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Temporal Factors Affecting Foraging Patterns of a Diurnal Orb-weaving Spider,

Micrathena gracilis (Araneae: Araneidae)

By

Mitchell Davis Long

An Undergraduate Thesis Submitted in Partial Fulfillment
of the Requirements for the
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ABSTRACT: Several studies have investigated the ecological factors that affect behavior in *Micrathena gracilis*, a diurnal orb-weaving spider that forages on flying insects during the day. However, none yet have considered how the temporal distributions of prey and predator occurrences shape their daily behavioral rhythms, especially web construction, which involves a heavy energetic investment well in advance of potential nutritional benefit. Recently, several orb-weaving spider species have been shown to exhibit a variety of abnormal rhythms, suggesting that circadian clock-controlled rhythms may play an unexpected role in behavioral evolution. Despite the appearance of significant insect abundance in the evenings, *M. gracilis* individuals stop foraging, take down their webs, and retreat before they can capitalize on this opportunity. Is the nutritional benefit of this forfeited prey significant compared to what they collect during the day, and if so, what potential cost might justify opting out of this potential gain? To investigate, sticky traps for prey collection and a camera array for recording predator activity were used at a local field site to survey what risks and rewards these spiders face throughout the 24-hour day. Spider activity and web captures in the field were also used to confirm behavioral patterns and capture success throughout the day. It was found that spiders begin foraging when prey becomes available but cease while prey is still abundant. These observations appear to support a theoretical model of behavioral decisions under predation risk. However, recorded predation events were rare, and predation was not confirmed outside of the foraging timeframe. These results support the notion that the circadian rhythm of *Micrathena gracilis* is shaped by factors other than prey availability, but the theoretical pressure from predation risk requires further investigation.

INTRODUCTION

A Diurnal Model of Foraging and Predation Risk Trade-Offs

Virtually all organisms are subject to selective pressures that drive their optimization for a given environment. Pressures to obtain food and mates weigh on the lifetime success of a given individual, but a lengthy string of repeated failures is generally required for these to significantly impact the lifetime fitness of the individual; one day of poor performance is likely to be negligible. Predation, however, is a pressure that can eliminate an individual's future fitness in a single event. A population ill-prepared for exposure to predators will experience extremely harsh selection in favor of the few that manage to survive, and the more frequently predation occurs, the stronger this selection will be.

Organisms regularly juggle numerous considerations when making decisions in the face of predation risks. Foraging behaviors encourage the nutritional intake for energy to expend finding a mate or producing and raising young, and mating behaviors encourage exposure for attention or moving to seek out a partner. At the same time, the risk of predation encourages forfeiture of risky behaviors that could lead to the death of the individual if discovered. Previous studies have considered how individuals from a myriad of species actively make decisions in response to the potential risk of and actual interaction with their predators (Lima and Dill 1990). While previous review has increased temporal resolution from evolutionary time over many generations to ecological time over an individual's lifespan, few studies have continued even further into considering environmental risks and rewards in the temporal context of a daily cycle.

It is here, on a moment-to-moment scale, that prey acquisition and predator risk truly occur, as the time of day determines what organism interactions are likely to occur.

Organisms adapt to these daily cycles through circadian rhythms, which are present in almost all taxa examined to date. A circadian rhythm allows an organism to coordinate daily processes with predictable environmental cues, such as bats expressing circadian entrainment that allows them to anticipate sunset and begin their nightly activities proactively rather than reactively (DeCoursey & DeCoursey 1964). These adaptations allow organisms to anticipate a variety of events in the environment, such as upcoming periods to capture prey or to avoid predators that become active, and disruptions are often severely detrimental, including with humans who may experience sleep and behavioral disorders as a result. These periods are especially key for orb-weaving spiders, which not only serve ecologically as both predator and prey simultaneously but also prepare well in advance for food availability by building their orbs, oftentimes before the first daily appearance of prey. This preemptive web-building also represents a significant energetic investment from silk production, and ill-timed construction may result in web destruction from passing animals or lowered capture success of targeted prey.

Several studies have demonstrated interesting circadian rhythmicity in orb-weaving spiders. *Cyclosa turbinata*, a species that forages on a large orb during both day and night using a collection of debris in the web to obscure its body, appears to modulate its web abandonment and thanatosis (apparent death) antipredator behaviors based on the time of day (Watts et. al. 2014). Doing so allows alternating between fleeing the web while prey is scarce and avoiding detection to minimize time lost returning while prey is abundant (Watts et. al. 2014). Female *Anelosimus studiosus*, a subsocial species that forages on sheet webs, also demonstrate flexibility

in both aggression and antipredator behaviors depending on the time of day and whether or not they are brooding, becoming more bold during periods of increased prey availability and when protecting their newborn young (Watts et. al. 2015). *Larinioides cornutus*, a species that forages on a large orb only during the night, displays variable aggression depending on time of day, becoming more aggressive at night when attacking prey but more timid during the day when hiding from predators (Jones et. al. 2011). The foil to this rhythm would be a diurnal species that forages only during the day and retreats in the evening—a behavior pattern seen in *Micrathena gracilis*, an orb-weaving species with ecological interactions that are well-understood but have yet to be analyzed in a temporal context.

A previous model of temporal variation in predation risk predicts that energetic state and environmental and internal parameters all interact to determine the optimal foraging behavior (Watts et. al. 2018). Individuals in a lower energetic state (having less energy available due to less prey consumed) should partake in riskier behavior in order to compensate, and individuals in a higher energetic state should avoid doing so; predation risk should severely decrease boldness even when prey encounter rate is high, but once predation risk subsides, boldness should increase to take advantage of prey availability (Watts et. al. 2018). The latter predictions of predation risk and prey encounter can be tested in the field, and the previously mentioned *M. gracilis* offers a potential case study that may fit these predictions.

M. gracilis individuals must balance successful foraging with predation risk in their natural environment. These spiders forage exclusively during the day, which, according to the predictions above, indicates that this is either the time of the highest prey availability or the time in which predation is relieved—or both. If predators are still present while prey becomes most

abundant, the potential benefit of prey capture must be substantial to justify the exposure to predators. Additionally, it might be predicted that *M. gracilis* may have some means of mitigating predation during the daytime while they are exposed.

Also of note is the time at which *M. gracilis* ceases foraging in the early evening and retreats to a nearby branch or foliage for protection. These spiders consume the orb of their webs just before sunset, taking in small prey that were ignored during the daytime. Several potential explanations for this timing may be proposed. Firstly, this may be the time of day when prey becomes significantly less abundant. Secondly, this may be when risk of predation or web destruction begins to climb as the evening progresses. Thirdly, foraging behavior may be suppressed when capture efficacy is reduced or if the environment is not conducive to web construction, and predator avoidance behavior may be suppressed if predation risk is perceived to be lessened.

Because the webs of *M. gracilis* are much more isolated in space between attachment points than typical orb-weaving spiders, the spider itself is highly exposed to any flying predators that might pluck it out of the web, suggesting that any predator presence is highly risky for these spiders. Additionally, the web itself is at risk of destruction from passing animals that may walk or fly through it, causing a loss of the small prey caught in the orb if the spider has not taken it down beforehand. If prey is available during the night, then perhaps these risks outweigh the potential benefit; if prey are not available, or are very sparse, then these risks inevitably outweigh the benefits because there are none to be had. Any destruction when there is no prey available results in a net loss to the individual spider. Interestingly, the frame strands between attachment points are sometimes left up after the orb is consumed, indicating that doing

so is either less risky because of their placements along foliage and branches or less detrimental to the spider should they be knocked down because these strands catch no prey. All considered, *M. gracilis* appears to pose a unique model of the balancing act between foraging and predation risk. Here, these ecological factors are investigated.

Spider Activity: Confirmation of Previous Study

As *Micrathena gracilis* are unusual among orb-weaving spiders in that they appear to be a strictly diurnally foraging species from observations in the field, their activity patterns should be quantified to put the behavior of the individual spiders in a temporal context. To verify previous observation and study, we expect specimens to forage exclusively during the day, following along the model of maximizing prey availability and minimizing predation risk.

