



## Evidence of circadian rhythm in antipredator behaviour in the orb-weaving spider *Larinioides cornutus*

Thomas C. Jones\*, Tamer S. Akoury, Christopher K. Hauser, Darrell Moore

Department of Biological Sciences, East Tennessee State University

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Ecologically, spiders are both predators and prey. Therefore, they must balance being aggressive enough to forage successfully, but not so aggressive that they become overly exposed to predation. Some species of spiders actively forage during clearly defined periods of the day, leading to the hypothesis that they should be less aggressive (or more defensive) during periods when they are not foraging, predicting that antipredator behaviour should be more pronounced during inactive foraging times. We tested the antipredator 'huddle response' in a nocturnal foraging orb-weaver, *Larinioides cornutus*, and found that, as predicted, the spiders huddled longer in the day than at night. We then conducted tests to determine whether the cycling of the response was regulated by an internal clock (circadian), and we found that huddle duration continued to cycle under constant dark (with periodicity significantly less than 24 h) as well as under constant light (periodicity nonsignificantly longer than 24 h). This work adds a novel behaviour to the list of behaviours under circadian control and also to the surprisingly short list of studies demonstrating circadian rhythm in spiders.

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It is commonly assumed that circadian rhythms are adaptive, directing the organism to perform each of its various functions, including behaviour, at the most appropriate time of day. Circadian rhythms typically are entrained by environmental cycles, most notably the daily alternation of light and dark. Entrainment ensures that the rhythm maintains a fixed phase relationship with the environmental cycle. Often, the entrained rhythm makes it possible for the organism to anticipate (i.e. perform a function ahead of) environmental changes such as sunrise or sunset. The entrained circadian rhythm thus may allow the organism to be proactive rather than reactive with respect to daily periodic environmental stimuli. Experiments conducted in the laboratory with abrupt changes in light levels are able to differentiate circadian-based anticipatory behaviour from behaviours that respond directly to (gradually) changing light levels. For example, the entrained circadian rhythm of activity in bats (DeCoursey & DeCoursey 1964) and flying squirrels (DeCoursey 1989) allows these nocturnal animals to anticipate sunset, thereby enabling them to begin their night-time activities at the appropriate light intensity level. In another laboratory study, performance of the calling song is primarily a nocturnal behaviour in male crickets (*Teleogryllus commodus*): it occurs throughout the night but actually begins

1–3 h before sunset (Loher 1972). In the field, honeybees, using their circadian clock-driven time-memory, anticipate the time of day at which they encounter profitable food sources on previous days by scheduling reconnaissance flights to that particular location in the environment, with the amount of anticipation depending on the amount of previous experience with that source (Moore & Doherty 2009). In an ecological sense, spiders are both predators and prey (Wise 1993). In particular, orb-weaving spiders aggressively attack insects caught in their webs, but are themselves subject to attack from wasps and birds (Foelix 1996). Most orb-weaving species are either nocturnal or diurnal, actively foraging during only one part of the daily cycle, and remaining secluded during the other (Carico 1986; Stowe 1986). In a sense, these spiders must behaviourally 'switch' from being predators to avoiding being prey on a daily basis. One would therefore expect there to be a selective advantage for spiders to anticipate dawn and dusk, particularly if prey levels are higher during these environmental transitions. However, very little information exists concerning the circadian control of behaviour in spiders. Most of the studies to date are concerned with locomotor activity (e.g. Seyfarth 1980; Schmitt et al. 1990; Suter 1993) or changes in sensitivity of the eyes (e.g. Yamashita & Nakamura 1999). Here, we present evidence for circadian regulation of an antipredator behaviour in the orb-weaving spider *Larinioides cornutus*.

An antipredator behaviour commonly observed in orb-weaving spiders is 'bailing out', in which the spider drops from the web and

\* Correspondence: T. C. Jones, Department of Biological Sciences, East Tennessee State University, Johnson City, TN, 37614, U.S.A.

E-mail address: [jonestc@etsu.edu](mailto:jonestc@etsu.edu) (T. C. Jones).

remains motionless with its legs flexed tightly to its ventral midline for a period of time (Rayor 1996). This behaviour is illustrated for the species used in the present study in Jones et al. (2011). Uetz et al. (2002) found that a colonial orb-weaving spider would express this behaviour in response to continuous vibrations applied to a support silk line. That study also found that the likelihood of exhibiting the response increased in those spiders whose neighbours had already been coaxed to bail out. The physical posture assumed by spiders when they bail out of their webs can be elicited in the laboratory, even if the spiders are removed from their web. Studies by Pruitt et al. (2008, 2010) on social cobweb-building spiders suggested that this 'huddle response' (also known as thanatosis, or death feigning) is part of an overall behavioural syndrome (sensu Sih et al. 2004) related to aggression: spiders that are more aggressive towards prey and conspecifics do not hold the huddle posture as long as less aggressive spiders.

