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Diel Periodicity in Activity and Location in the Web of the Common House Spider (Achaearanea tepidariorum).

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Diel Periodicity in Activity and Location in the Web of the Common House Spider (*Achaearanea tepidariorum*)

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By

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ABSTRACT

Circadian rhythm is a type of endogenous clock that controls daily behavioral patterns in most organisms. Spiders have been shown to exhibit both circadian and non-circadian rhythms in their behaviors. This rhythmicity may allow spiders to cope with diel changes in environmental conditions. Both diurnal and nocturnal behavior have different sets of costs and benefits to a species' survival. *Achaearanea tepidariorum* is one species in which potential circadian rhythmicity has never been studied. Due to its foraging behavior, it was predicted that its daily activity would be arrhythmic. We recorded the positions within the web of forty individuals throughout the day, and then observed their daily activity via use of an actogram apparatus. Analysis of the resulting actograms and web position data revealed a significant nocturnal periodicity in the spiders' activity, as well as possible anticipation of the daily cycle. This nocturnal periodicity, coupled with specific web-building behavior, may be the result of this species balancing the costs and benefits of predation and foraging. More studies are needed to provide more information about the circadian behavioral patterns of *A. tepidariorum*.

INTRODUCTION

Circadian rhythm is a type of endogenous clock that regulates day-to-day physiological changes and behavioral patterns, such as when to sleep, when to eat, or when to mate. In vertebrates, this internal rhythm is primarily controlled by the SCN in the nervous system (Morin 1994). However, not all rhythmic behavior is considered circadian. If behavior patterns are circadian, then they will still be performed under constant conditions with approximately the same periodicity, a phenomenon called “free-running.” Non-circadian rhythms are affected by external cues only, and do not involve an internal clock. Thus far it has been found that all eukaryotic organisms and some prokaryotes exhibit some circadian rhythm in daily patterns (Dvornyk et al. 2003). Rhythmic behavior is important to an organism’s survival, in that it can allow them to “anticipate” the daily cycle rather than simply responding to immediate conditions. It can also allow an organism to be active during more favorable environmental conditions, and aid in predator avoidance.

Rhythmic patterns have been studied in a few aspects of the behavior and physiology of spiders. The rhythmicity of web-building has been studied in several species of spider, and is likely to be non-circadian in nature, triggered by external cues. Studies have confirmed that web-building is primarily a nocturnal activity in most species (Stowe 1978). Activity-recording devices confirmed that the web-building behavior of *Araneus diadematus* is triggered by the onset of darkness (Ramousse & Davis 1976), and in another study it was observed that during a total solar eclipse, *Metepeira incrassata* dismantled its web at mid-day after the onset of darkness, then began to rebuild when the sun reappeared (Uetz et al. 1994), further confirming that external cues are needed to trigger web-building behavior.

Foraging is another behavior that is affected by non-circadian rhythms in spiders. For example, under field conditions the nocturnal orbweaver *Eriophora edax* is more likely to build its webs, catch prey, and eat its meals at specific intervals during the night, suggesting rhythmicity due to external cues, though there were no tests conducted under constant conditions (Ceballos et al. 2005). Gillespie and Caraco found that variations in habitat and prey abundance affect the times at which populations of *Tetragnatha elongata* will forage (1987). Again, this study was conducted in the field, and not under constant conditions.

Patterns of movement are affected by circadian rhythm in spiders. An endogenous circadian clock was found to govern the locomotor activity of spiders (Suter 1993). In his experiment, an activity monitor was used in which the spiders' activity was recorded via infrared detection, much like the apparatus used for the observations of this study. The results showed that the two species studied exhibited circadian rhythmicity, as well as other higher frequency rhythms, as evidenced by the presence of free-runs in the resulting actographs. Wandering spiders tend to be more active at specific periods during the night (Norgaard et al. 2006), especially the males (Schmitt et al. 1990), showing a strongly nocturnal periodicity. Another example of circadian patterns of activity is shown in the colonial spider *Mallos gregalis*, which changes its position in its web according to the time of day (Tietjen 1982).

The environment is a key factor in the rhythmic patterns of spiders, since it has several factors that can potentially vary on a diel cycle with which individuals must be able to cope. One such factor is temperature. Spiders are ectotherms, and may be less able to respond to predators or prey at night, when the air tends to be cooler, potentially lowering their metabolism. Humidity is also a factor, since many spiders take in water through the air (Kaston 1965). Variations throughout the day may drive a species to be more active only at certain points when there is more or less water available. Prey density and predation risk are other major factors, since spiders must balance the benefits of catching enough prey with the costs of potentially becoming prey themselves. An example of possible predator avoidance due to rhythmic behavior is illustrated by two species of wolf spider, *Pardosa milvina* and *Hogna helluo*. These spiders often occupy the same microhabitats and use it in similar ways, but *P. milvina* is significantly more active during the day than *H. helluo* (Marshall et al. 2002). This could be due to the fact that *P.*

milvina is frequently preyed upon by *H. helluo*, and as a result it changes its behavior when it is in the presence of this predator (Walker & Rypstra 2003).