Prey Availability: A Theoretical Driver of Activity Periods

Many studies have investigated what prey orb-weaving spiders capture, and some compare these captures to a broader profile of what insects are available in the environment (Chacon & Eberhard 1980; Uetz et. al. 1978; Biere & Uetz 1981). Such studies of *Micrathena gracilis* in particular construct a picture of prey selectivity in the species guided by different behavioral responses (Uetz & Hartsock 1987). Due to their web positioning above the ground between distant anchor points, these spiders capture flying insects almost exclusively, largely from the Orders Diptera, Coleoptera, Homoptera, and Hymenoptera, which encompass the majority of the available prey in the microhabitat the spiders prefer (Uetz & Hartsock 1987; Biere & Uetz 1981). *Micrathena gracilis* appear to specialize in the active capture of rarer,

larger insects between 4-8 mm that offer more biomass, generally ignoring more abundant, smaller prey less than 3 mm that strike the web and remain trapped until the evening (Uetz & Hartsock 1987). The spiders largely detect these insect strikes through vibrational cues in the web, which contributes to their ability to discriminate insect size before approaching: larger prey items that remain caught in the web create more vibration over a period of a few seconds, increasing the likelihood that the spider responds and invests the energy (venom, silk, and movement) needed to secure the item. Smaller prey items that fail to catch the attention of the spider or that are actively ignored remain in the web until it is taken down at night, likely resulting in some caloric benefit without any investment from the spider beyond what has already been invested in web construction (Uetz & Hartsock 1987). Particularly large prey items are likely to escape instantaneously (Uetz & Hartsock 1987), which prevents exposure of the spider to the danger of a counterattack when approaching prey with a size advantage and provides possible explanation for why the spiders sometimes hesitate momentarily before approaching an insect that has struck the web. This also follows the theoretical model of forfeiture of some potential nutritional benefit if risk of predation (or in this case, being killed from the potential prey item defending itself) or the potential loss in otherwise captured prey (from the spider being knocked out of the web or fleeing and being unable to capture abundant prey) is high.

Recently, spiders have been shown to exhibit significant and unexpected variability in their circadian rhythms, likely capable of differences in individual expression which provide the raw material for potential evolutionary change (Moore et. al. 2016). As previously noted, orb-weavers must prepare well in advance for the insects they intend to catch and are ill-suited

for opportunistic predation. *Micrathena gracilis*, confirmed by field observations, consistently begins to forage in the mid- to late-morning and concludes with web takedown in the early evening. If insects are available in abundance on either end of this foraging period, then following the theoretical model of activity aligning with prey availability, *M. gracilis* will likely adapt to extending the foraging period earlier or later to take advantage of the availability of prey, taking in more biomass and thus being able to dedicate more energy to more or higher quality offspring. Thus, it logically follows that with no other significant pressures in play, *M. gracilis* foraging activity should align with the availability of prey in order to maximize nutritional gain from energetic investment in web construction. It also follows that periods of spider inactivity should align with times when the prey these spiders are typically able to capture is less abundant, especially if available prey during these periods is comprised largely of prey types that *M. gracilis* struggle to capitalize on, such as *Lepidoptera* that are difficult to catch with web adhesive due to the powdery scales that prevent adhesion to the insect's body. *M. gracilis* deciding how to respond to prey through vibrational cues further supports that foraging in increasingly dim conditions as the evening progresses should not pose a significant challenge. Deviations from the ideal foraging time are predicted to be due to other challenging ecological factors, such as temperature stress and especially predation risk, that outweigh the potential benefit of continuing to forage, according to the theoretical model of risk aversion.

While previous studies have compared what *Micrathena gracilis* have been observed capturing to what is available in the environment over the course of daily cycles, no studies have framed the available prey in terms of temporal availability. By observing trap captures over the

course of several full 24-hour daily cycles, a profile of insect availability over 2-hour time periods can be constructed which can be considered for support of the theoretical model.

Predation Risk: A Theoretical Driver of Inactivity Periods

The antagonist of activity periods, according to the theoretical model, is the risk of predation, made especially potent by the risk of instantaneous, complete elimination of potential fitness. If predation may begin to offer an explanation for why these spiders forego additional nutritional intake, another aspect of their physiology must be considered related to their defenses: their pronounced abdominal spines. The development of spines on mature females continues to lack significant, empirically-based explanation. A phylogenetic analysis of the evolution of sexual dimorphism and development of spines in females throughout the *Micrathena* genus showed substantial variation, with spines ranging from complete absence to highly exaggerated, suggesting that spine evolution is relatively rapid with many examples of convergence, indicating similar ecological conditions for many species (Magalhães & Santos 2012). Historically, the function of abdominal spines has been assumed to be predator defense, as the females that forage throughout the summer are increasingly exposed to predators as they sit in their webs out in space. This risk may be exacerbated by the lack of stabilimenta (Opell et. al. 2006) that may provide camouflage for the spider or increased visibility to avoid web destruction (Blackledge 1998) and the absence of hiding places near the web that provide opportunity to retreat to cover (Eberhard 2007). Courtship in *Micrathena* is largely based on tactile stimulus from web plucking rather than visual stimuli, so the spines are unlikely to serve a purpose in sexual selection (Magalhães & Santos 2012). Abdominal spines may specifically discourage

predation by wasps and smaller birds, as the increased spatial profile of *M. gracilis* in particular may make it difficult for a bird to swallow whole prior to gizzard processing or for a wasp to bring the larger body back to a nest for packing into cylindrical tubes (Magalhães & Santos 2012). This may also be an explanation for why spines do not develop in males, as they do not spin webs to forage and thus lack the same exposure to predators, benefiting more from the increased mobility of their smaller size and lack of spines (Magalhães & Santos 2012). The patterns of spine development and variation are very similar to that observed in *Gasteracantha* species, which also lacks significant explanation for the function of spines (Levi 1978).

Additionally, the black-and-white coloration of female *M. gracilis* makes no statistically significant difference in prey capture success (and may even slightly decrease prey capture), indicating that it may contribute to crypsis to aid in avoiding visual predators, either while in the web or while retreated overnight along exposed tree bark (Vanderhoff et. al. 2008). The idea that the white coloration observed in spider abdomens aids in deterring predators is supported by it being composed of a metabolic waste, guanine, that can be seen through the cuticle, likely serving as an indicator of foul taste (Anderson 1966). Recent phylogenetic analysis of guanine coloration in spider species found in Britain, for example, have shown that increased presence of guanine causing a white or silver coloration is more commonly associated with spiders that tend to live in more open and exposed habitats, especially in spiders that are relatively large (Oxford 1998).

While previous studies focus on interactions with predators in which spines would be beneficial, these spines would not aid in protection from organisms capable of chewing or breaking off spines before ingesting, such as mammals with developed jaws. Of particular

interest in the ecosystems where *M. gracilis* are found are various types of bats, which begin to hunt before sunset and continue into the middle of the night, swooping through open areas to collect flying insects such as *Lepidoptera* (DeCoursey & DeCoursey 1964). These bats may pose a significant threat for *M. gracilis* should they remain exposed in the evening where bats may easily collect them from their spatially isolated webs; these spiders are of a size that could provide enough biomass to be worth the effort while not being so large that they are difficult to consume while airborne. Additionally, because bats hunt by echolocation in poor light conditions, the potential crypsis or visual deterrent provided by the spiders' coloration provides no protection from these predators. Bats or ecologically similar predators, especially those that thwart the spiders' defenses other than fleeing, may provide the predation risk that drives periods of inactivity for the purpose of risk aversion that the theoretical model predicts.

METHODS

Study Species

Micrathena gracilis is a species of diurnal, orb-weaving spider that is commonly found in forested environments throughout the Eastern and Northern United States (Levi 1978). The species is sexually dimorphic, with females growing larger (0.5-2 cm) with pronounced abdominal spines and males remaining smaller (>1 cm) without spines after hatching in the spring (Bukowski & Christenson 1997). In summer, female spiders construct relatively small orbs (8-19 cm in diameter) with very tightly packed capture spirals (averaging 1.3 cm between threads) in the morning (Opell et. al. 2006), typically completing spirals and taking position in the center to forage by 10:00 AM (Biere & Uetz 1981). They forage throughout the daytime, take down their capture spirals in the evening, and sometimes leave the frame strands up to reuse them the following day (Hodge 1987a). After taking down their webs, these spiders retreat to a nearby branch or other cover to wait for morning.

Micrathena gracilis have strong affinity for deciduous forests that provide a shady habitat, protection from wind, and many potential attachment points for their webs (Hodge 1987a & 1987b). These sites also facilitate their reproductive cycle, as females will oviposit egg sacs into curled, dried leaves in the fall which will hatch the following spring (Moya et. al. 2010). Once situated in their preferred habitat, these spiders typically reside in the same area unless they experience significant stressors, usually in the form of excessive UV exposure (Biere & Uetz 1981) or dramatic energetic loss from web destruction or several days with no success foraging (Hodge 1987b). They exhibit temperature regulatory behaviors by orienting in the web to

minimize UV radiation exposure from the sun, likely to compensate for variable sunlight exposure in patchy deciduous understory, as their body temperature rises significantly more than the ambient air when exposed due to their mostly dark black coloration (Biere & Uetz 1981). The spiders' webs are also somewhat vulnerable to UV exposure, which decreases the efficacy of the adhesive over time (Stellwagen et. al. 2015). The webs exhibit a relatively high degree of adhesive strength, encouraging the capture and prolonged retention of all but the largest insects capable of escape, and do not reflect UV light (Opell et. al. 2006). These webs are constructed relatively far out in space from attachment points, spanning over 3 m in some locations, and can be centered over 5 m above the ground. Orientation angle relative to the ground and compass direction of the web face have been shown to make no significant impact on foraging success and are thus likely determined by availability of attachment points rather than an optimal positioning (Biere & Uetz 1981).