A recent study of the effect of biogenic amines on the huddle response in the orb-weaving spider *Larinioides cornutus* found that experimentally elevating octopamine significantly shortened the duration of the huddle response, while elevating serotonin significantly prolonged it (Jones et al. 2011). That study found that the effect of serotonin decreased over the first 6 h after treatment, but then increased and was most pronounced 24 h after dosing, leading to the speculation that these spiders may show rhythmicity in antipredator behaviour. In the present study we explored whether the huddle response of the nocturnal orb-weaver *L. cornutus* (Araneidae) shows diel periodicity, and if so, whether periodicity is regulated by an internal (i.e. circadian) clock. We hypothesized that these nocturnal spiders would huddle longer during the day than at night, reflecting the fact that they forage at night but not during daylight hours. Our rationale was that there is a significant cost to bailing out of the web at night, in terms of missed prey capture opportunities, that does not exist during the day. Alternatively, the predation risk for the spider (particularly from wasps and birds) may be higher for the spider during daylight hours than at night.

## METHODS

### *Study Species, Collection and Housing*

*Larinioides cornutus* (Clerck 1757) is an orb-weaver in the family Araneidae, which is common to Europe and North America (Levi & Levi 1990). It is a nocturnal spider, constructing its web at dusk and

actively foraging throughout the night, then removing its web at dawn, and remaining in a hidden retreat during the day (Bellmann 1997). Female adult *L. cornutus* were collected in September and October 2009 from buildings and shrubbery in northeastern Tennessee (U.S.A.). The spiders were extracted from their webs and individually housed in 250 ml plastic deli containers. Spiders that were housed for more than a few days were given water twice a week, fed crickets every other week, and kept at approximately 23 °C under 12:12 h light:dark cycle.

### *Quantifying the Huddle Response*

Web-building spiders typically show an antipredator huddle response in which they draw their legs in tight to their body and remain motionless. If left undisturbed, the spiders will break out of the huddle after a period of time. This huddling appears to be an 'all-or-nothing' response, and there is no known effect of stimulus strength on huddle duration in *L. cornutus* (T. C. Jones, unpublished data) or in other spiders (Pruitt et al. 2008, 2010). There is also no evidence of habituation to the stimulus (Jones et al. 2011). We used the method of Jones et al. (2011) to quantify the response. Individual spiders were removed from their containers and placed in a glass bowl (15 cm diameter, 6 cm high), and were given 30 s to acclimate to the dish. To trigger the huddle response we delivered a puff of air from approximately 10 cm away. The air movement deflects fine sensory hairs (trichobothria) on the spider's legs, stimulating the stereotypical huddle response (Foelix 1996). We determined the duration of the huddling response to the nearest second with a stopwatch from the moment the spiders initiated the huddle to the moment that they broke out of it. Individuals that did not huddle after three attempts to initiate the response received a score of 0 s; individuals that initiated a response but immediately broke out of it, received a score of 1 s. We cleaned each dish with ethanol between trials.

### *Measuring Diel and Circadian Rhythmicity in the Huddle Response*

For this part of the study, adult *L. cornutus* were housed in a light-controlled room under an LD 12:12 h for at least 5 days prior to testing. The room was carefully sealed against light leaks, and the door was double-screened with black-out curtains to prevent light from leaking in when opened. All dark observations were conducted under low light filtered with two layers of GamColor® Medium Red XT gel. Ten spiders were tested for 72 h under LD

**Table 1**  
Chi-square and *F* periodogram analyses of huddle response duration for individual spiders under LD 12:12 h, DD and LL

LD 12:12 h			DD			LL		
ID	$\chi^2$ $\alpha=0.001$	<i>F</i> $\alpha=0.01$	ID	$\chi^2$ $\alpha=0.001$	<i>F</i> $\alpha=0.01$	ID	$\chi^2$ $\alpha=0.001$	<i>F</i> $\alpha=0.01$
Lc-22	23.9	23.9	Lc-C	22	22	Lc-I	26.7	26.7
Lc-14	23.9	23.9	Lc-P	19.9	19.9	Lc-XI	26.7	26.7
Lc-1	28	28	Lc-12	19.9	21.3	Lc-HHH	26.7	26.7
Lc-12	28	28	Lc-D1	20	20	Lc-CCC	22	22
Lc-CCC	23.9	23.9	Lc-JJJ	24	24	Lc-D2	<b>NS</b>	<b>NS</b>
Lc-QQQ	23.9	23.9	Lc-D2	23.9	23.9	Lc-X2	<b>29.5</b>	<b>NS</b>
Lc-JJJ	23.9	23.9	Lc-CCC	23.9	23.9	Lc-NNN	23.9	23.9
Lc-HHH	23.9	23.9	Lc-1	25	25	Lc-X4	<b>NS</b>	<b>NS</b>
Lc-11	23.9	23.9	Lc-11	18.7	18.7	Lc-II	27	27
Lc-26	23.9	23.9	Lc-22	22	21.4	Lc-JJJ	28.7	28.7
			Lc-18	23.9	23.9	Lc-12	20.6	20.6
			Lc-MM	22.7	22.7	Lc-M	28	28
			Lc-LL	21.3	21.3	Lc-C	28.7	28.7
			Lc-HHH	19.9	19.9	Lc-X5	20	18
			Lc-26	<b>NS</b>	<b>NS</b>	Lc-X3	23.9	23.9

Given are the main periods ( $\tau$ ), in hours, that were significant at  $\alpha = 0.001$  for chi-square periodograms and that were significant at  $\alpha = 0.01$  for *F* periodograms (individuals with nonsignificant periodograms are indicated in bold).

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