame thread, whereas *Araneus* always used the auxiliary spiral to cross between radii. As well as this, *Araneus* walked in 'ruts' whereby the same turn of auxiliary spiral was followed for several turns until it cut the spiral and switched to the next turn closer towards the hub, acting as a bridge between radii. *Uloborus* did not exhibit this mechanism of building behaviour *(Zschokke & Vollrath, 1995)*.

Temporally, the two species also differed slightly. Both species exhibited high maximum displacement speeds during radii construction. Furthermore, both exhibited roughly linear increases of displacement speeds when constructing the auxiliary spiral. Following this, construction of the capture spiral in *Araneus* from the periphery inwards commenced at a slower pace, before decreasing in speed further until it was equivocal to the speed of initial auxiliary building. In contrast, in *Uloborus* the pace

of capture spiral construction was even slower, approximately one sixth of the speed of auxiliary spiral construction, and remained constant throughout. The spiral construction speeds are reflective of how uloborid species are limited by silk production speed whereas araneid species are limited by the time taken to attach the capture spiral to the radii *(Zschokke & Vollrath, 1995)*.

Although these mechanisms are not at a neurophysiological and cellular anatomical scale, the experiments explain to an extent why orb-weaving takes place in terms of how the organisms' bodies work.

Development

Tinbergen's final question is likewise on an organismal scale and asks how the behaviour develops throughout the animal's life history, specifically asking whether it is learnt or innate behaviour *(Dawkins, 2018)*.

In orb-weavers, it is thought that web building behaviour is genetically determined and is not affected as a result of experience. The first orb webs of juveniles appear sufficiently similar to those from later stages to support this hypothesis. In a paper by Hesselberg, the webs of two species, *Nephila clavipes* and *Eustala illicita*, were analysed at three different developmental stages. In *N. clavipes*, all age classes were easily recognisable as typical orb webs and showed no change in web parameters, except in total size of the web. Results were similar in *E. illicita*, except that earlier stages were shown to be more symmetrical and less likely to contain a free sector. This supports the 'biogenetic law' hypothesis, which states that an organism's ontogeny follows the same pattern as the evolutionary changes in its ancestry *(Nelson G, 1985; Hesselberg, 2010)*.

The lack of major differences in young and adult spiders behaviour regarding web building and structure implies genetic and therefore innate origins of the behaviour. Additionally, it refutes the size limitation hypothesis, which may be explained by the relative size of the brain in young spiders, which takes up almost all of the cephalothorax *(Hesselberg, 2010)*.

Conclusion

Tinbergen's four questions are a useful method of investigating the evolution of orb-weaving behaviour in spiders, considering both the ultimate and proximate scale of adaptiveness. Following consideration, the question that remains is whether the behaviour is at its maximisation peak, or whether it will continue to evolve to optimise the fitness of spiders even further. The behaviour may now be acting as a gateway to novel strategies and web-types to further increase fitness and promote diversification in *Araneae*.

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