Study Environment

The study plot used was a small, fenced woodlot in Washington Co., Tennessee. The plot consisted of patchy deciduous forest characteristic of the natural habitat of *Micrathena gracilis*, with scattered shrubbery and grasses in the understory and a relatively high canopy providing a large shaded area. All days used for the study were warm with a mean high of 28.06 °C (SD: 3.03 °C) and a mean low of 15.00 °C (SD: 3.11 °C), sunny or partly cloudy, and had no precipitation. Sunrise and sunset times and temperatures at 10:30 AM and 7:30 PM were retrieved from weather records after the study concluded in order to explore daily cycles of

abiotic factors that influence spider behavior. Data was collected once per week for four weeks, beginning on August 29th, 2019 and ending on September 20th, 2019.

Spider Activity

For observation and web captures of *Micrathena gracilis*, the study site was seeded with specimens collected from several local (<40 km from study plot) areas: Bays Mountain Park (a nature preserve in Kingsport, TN), Winged Deer Park (a public park in Johnson City, TN), and University Woods (near ETSU's campus in Johnson City, TN). Spiders were released onto shrubbery and trees resembling typical retreat locations either the night before or the morning of the beginning of 24-hour observation periods. Spiders released in the morning were kept in a dark cooler overnight beforehand to minimize artificial light exposure and possible shifts in activity periods. Spiders were observed through the 24-hour observation periods often, and web-building and prey capture times were recorded. Spider observations were typically made at least each hour, allowing higher resolution in recording these events. In total, 29 spiders were observed over a 4-week span.

To aid in determining when *M. gracilis* were truly inactive versus being taken by predators or otherwise disappearing, spiders were located as much as possible even while outside of the web. Only spiders present in web centers at some point in the hour time block were considered to be foraging for the hour and able to take advantage of prey becoming available to them on the web. For example, if a spider was visually observed in the plot but did not complete web construction until 10:30 AM, then it was considered not foraging for the hour time block ending at 10:00 AM but was considered foraging in the hour time block ending at 11:00 AM. If

spiders were observed in retreat or did not have a completed web, they were marked as not foraging unless they spent at least a portion of the hour foraging on a completed web later on in the hour. If spiders were found dead, they were marked as not foraging for the remainder of the day, as these deaths are considered a cutoff point for when the spider should retreat and cease foraging due to predator activity. If spiders could not be found during an hour period, such as in the morning before web building occurred, no observation could be made, and no status was recorded until the spider was found.

Prey Availability

While observing activity, *Micrathena gracilis* prey captures were also observed and recorded. If prey striking the web was actively consumed, it was added to totals of prey captures. If prey strikes were ignored during an hour in which the spider was actively foraging, the prey was still counted towards prey captures, as it would have become available to the spider during web consumption in the evening and contributed towards the hypothetical nutritional gain for foraging during that time block. If prey escaped or disappeared from the web before the web was taken down, it was assumed to be unavailable to the spider for consumption and not counted in prey totals. If prey struck a web that remained up after a spider disappeared or retreated, it was not counted in prey totals, as it is assumed that the spider gave up consumption of these prey items through direct attack or later web consumption in order to avoid stressors or threats.

To collect flying insects and create a profile of what insects are theoretically available for spider consumption throughout the day, adhesive traps were used for collection. Around the study plot, 5 lines of nylon fishing line were tied approximately 1.5-2 meters above the ground

between trees measuring roughly 3 meters apart. The adhesive traps used measured approximately 6" by 8" (15 cm by 20 cm), were yellow in color, and had adhesive on both sides that was covered by wax paper until removed. On each line, 2 traps were attached by 2 twist-ties each to minimize wind disturbance. Each trap was placed roughly 1 meter away from the nearest attachment point on the tree and the other trap on the line. To begin collection, the wax paper was removed from 1 adhesive face per trap to expose it. Within each pair on a given line, the traps were exposed in opposite directions to sample in each direction. 20 of these traps were used, each with 2 adhesive faces, one of which was exposed per collection period, yielding a total of 40 collection samples over 4 24-hour collection periods. Every 2 hours after exposure, the traps were photographed for later reference. At the end of the 24-hour period, the traps were taken down and re-covered with the wax paper for later analysis.

Once traps were taken down, the photographs between consecutive 2-hour blocks were compared to identify which insects arrived on the trap during the time period in a manner similar to previous studies (Watts et. al. 2014). Insects appearing at the end of a time block that were not present at the end of the previous time block were assumed to have struck at some point between the two. Once noted, the insects were identified to the Order level using a light microscope and measured lengthwise to the nearest millimeter. Insects were measured for body length, not including wings or antennae if they projected further than the main body. All of this data was tabulated for later analysis. Insects that escaped from traps before the end of the 24-hour period were removed from the dataset, as they were unable to be assuredly identified using a microscope and are assumed to also likely escape from the webs of *M. gracilis*. Other spiders that were trapped (largely during the night) were excluded from the data, as they are

assumed to be invalid prey for *M. gracilis*. Based on a previous study's observation that insects greater than 9 millimeters were able to escape *M. gracilis* webs at a rate greater than 75%, insects measuring greater than 10 millimeters were removed from the dataset on grounds that they are overwhelmingly likely to escape predation in the web due to stronger forces applied when striking capture strands and a size advantage on the spider, making it difficult to bite and envenomate (Uetz & Hartsock 1987).

Predation Risk

To confirm that bats were present around the study plot and could potentially hunt *M. gracilis* in the area, a Wildlife Acoustics Echo Meter Touch 2 for iOS and an iPhone SE were used to listen to and record bat calls for later identification. These recordings began between 6:00 and 7:00 PM and concluded between 9:00 and 10:00 PM during the first and second 24-hour periods of data collection. Once a potential bat call was recorded, the Echo Meter Touch 2 produced an auto-identification based on known call patterns of local bat species during echolocation, and to further validate this identification, the recorded sound files were processed with the Sonobat Bat Call Analysis Software. Calls were tested for clarity of sound quality and a 95% probability of positive identification.

To investigate the potential for predation by bats and any other threats, *M. gracilis* specimens were collected and frozen shortly after to serve as bait for predators. Because specimens cannot be observed remaining in their webs throughout the day, these specimens aimed to simulate the spiders remaining exposed out in space over a longer period of time. The frozen specimens were strung up with a needle and extremely fine thread by piercing them

through the center of the abdomen and placed in an area of the study plot similar to their natural habitat and separate from the traps and released specimens. These lines were attached to trees, bushes, and a shed structure with duct tape. Directly underneath each spider, an IR CCTV camera feeding to a Q-See DVR for recording was placed pointing upwards with the spider centered in the frame. A total of 8 cameras were used to record 8 specimens to start, and if a specimen fell or was extensively damaged, it was replaced after the first 2 weeks. A total of approximately 10 spiders were used in all over the course of 4 weeks. Care was taken to ensure the spiders were framed against a solid background (in this case, the sky above) to make finding the moment that a spider disappeared possible in the footage. If the spiders were against a moving or patchy background, such as leaves, then identifying the moment of disappearance was, in some cases, impossible, especially if the line simply fell without making obvious movement in frame. While this led to placement in a slightly more open and grassy area than the patchy wooded area used for the traps and specimens, these sites were no more than 30 feet apart, and were thus assumed to have equal risk for the same potential predators. Specimens were simply adjacent to the trees and undergrowth on the outskirts of a clearing as opposed to dispersed among the trees. Lines were checked periodically, and if a spider or line was missing, the footage for that channel was reviewed to identify the moment the spider disappeared if possible. The reason for disappearance was noted if it could be reasonably deduced, and in one case, the footage was exported for later reference.

RESULTS

Study Environment

Sunrise and sunset times and temperatures at 10:30 AM and 7:30 PM were retrieved from an online database to add context to the timing of spider activity. This data is tabulated below (Table 1).