Whether an organism is diurnal or nocturnal is a major factor in its survival and ecology, as each comes with its own set of tradeoffs. Diurnal species of spider are relatively uncommon and thus potentially may experience less competition for resources (Wise 1993). However, they are also more prone to predation by diurnally active birds and wasps, the most common predators of spiders. As a result, many diurnal spiders, such as those in the genus *Argiope*, possess bright warning colors to warn predators that they are inedible due to the production of harmful chemicals (Foelix 1996). Others, such as those in the genus *Micrathena* or *Gasteracantha*, are equipped with spines to make it difficult for birds to swallow them (Cloudsley-Thompson 1995). Nocturnal spiders are far more common than diurnal species, encompassing most species of orb-weavers. By remaining in their retreats during the day, these spiders avoid diurnal predators and have no need for special adaptations to defend against them. However, nocturnal species also must deal with potentially higher resource competition from other spiders (Wise 1993).

The focal species of this study is *Achaearanea tepidariorum*, the Common House Spider. This species is a sit-and-wait predator and builds three-dimensional tangle webs in corners and cracks, often in artificial structures (Benjamin & Zschokke 2003). This three-dimensional structure is hypothesized to be an antipredator adaptation (Blackledge et al. 2003), since the spider will be able to sense vibrations of movement coming from any side (Zevenbergen et al. 2008). The web is a permanent structure, and the resident spider does not leave it at any point of the day. *Achaearanea tepidariorum* is a common test subject, particularly in studies of the effects of the environment on behavior. For example, it was found that temperature affects the efficiency of this species' web-building behavior, specifically the amount and type of silk that the spiders used (Barghusen et al. 1997). Temperature, photoperiod, and food supply were also found to affect the seasonal life cycle of *A. tepidariorum*, specifically the timing of diapause (Tanaka 1991). However, its behavior in relation to circadian rhythm has never been studied, and it is unknown whether this species is diurnal or nocturnal. Since *A. tepidariorum* never leaves its web, it can potentially capture prey at any time of day. Results of a previous study of several species of spider suggested that continuously foraging species are arrhythmic in regard to certain behaviors (Jones et al., *in prep*). We thus hypothesized that it would be arrhythmic in its activity as well.

METHODS

Web Position—To determine if *A. tepidariorum* is a round-the-clock forager, we monitored the spiders' movements within their webs throughout the day. We caught forty individual females from different locations in Washington County, TN. The spiders were housed individually in lidded plastic cups (8 cm diameter, 6 cm height). The spiders were entrained to a 12/12-hour LD light cycle for one week, and then we monitored their movements by measuring their positions in their webs every four hours for two full days. Position measurements were taken in centimeters. First the distance from the bottom of the cup to the nearest edge of the spider's body (cephalothorax and abdomen) was measured, and then the distance from the spider to the nearest side was measured.

LD and DD Observations—We then measured the spiders' activity levels with a modified *Drosophila* activity monitor (Trikinetics Inc.). Thirty-two of the spiders were housed in individual closed-ended glass tubes (10 cm length, 2.5 cm diameter), and their movements were recorded by a network of infrared beams. The apparatus with the spiders was placed into an incubator to control the temperature, humidity, and light conditions. Temperature and humidity were kept at a constant level (25°C, humidity maintained by cups of water). The apparatus recorded the spiders' movements every 6 minutes for a period of 10 days. The spiders were recorded under LD conditions for the first 5 days. They were then taken out for feeding and we cleaned the tubes (a 3-hour gap), then we placed them back into the apparatus and observed them under DD conditions for 5 additional days. ClockLab (Actimetrics, Wilmette IL) was used to determine whether there was a significant periodicity in the spiders' activity.

RESULTS

Web position—Mean positions within the web under LD 12:12 were analyzed with a repeated measures ANOVA test, to account for multiple measurements done with each individual. Little consistency was found in the mean positions of the spiders during dark hours in terms of both distances from the side (Fig. 1) and from the top (Fig. 2) of the cups. However, differences in position at specific times during the day were found to be significant (Repeated Measures ANOVA, $F_{5,679} = 50.2$ and $F_{5,679} = 34.1$, $p<0.001$), specifically the spiders' position in their webs during the period just before darkness (1900 hrs), when they would drop toward the middle and side of the web. In terms of distance from the side, the spiders would move closer to the wall of the cup (Fig. 1). During the same time period, they would also drop down toward the middle or bottom of the web (Fig. 2).