Date of Data	Sunrise Time	Sunset Time	10:30 AM Temp.	7:30 PM Temp.
8/30/2019	6:59 AM	8:00 PM	20.0 °C	22.2 °C
9/7/2019	7:05 AM	7:48 PM	22.2 °C	23.3 °C
9/14/2019	7:10 AM	7:38 PM	25.0 °C	22.2 °C
9/20/2019	7:15 AM	7:29 PM	18.3 °C	21.7 °C
	Average Sunrise	Average Sunset	Avg. 10:30 AM Temp.	Avg. 7:30 PM Temp.
	7:07 AM	7:44 PM	21.35 °C	22.35 °C

Table 1: Abiotic data from data collection periods.

Average sunrise during data collection was around 7:07 AM, and average sunset was around 7:44 PM. The average temperature at 10:30 AM, a typical time in which *M. gracilis* individuals are nearing completion of their webs, was 21.35 °C. The average temperature at 7:30 PM, a typical time in which individuals are taking down their webs, was 22.35 °C.

Spider Activity

Observations of the 29 specimens of *Micrathena gracilis* released at the study plot were tabulated and yielded the following chart (Figure 1).

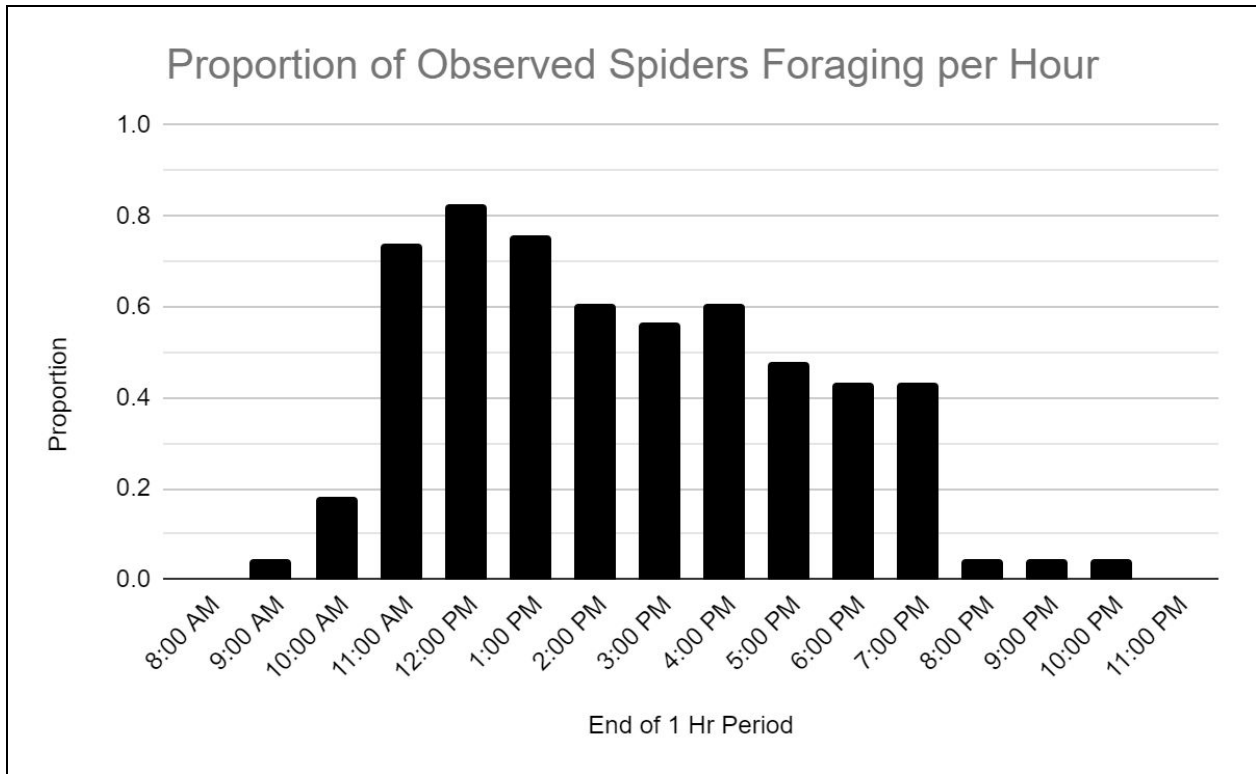


Figure 1: Proportion of observed spiders foraging per 1 hour block.

The majority of individuals completed their orb and began actively foraging between 10:00 AM and 11:00 AM, with the highest proportion of spiders foraging between 11:00 AM and 12:00 PM, and most spiders consumed the capture spiral and ceased foraging between 7:00 PM and 8:00 PM with few exceptions. As the day went on, individuals lost their webs or were repelled from the web by unknown stressors, causing a gradual decrease in foraging spiders that was not due to the spiders deciding to cease foraging early.

Prey Availability

The average liquid biomass available through direct prey capture or corollary web consumption per observed foraging spider per 1 hour block was calculated using a linear regression model (Sage 1982) for calculating wet and dry biomass based on Diptera prey length, which has been shown to be the most common prey type for *M. gracilis* (Uetz & Hartsock 1987). This data, including all hours in which at least one spider was observed foraging, was tabulated and yielded the following chart (Figure 4).

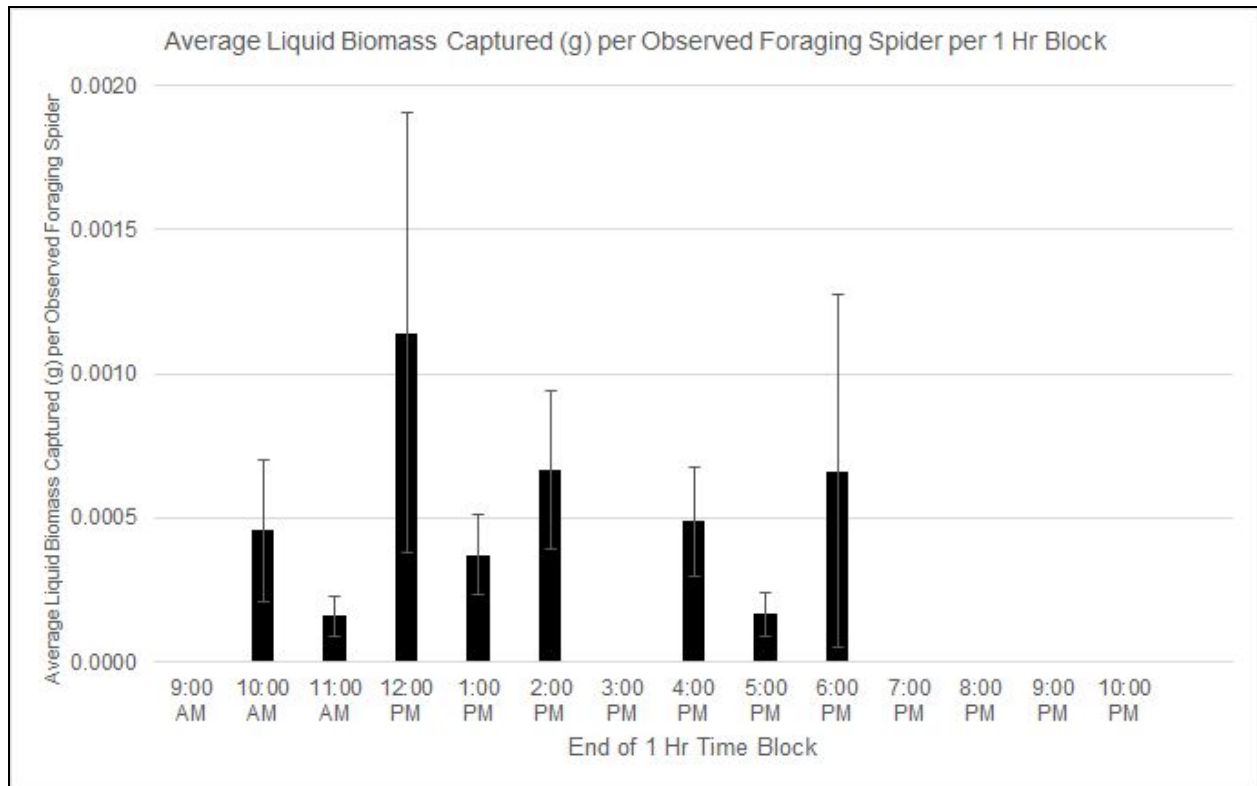


Figure 4: Estimated mean liquid biomass intake per foraging spider per hour with standard error bars.

While at least one spider was observed foraging between 8:00 AM and 9:00 AM, the first recorded prey available to *M. gracilis* foraging in the web was noted between 9:00 AM and 10:00 AM. A consistent amount of prey remained available most hours through the remainder of the day, with the last prey observed being caught by foraging spiders was between 5:00 PM and 6:00 PM. No prey was observed in the webs with an actively foraging spider after 6:00 PM.

Data for flying insects collected in the sticky traps were tabulated and used to calculate the average number of insects trapped per trap per hour during each of the 4 weeks. This data produced the following chart (Figure 5).

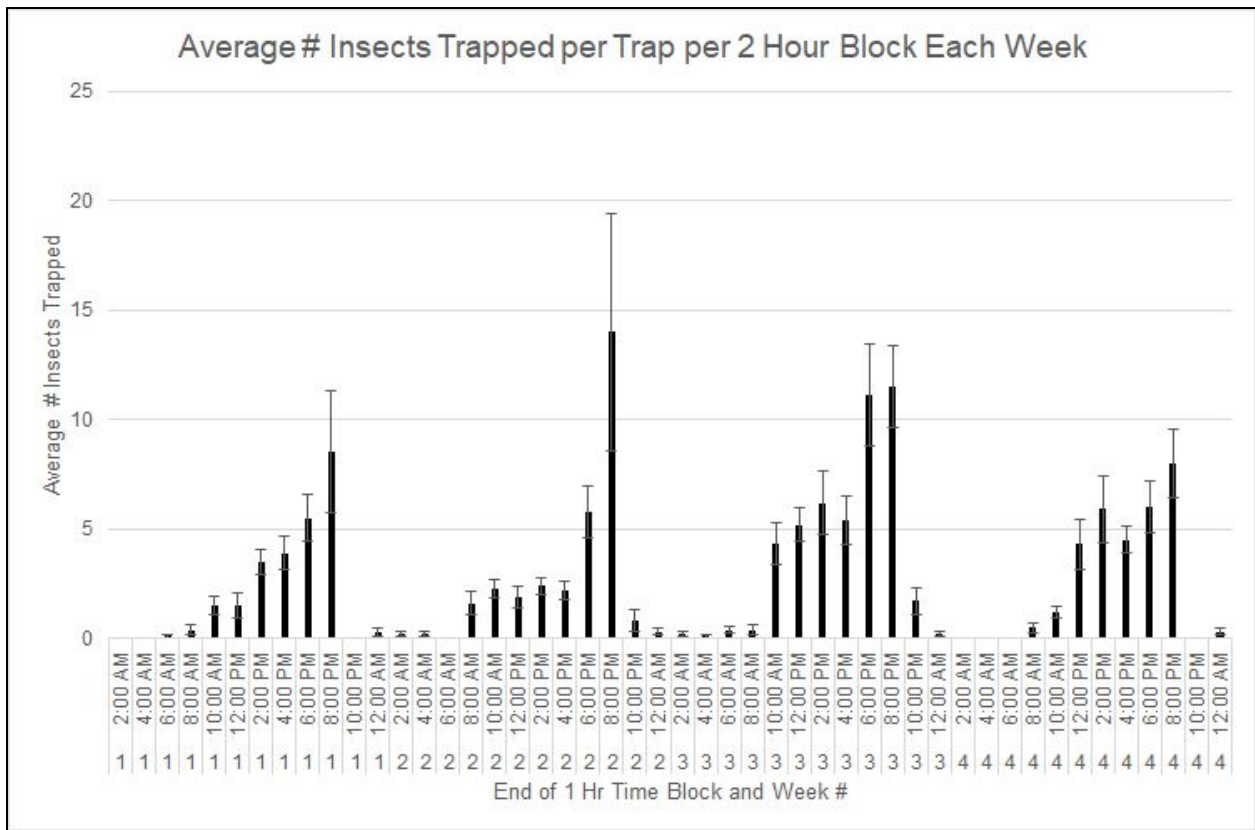


Figure 5: Mean number of insects trapped per sticky trap per hour per week with standard error bars.

All weeks showed a roughly linear increase in captured prey totals per 2 hour block during the daytime, typically beginning between 6:00 AM and 8:00 AM each day. All weeks displayed a highly increased average amount of prey capture in the evening hours, especially between 4:00 PM and 8:00 PM. The highest average number of insects per trap in all weeks was observed to be between 6:00 PM and 8:00 PM. After 8:00 PM, all traps showed a significant drop in captures which persisted overnight. Very little prey was captured between 8:00 PM and 6:00 AM over all 4 weeks.

To account for various Orders of insects offering varying biomass per insect, the lengths of each insect captured were converted into the trapped liquid biomass using the corresponding Order's linear regression model (Sage 1982). The trapped biomass measurements were averaged per trap per 2 hour block per week. This data produced the following chart (Figure 6).

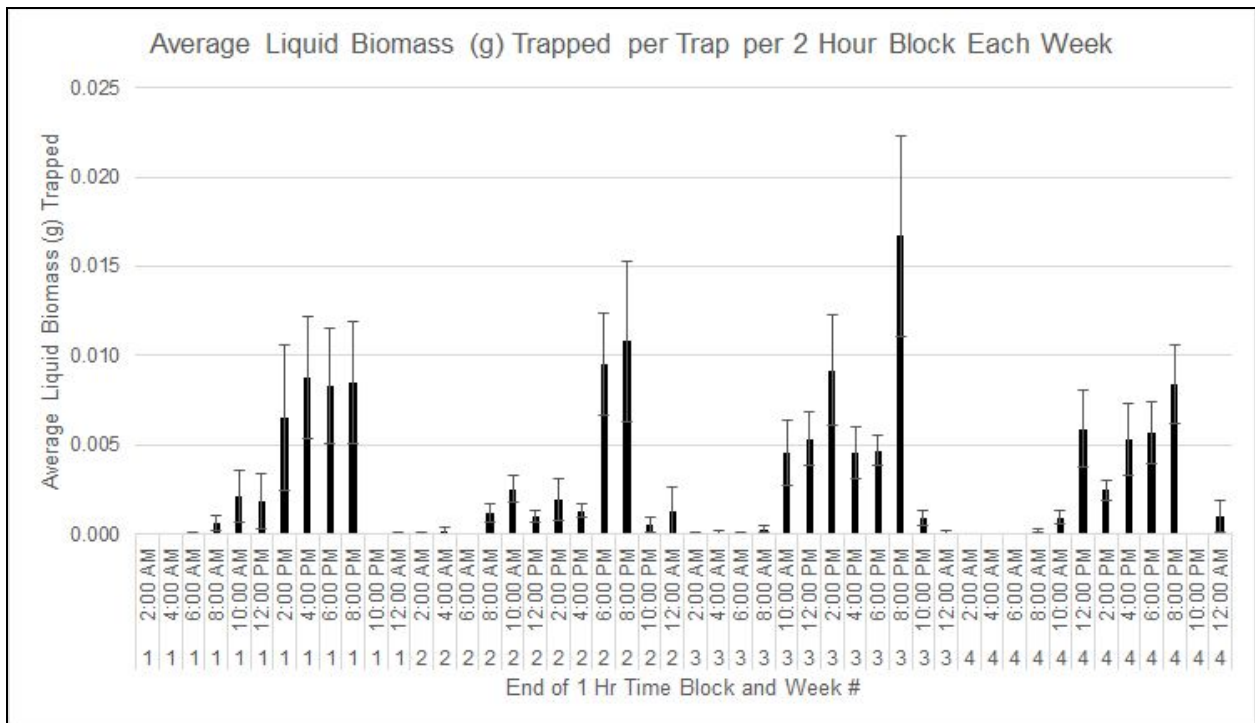


Figure 6: Mean estimated liquid biomass captured per trap per 2 hour block per week with standard error bars.

As with total insects captured per trap, traps showed a gradual increase in liquid biomass captured per 2 hour block throughout the day beginning largely between 6:00 AM and 8:00 AM. The highest estimated biomass captured was between 6:00 PM and 8:00 PM for the latter 3 weeks, while the highest for the first week was between 2:00 PM and 4:00 PM, only slightly higher than between 6:00 PM and 8:00 PM. Biomass availability rapidly decreased after 8:00 PM and remained low throughout the night until after 6:00 AM.

All calculated biomass estimates were totaled per 2 hour block and used to calculate the average biomass trapped per trap location over the course of 4 collection days. This data yielded the following chart (Figure 7).