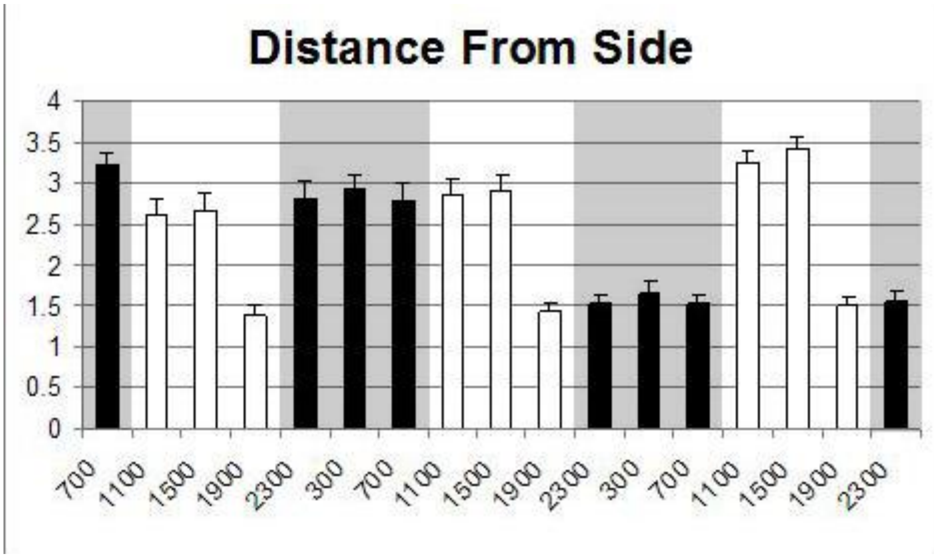

Fig. 1—Mean web-position from the side of the cup. Light observations began at 1100 hrs, dark at 2300 hrs. Measurements taken in cm every 4 hrs. Distances measured and recorded in cm from side of the cup to nearest part of the spider's body. Y-axis represents distance in cm from the side of the cup, x-axis represents time of measurements. Repeated measures ANOVA: $F_{5,679} = 50.2$, $p<0.001$.

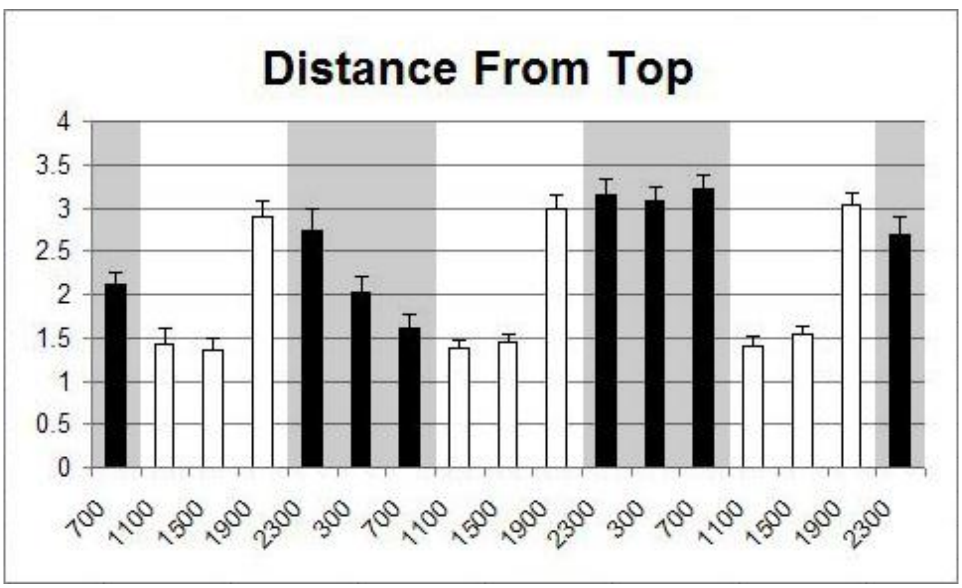

Fig. 2—Mean web-position from the top of the cup. Distances measured and recorded in cm from bottom of the cup to nearest part of each spider's body. Repeated measures ANOVA: $F_{5,679} = 34.1$, $p<0.001$.