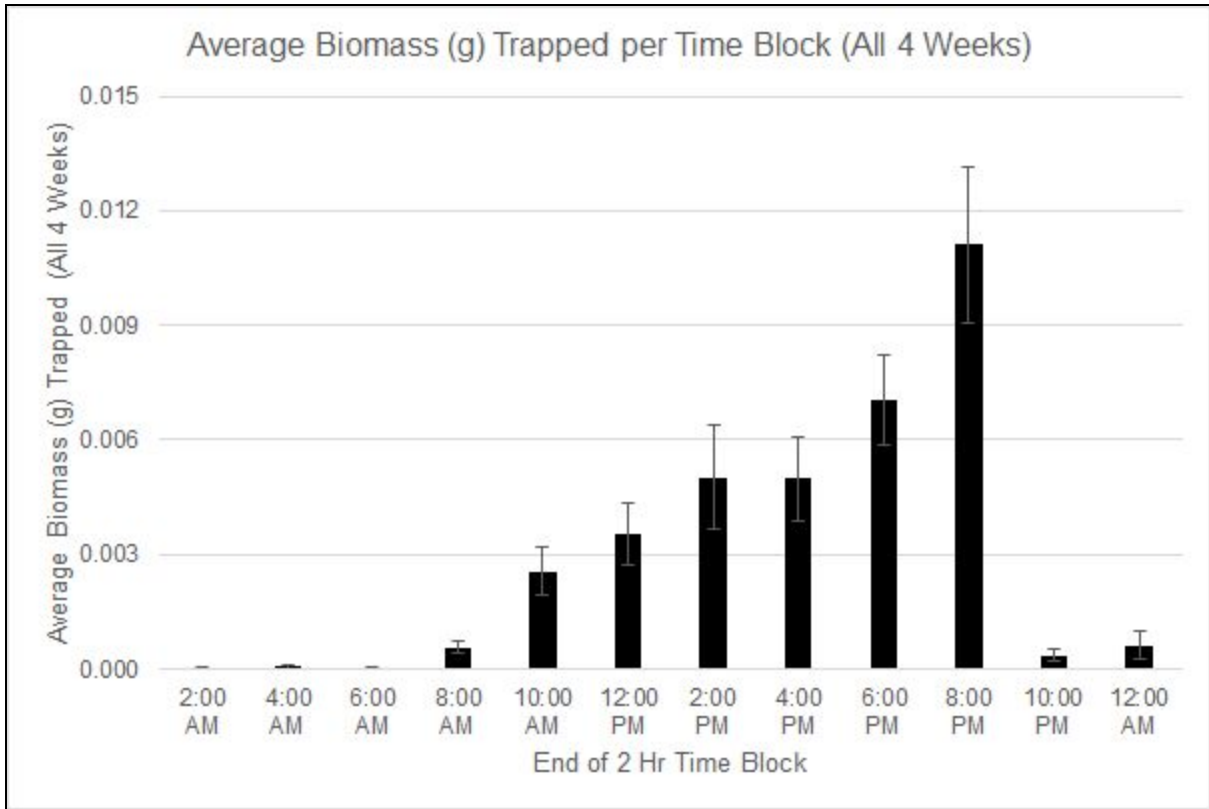


Figure 7: Mean biomass trapped per time block over all 4 collection days with standard error bars.

Averaging all 4 weeks' data yields decreased variance in each of the 2 hour blocks' measurements. The clear increase in trapped biomass as the day progresses, beginning around 8:00 AM each day, appears consistent in all weeks. The sharp decline in prey availability after 8:00 PM also appears consistent in all weeks.

In order to provide context for the Orders of insects being trapped that are assumed to be eligible prey for *M. gracilis*, the average biomass per 2 hour block for 4 collection periods can be represented by the portion of biomass contributed by a given Order. The average biomass

trapped by Order and proportions of biomass by Order yield the following charts (Figures 8 & 9).

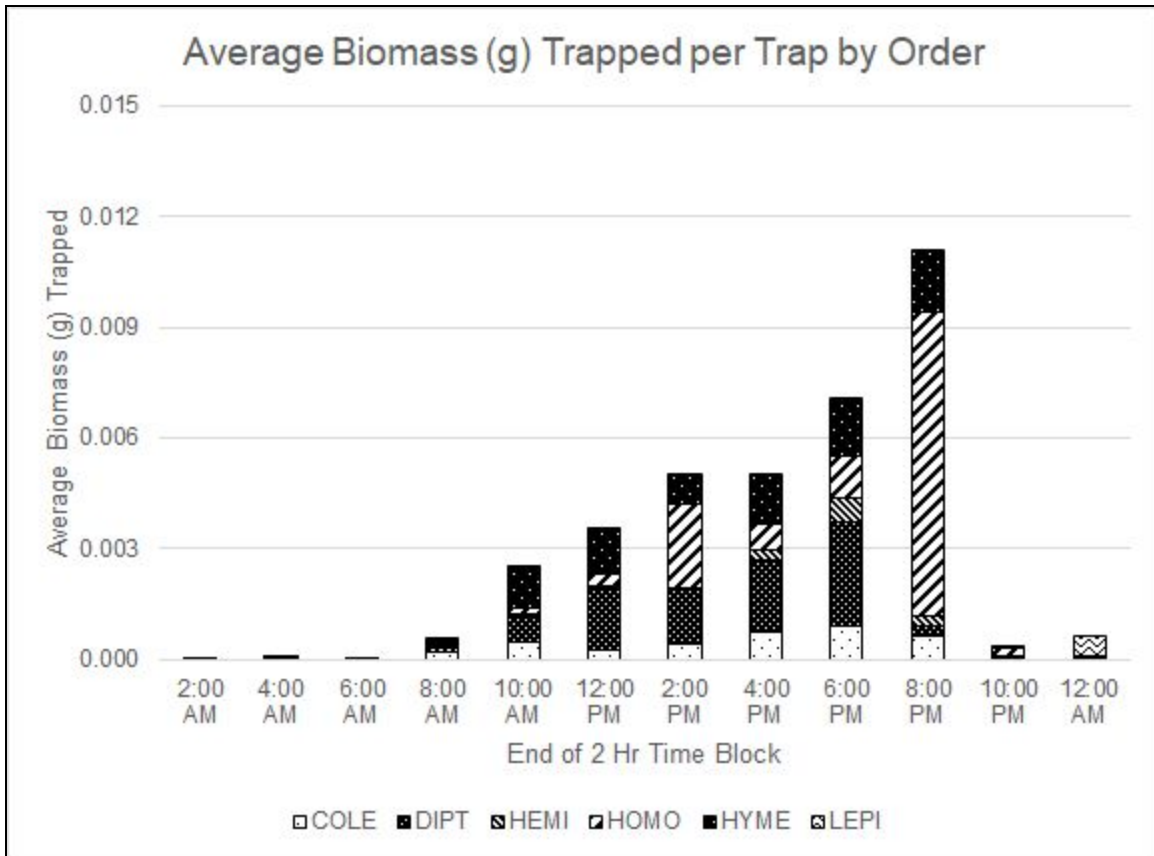


Figure 8: Average biomass trapped per time block broken down by Order.

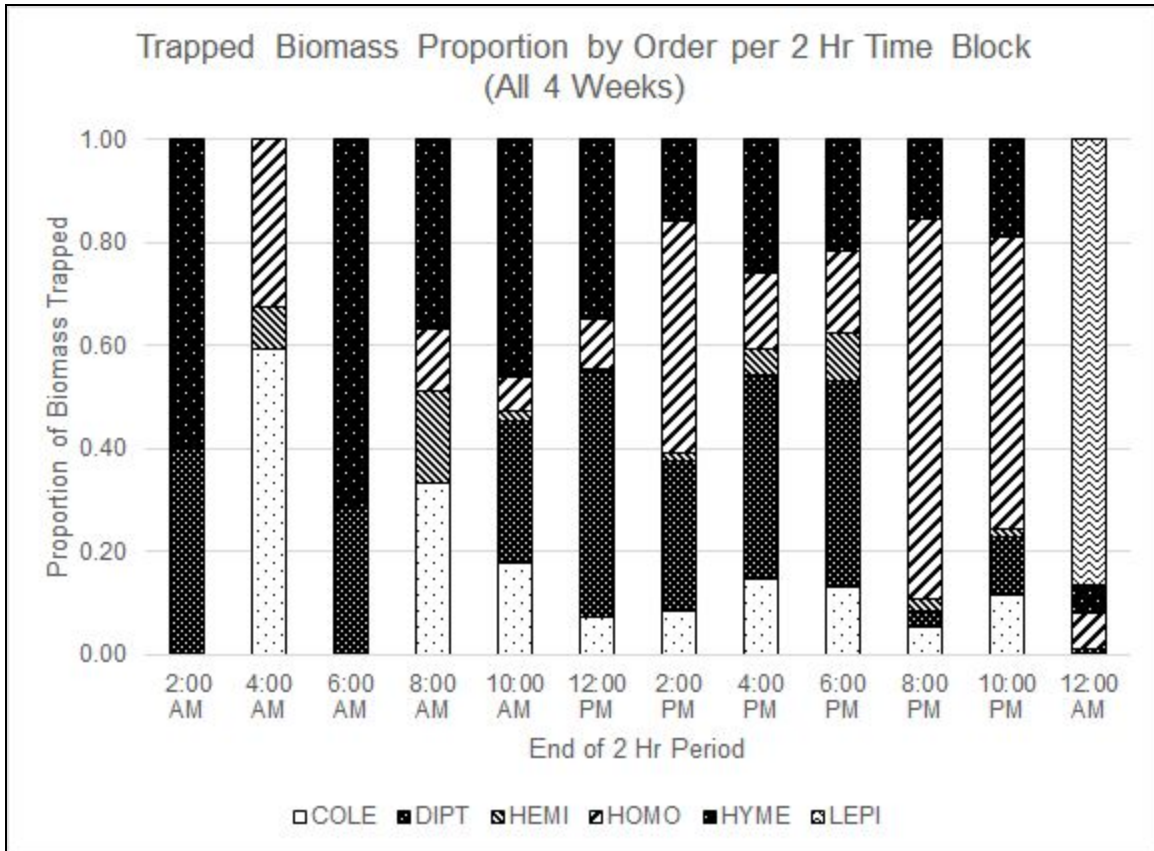


Figure 9: Biomass proportions per time block by Order. Note that these proportions, especially overnight, may be in relation to a relatively miniscule biomass.

Throughout the day, Coleoptera contributed a small but consistent amount to biomass collected. Diptera, a known preferred prey item for *M. gracilis* (Uetz & Hartsock 1987), appeared in increasing amounts from 8:00 AM to 6:00 PM, which aligns with the spiders' typical activity patterns. Hemiptera contributed a relatively small amount to biomass, largely in the afternoon. Homoptera contributed the vast majority of biomass available between 6:00 PM and 8:00 PM during collection periods. Hymenoptera contributed a consistent amount of biomass

during the day, much like Diptera. Finally, Lepidoptera contributed a small amount of biomass during the night when *M. gracilis* are no longer foraging.

Predation Risk

Several potential bat calls were recorded and auto-identified using the Echo Meter Touch 2, including calls from *Perimyotis subflavus* (tricolored bat), *Nycticeius humeralis* (evening bat), *Myotis grisescens* (gray myotis), *Lasionycteris noctivagans* (silver-haired bat), *Lasiurus cinereus* (hoary bat), and *Corynorhinus townsendii* (Townsend's big-eared bat). These calls were analyzed with the Sonobat software, and one single call was of high enough sound quality to confirm an identification with 95% confidence: *Perimyotis subflavus*, or tricolored bat. Thus, bats were found to be present near the study plot, and this was pursued with the camera array.

Frozen spiders that were hung as predator bait were difficult to track and only yielded one predation event: a single spider was taken during the day by a male Northern Cardinal (*Cardinalis cardinalis*). A photograph of the footage in which this was observed is shown below (Figure 10).



Figure 10: A male Northern Cardinal (*Cardinalis cardinalis*) taking *Micrathena gracilis* bait.

Over the first 2 weeks of observation, 8 spiders were placed over cameras. 6 spiders remained on the lines with no change. The lines of the 2 missing spiders fell due to light rain or the adhesive of the tape used to secure the line giving out. Only roughly half of the spiders could be consistently observed in the camera feed, as the other half were placed against an inconsistent background that made identifying the spider's presence in frame impossible. The 2 fallen spiders were replaced with 2 freshly frozen spiders, and the spiders that could not be readily observed in frame were moved to a new location against the sky as a precaution so observation could continue. With 8 spiders in total on lines again, observation continued for another 2 weeks. Roughly a week into the second 2-week period, the cardinal predation event was observed. 1 other line was also knocked down due to rain. The remaining 6 spiders remained on their lines for the remainder of the second 2-week period with no change.

Spiders were observed to dry out significantly over the first few days on the lines. In most cases, after a week of exposure, the spiders were reduced to a dried, brittle exoskeleton with no moisture within.

An additional observation was made of a yellow jacket (*Vespula sp.*, possibly either *maculifrons* or *acadia*) killing a spider in its web during the web observation study in response to striking the web and the spider attempting to attack it.

DISCUSSION

Spider Activity

As predicted, released *M. gracilis* individuals constructed webs and behaved normally in the study plot due to the close representation of their natural habitat in deciduous forest with a patchy understory. When capturing spiders for later release, care should be taken to avoid disrupting the spiders' rhythms, especially when studying them in a temporal context.

In the field, the observed proportions of foraging spiders during each hour of 24 hour days in Figure 1 supports exclusively diurnal foraging behavior in *M. gracilis*, which sets the timeframe for the ecological pressures that the theoretical model predicts. The period in which individuals forage most commonly was determined to be between 11:00 AM and 7:00 PM. Individuals became active well after sunrise, indicating a delay between sunrise and even the early stages of web construction, but retreat was strongly correlated with sunset. During this time, spiders may or may not need to replace frame strands that were left up overnight, and becoming active slightly earlier than prey becomes available offers an opportunity to do so if

necessary. The consistency of this range throughout the observed specimens supports the notion of strong selection for this range of time, which appears to be the increasing availability of prey corresponding to increasing activity, confirming the theoretical model.

Interestingly, a small proportion of spiders was observed foraging before and after the typical timeframe, indicating that there was some variation in foraging timing in the released population. This may have been caused by the process of transporting the spiders to seed in the plot disrupting their circadian rhythm, but if natural, it may demonstrate the prediction of the theoretical model that lower energetic state individuals will engage in riskier behavior to compensate for decreased foraging success in previous days. The energetic state of these individuals was not tested. This may also indicate that the spiders' cue for beginning web construction may not be consistent on a day-to-day basis. Light from sunrise or an increase in ambient temperature due to solar radiation are likely candidates to trigger activity, and these factors will inevitably vary between days. Once spiders are attentive to their surroundings while foraging, they may be better able to discern the cues for web deconstruction, allowing for consistent retreat timing. This may be due to a gradual decrease in lighting or the ambient temperature as the sun begins to set. While spiders responded consistently to sunrise and sunset and the corresponding temperatures during the study period, investigating how consistent daily light conditions interact with experimentally manipulated temperatures and vice versa may clarify a distinction between the two. Another unexplored possibility is whether endogenous circadian rhythms play a role in retreat timing.

Prey Availability

The liquid biomass captured by *M. gracilis* individuals under observation in Figure 4 shows that foraging success varies throughout the day. Most spiders foraging during each hour block realized some nutritional benefit, and the highest average spider income occurred between 11:00 AM and 12:00 PM. The second highest income occurred between 5:00 PM and 6:00 PM but had high variance. No captures were observed after 6:00 PM, partly due to the large proportion of spiders that ceased foraging around this time, but this may also be due to the spiders being unlikely to capture the types of insects available during this time, such as Homopterans that were not common in other studies.

The average length and biomass of insects captured in the sticky traps in Figures 5 and 6 demonstrate that not only are there a high number of insects available in the evening when spiders are no longer foraging but that these insects could contribute a significant amount to biomass intake should the spiders remain on their webs longer in order to take advantage of them. This apparent discrepancy remains reasonable when considering the theoretical model of ceasing foraging because of predation risk, which will be discussed in the following section.

An important conclusion from the averaged data in Figure 7 remains that flying insect availability is coupled closely with the timeframe in which spiders begin foraging. As noted earlier, spiders delay foraging activity until significantly later than sunrise, indicating that the spiders reduce energetic expense in the early morning until a time at which beginning to forage becomes more profitable, which aligns with the predictions of the theoretical model. Individuals completing their webs around 10:30 AM allows them to take advantage of the gradual rise in insect availability through the day without constructing webs too early and increasing the timeframe in which they could be damaged by weather, UV exposure, or other animals.