LD and DD Activity—Most of the individuals exhibited a clear nocturnal activity pattern under LD, as shown by the actograms (Figs. 3-8). Interestingly, the main bout of activity of these spiders did not begin as soon as the lights went out. Instead, the spiders began their activity around an hour after darkness fell. Under DD, the spiders exhibited shorter bouts of activity, but for most this began after what was anticipated lights-out, and most showed clear patterns of free-running during this part of the observation. All but one individual (n = 31) showed significant free-runs under DD, and had periods of less than 24 hrs (Chi square periodograms, $p < 0.001$ or 0.005. Mean 23.89 hrs, S.D. = 3.39). Some individuals did not show a clear nocturnal pattern under LD, but still showed clear free-runs under DD (Fig. 4, 7). Others had free-runs which were less readily apparent, but were still significant (Fig. 6). A few individuals had actogram patterns that were entirely unclear, but again, still had significant free-runs under DD (Fig. 5).

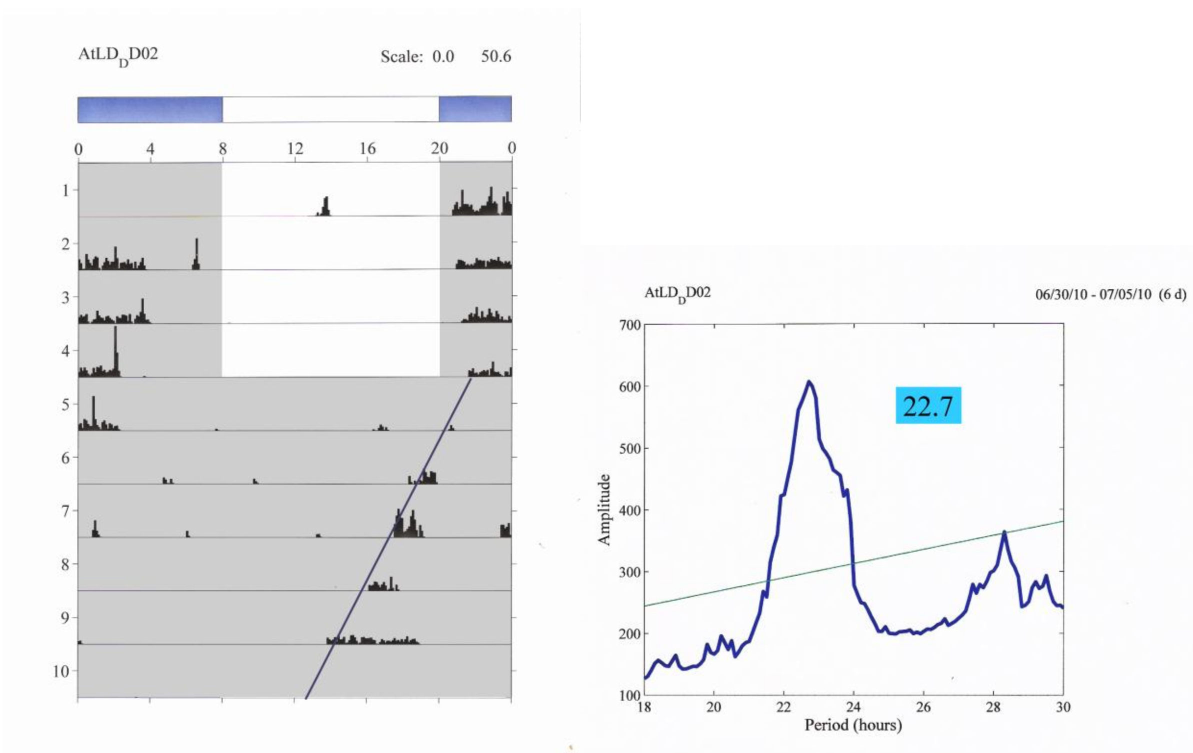

Fig. 3—Actogram (left) and periodogram (right) documenting the activity of Spider 02. Y-axis of the actogram represents the day, the x-axis time. LD period lasted between days 1 and 5, DD between days 5 and 10. Periodogram for DD created on a scale of 18-30 hours, and significance analyzed with Chi-square Periodogram test. Period number corresponds to the most significant peak. Period for Spider 02 was 22.7 hrs, p<0.001.

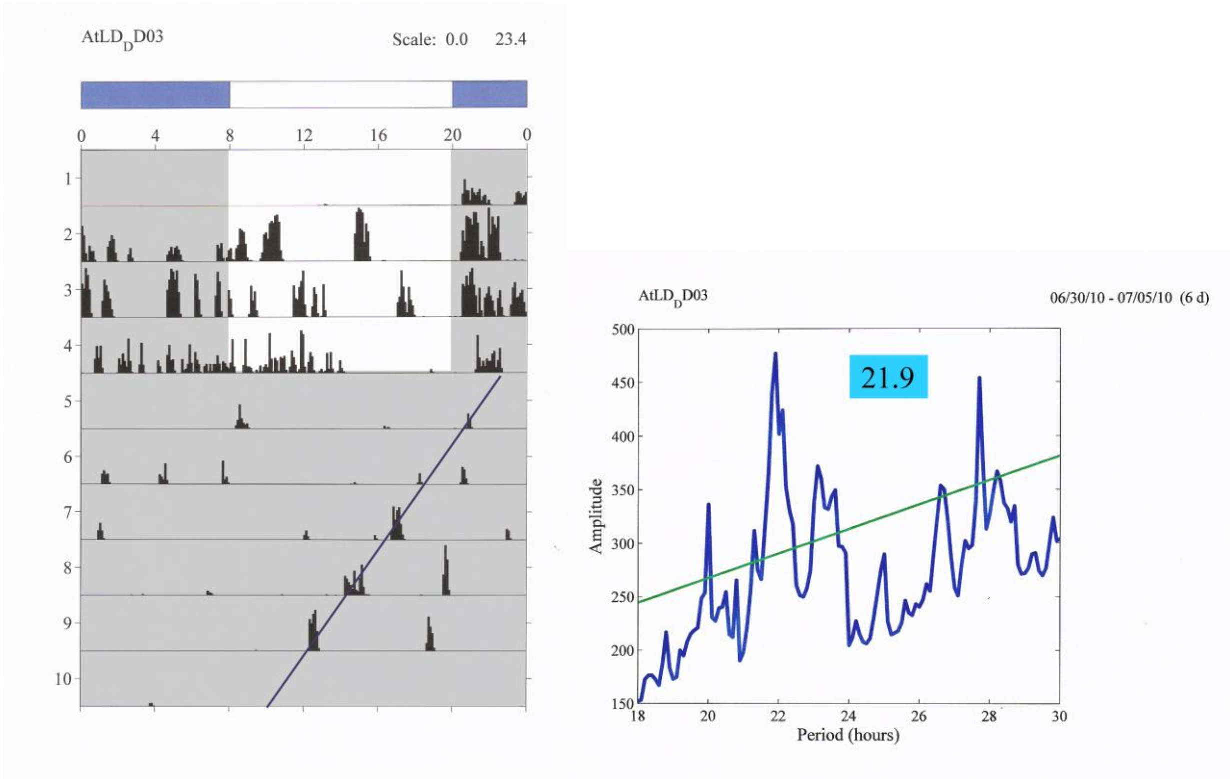

Fig. 4—Actogram and periodogram documenting the activity of Spider 03. Period was 21.9 hrs, p<0.001.

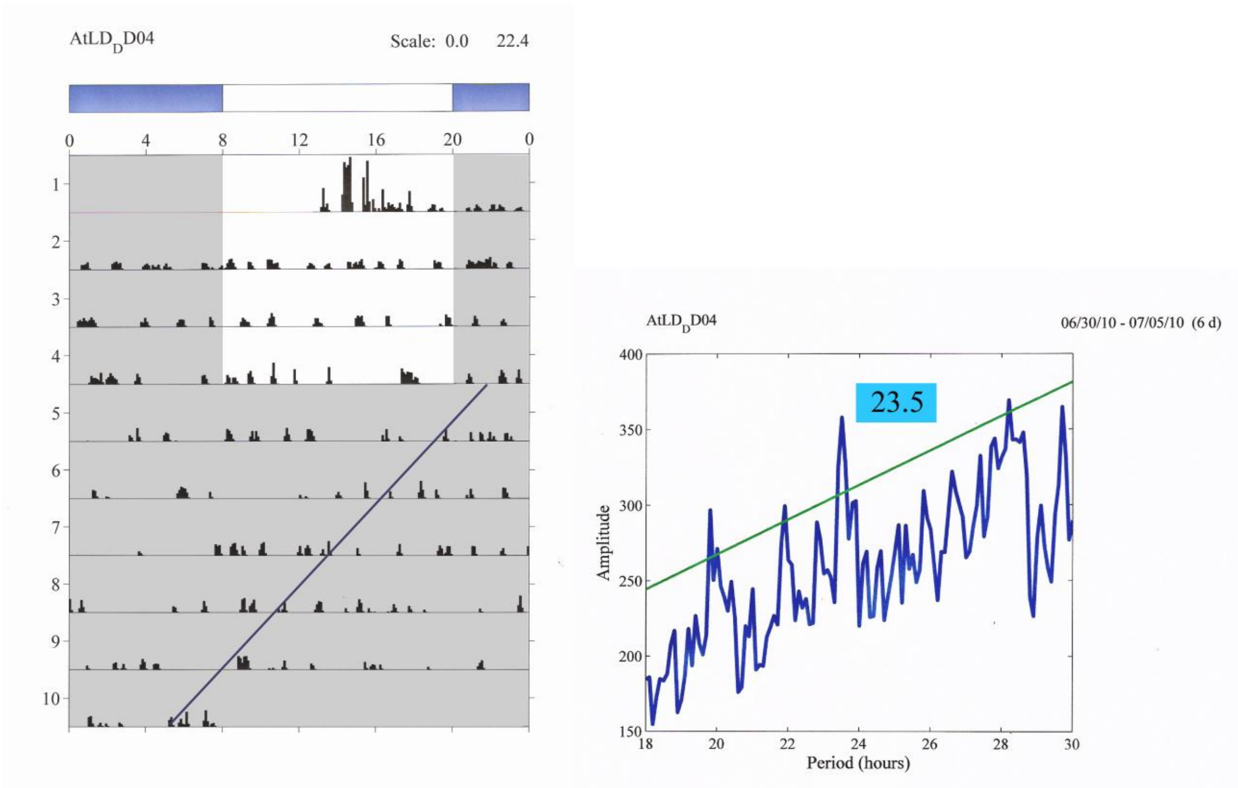

Fig. 5—Actogram and periodogram documenting the activity of Spider 04. Period was 23.5 hrs, p<0.001

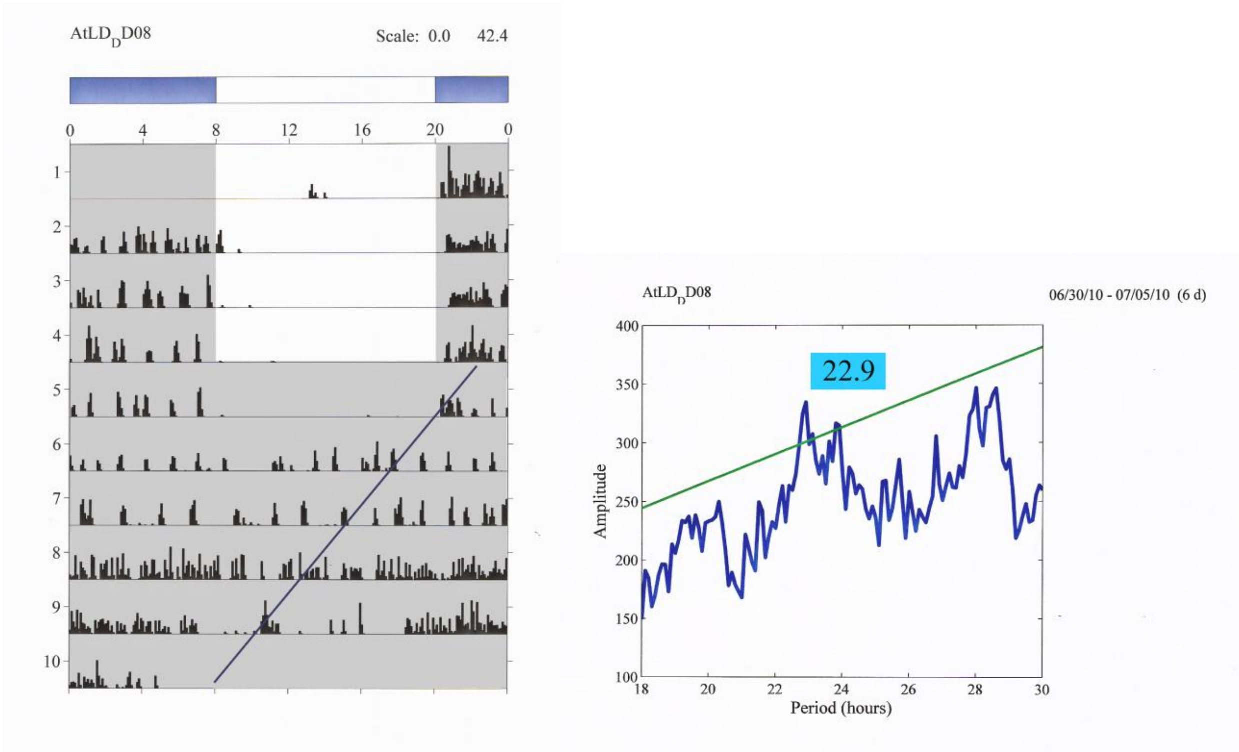

Fig. 6—Actogram and periodogram documenting the activity of Spider 08. Period was 22.9 hrs, p<0.001.

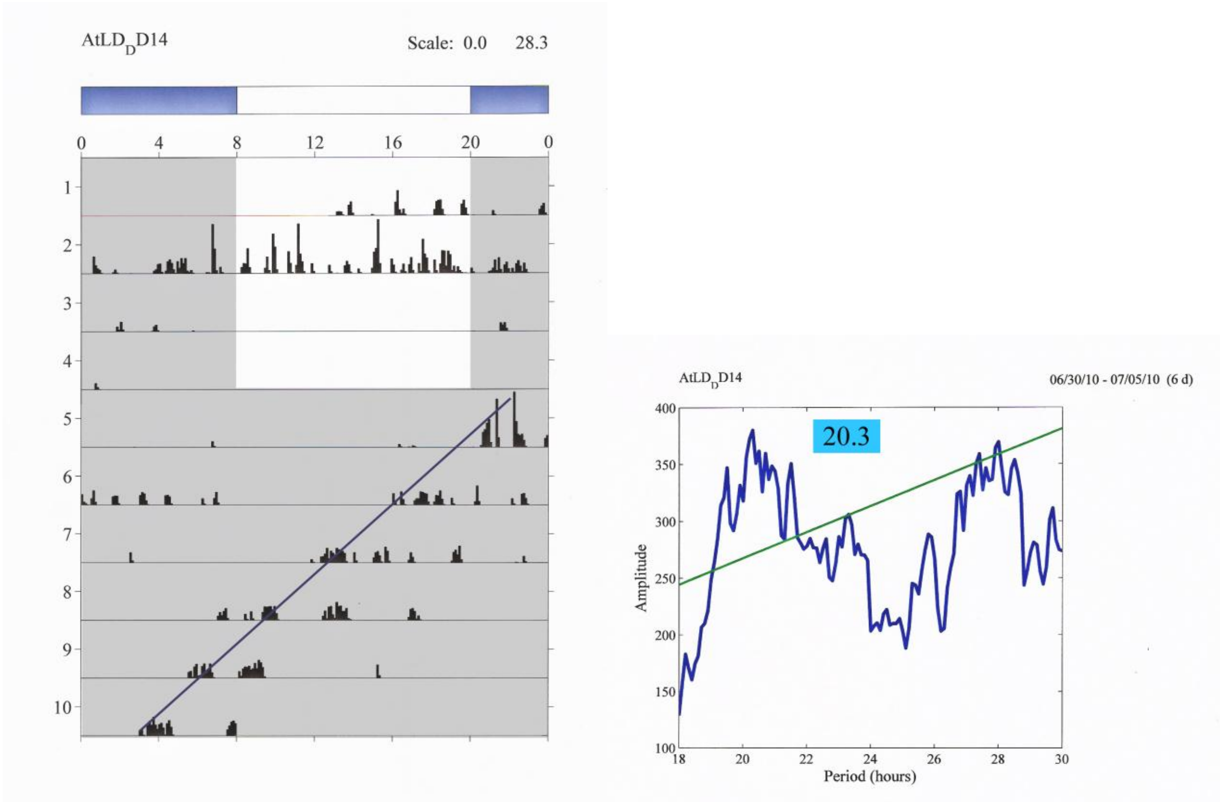

Fig. 7—Actogram and periodogram documenting the activity of Spider 14. Period was 20.3 hrs, $p<0.001$.

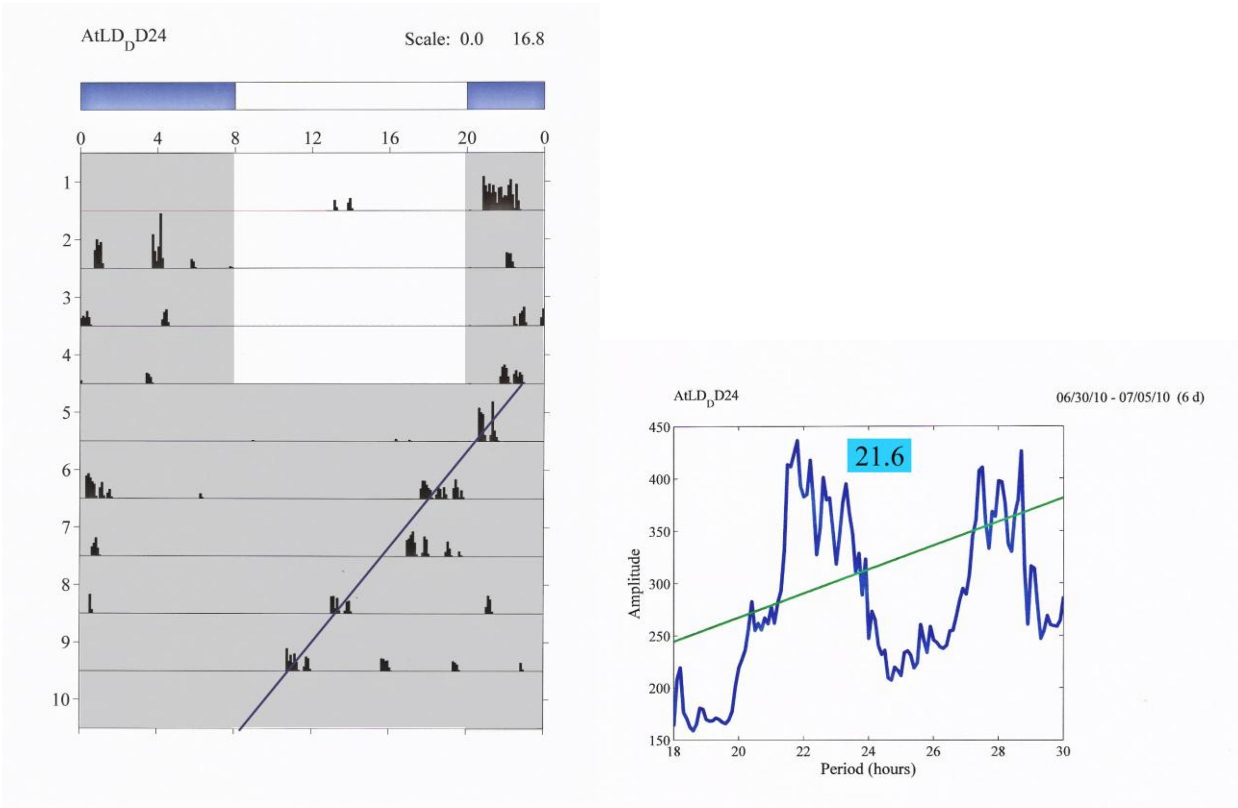

Fig. 8—Actogram and periodogram documenting the activity of Spider 24. Period was 21.6 hrs, $p<0.001$.

DISCUSSION

A. tepidariorum normally does not leave its web, and is potentially a round-the-clock forager, so we predicted that it would be arrhythmic in its activity. However, our results clearly show that this species has nocturnal activity patterns. We speculate that the spiders may be performing web-maintenance behavior during this time, and not strictly foraging. By being active during darkness, the spiders may potentially be balancing the risks of predation with the benefits of better access to prey. Since the most common predators of spiders are diurnal, the spiders would most likely move to a more defensible position in the web during the day, which is what our results suggest they do. The web position observations showed that during the day, the spiders generally stayed closer to the top of the web (Fig. 2), which, while possibly making it more difficult to respond to prey quickly, would allow them to stay hidden from predators. During the night, the change in position to the center of the web may allow the spiders to attack prey more quickly, due to better access.

Results also confirmed the presence of an endogenous clock in this species. This was shown by the free-runs during the DD period of the LD and DD observations. In regard to web position, the spiders seemed to “anticipate” the coming of darkness by dropping down and to the side of the web prior to lights-out, more evidence of an endogenous circadian clock at work, as also found. This perceived anticipation of the daily cycle may allow the spiders to take advantage of different foraging situations. For example, by dropping down to a more favorable foraging position just before the onset of darkness, a spider may be able to take advantage of potentially higher prey densities during the crepuscular period. During this time they may be involved in web-building activity to prepare for the possible influx of prey.

The LD and DD observations also revealed that though the spiders changed position prior to darkness, they only became active about an hour *after* the onset of darkness. We do not readily have an explanation for this behavior. We speculate that the spiders may be taking this time to sit and wait for prey, then after time has passed they begin activities like web-building. More observations are needed to confirm the true reasons for this behavior.

We found that *A. tepidariorum* exhibits clear nocturnal circadian activity patterns, contradictory to our prediction that this species would be arrhythmic. The spiders also showed possible anticipatory behavior in their daily movements, as shown by their dropping toward the center of their webs prior to nightfall. However, they only became active after approximately an hour after darkness. Future studies will be needed to document the specific activity of the spiders during this period. In addition, studies of the antipredator behavior of this species may be conducted, in relation to its circadian activity patterns. This would be in comparison to the study conducted with the orb-weaver *Larinioides cornutus*, which was found to exhibit anti-predatory behavior in a nocturnal circadian pattern (Jones et al., *in prep*).

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