While significantly more insect biomass becomes available between 6:00 PM and 8:00 PM, as shown in Figure 8, the majority of this biomass is contributed by Homoptera. Hymenoptera remains available as well. Diptera, a known preferred prey of *M. gracilis*, nearly disappears after 6:00 PM, likely due to the gradual decline in lighting that limits visual information these insects use to navigate in flight (Uetz & Hartsock 1987). While the biomass totals suggest that this period would be highly beneficial for spiders to forage through, previous studies have shown that Homoptera are the least preferred insects that have been observed being caught in the web (Uetz & Hartsock 1987). Thus, while these spiders may theoretically be able to take advantage of these insects during this period, in reality, the actual benefit realized may be substantially lower. This may be due to differences in the positioning and appearance of sticky traps and the spider webs causing differences in insect perception that drive decisions on whether to land on the surface or fly through the space it occupies. The same lack of capitalization on availability is true of Hemiptera, though to a lesser degree: no recorded captures of Hemiptera by *M. gracilis* were made in other studies (Uetz & Hartsock 1987). The biomass that these spiders are taking advantage of appears to be largely determined by Diptera and to a lesser extent by Hymenoptera, Coleoptera, and Homoptera which aligns better with foraging activity patterns, but the mechanisms for such stark differences in capture rates of different Orders are unclear. Further investigation into what Orders *M. gracilis* actually capture as prey and why certain plentiful insect Orders avoid capture to such a high degree should elucidate whether this increased biomass from the large presence of insects in the evening is something these spiders can take advantage of.

Predation Risk

The confirmation of bat presence, obtained from the recording of a tri-colored bat (*Perimyotis subflavus*), in the study plot allows the lack of predation events observed by the camera array to offer more significance. Over a total of roughly 3 weeks with multiple spiders available on fishing line, no predation by bats was observed, which supports the expectation that these predation events are relatively rare and difficult to observe but offers no support that they occur at all. This may have been influenced by the tendency of spider bait to dry out and become unappetizing for predators or by the fishing line used to expose the frozen spiders making them appear difficult to consume by aerial predators. Especially in the case of bats, where the predators may be able to detect the relative density of a prey item, dried spiders may be differentiated from live prey and may not justify consumption effort. Another factor is the area of the study plot: while the plot itself was a well-grown woodlot, it was surrounded by urban development that may have been non-conducive to bat foraging due to noise and lack of habitat. Additionally, other light sources outside of the study plot, such as street lights, may provide more prey for bats, discouraging them from exploring other areas where prey may be harder to come by. Repeating a similar setup in a more isolated environment where bat activity is more common may provide better support for the hypothesis that bats will take spiders when available.

The observed predation by the Northern Cardinal in Figure 10 showed the bird hovering around the spider before plucking it off the line, indicating that predators that are able to avoid entanglement in the spider's web are more likely to consume them. While spines have been typically thought to provide defense from avian predators, this observation contradicts this. This may be due to the brittleness of the spider's abdomen allowing the bird to simply crush it in the

beak before swallowing, but the bird may have also failed to swallow the spider later on off-camera. In general, the true function of spines appears to be poorly understood in the literature, aside from the assumption that they deter predators, and deserves further investigation. Risk of web damage may also be high in environments with larger birds and mammals moving through the understory.

The attack on one *M. gracilis* individual by a wasp adds another potential threat in the environment, but the wasp did not take the spider's abdomen after killing it. The wasp simply stung until the threat was neutralized and escaped the web afterwards. This event appeared more as a situational defensive response rather than a predatory one, but Homopterans are known predators and parasites of orb-weaving spiders that may be thwarted by *M. gracilis* avoidance during the daytime.

While the identification of the various forms of predation that *M. gracilis* individuals are threatened by is weak, the significant discrepancy between spider activity periods and prey availability demonstrate that, according to the theoretical model, even rare predation is likely exerting a significant selective force on *M. gracilis* circadian rhythms. Further work to confirm this predation and weigh its selective importance is required, though study of predation events is notoriously difficult due to the spontaneous and irregular nature of these events.

A Theoretical Model of Diurnal Behavioral Optimization

Here, we offer support that *Micrathena gracilis* is concentrating foraging efforts both spatially, with small, dense orbs, and temporally, with exclusive daytime foraging that excludes a significant amount of potential prey. Tight web construction allows the easier capture of not

only larger prey items that become ensnared in multiple capture lines and may provide enough sustenance for an entire day but also smaller prey items that provide a passive income of nutrients that aid in balancing out the maintenance costs of the web for the day if no other prey is captured. Prey becomes available in the morning, triggering the spiders' activity, and despite abundant prey in the evenings, continued activity is masked by the threat of predation. As night approaches, prey becomes less abundant, and *M. gracilis* avoids the continued risk of both predation and web destruction by consuming the orb, extruding a final nutritional benefit from the day before, and retreating overnight. Leaving frame strands remaining allows the conservation of both time and a small amount of silk should the spider establish itself in a position where the frame is undisturbed, especially high off the ground where few animals would reach or collide with them. These spiders appear to be a strong fit for the theoretical model presented of balancing foraging behavior with risk of predation, and this model of circadian rhythms should always be considered in experiments in which biological processes or behaviors that are affected by the time of day are tested.

REFERENCES

- Anderson, J. F. (1966). The excreta of spiders. *Comparative Biochemistry and Physiology*, 17(3), 973–982. doi: 10.1016/0010-406x(66)90136-8
- Biere, J., & Uetz, G. (1981). Web Orientation in the Spider *Micrathena Gracilis* (Araneae: Araneidae). *Ecology*, 62(2), 336–344. doi:10.2307/1936708
- Blackledge, T. A. (1998). Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *Journal of Zoology*, 246(1), 21–27. doi: 10.1111/j.1469-7998.1998.tb00128.x
- Bukowski, T., & Christenson, T. (1997). Natural History and Copulatory Behavior of the Spiny Orb-weaving Spider *Micrathena gracilis* (Araneae, Araneidae). *The Journal of Arachnology*, 25(3), 307–320. Retrieved March 19, 2020, from www.jstor.org/stable/3705597
- Chacon, P. & Eberhard, W. G. (1980). Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bulletin (British Arachnological Society)*, 5(1), 29–38.
- DeCoursey, G. & DeCoursey, P. J. 1964. Adaptive activity rhythms in bats. *Biological Bulletin*, 126, 14–27.
- Eberhard, W. G. (2007). Stabilimenta of *Philoponella vicina* (Araneae: Uloboridae) and *Gasteracantha cancriformis* (Araneae: Araneidae): Evidence Against a Prey Attractant Function. *Biotropica*, 39(2), 216–220. doi: 10.1111/j.1744-7429.2006.00254.x
- Hodge, M. A. (1987a). Macrohabitat Selection by the Orb Weaving Spider, *Micrathena Gracilis*.

- Psyche: A Journal of Entomology*, 94(3-4), 347–361. doi: 10.1155/1987/21317
- Hodge, M. A. (1987b). Factors influencing web site residence time of the orb weaving spider, *Micrathena gracilis*. *Psyche: A Journal of Entomology*, 94(3–4), 363–371. doi: 10.1155/1987/68503
- Jones, C. J., Akoury, T. S., Hauser, C. K., & Moore, D. (2011). Evidence of circadian rhythm in antipredator behavior in the orb-weaving spider *Larinioides cornutus*. *Animal Behaviour*, 82(3), 549–555. doi: 10.1016/j.anbehav.2011.06.009
- Levi, H. W. (1978). The American orb-weaver genera *Colphepeira*, *Micrathena*, and *Gasteracantha* north of Mexico (Araneae, Araneidae). *Bulletin of the Museum of Comparative Zoology at Harvard College*, 148, 417–442.
- Lima, S. & Dill, L. (1990). Behavioral Decisions Made under the Risk of Predation: A Review and Prospectus. *Canadian Journal of Zoology*, 68, 619–640. doi: 10.1139/z90-092
- Magalhães, I. L. F. & Santos, A. J. (2012). Phylogenetic analysis of *Micrathena* and *Chaetacis* spiders (Araneae: Araneidae) reveals multiple origins of extreme sexual size dimorphism and long abdominal spines. *Zoological Journal of the Linnean Society*. doi: 10.1111/j.1096-3642.2012.00831.x
- Moore, D. M., Watts, J. C., Herrig, A., & Jones, T. C. (2016). Exceptionally short-period circadian clock in *Cyclosa turbinata*: regulation of locomotor and web-building behavior in an orb-weaving spider. *Journal of Arachnology*, 44(3), 388–396. doi: 10.1636/JoA-S-16-014.1
- Moya, J., Quesada-Hidalgo, R., Barrantes, G., Eberhard, W., Escalante, I., Esquivel, C., Rojas,

- Andrés, R., Triana, E., & Arias, A. (2010). Egg sac construction by folding dead leaves in *Pozonia nigroventris* and *Micrathena* sp. (Araneae: Araneidae). *Journal of Arachnology*, 38(2), 371–373. doi: 10.1636/hi09-74.1
- Opell, B. D., Bond, J. E., & Warner, D. A. (2006). The effects of capture spiral composition and orb-web orientation on prey interception. *Zoology*, 109(4), 339–345. doi: 10.1016/j.zool.2006.04.002
- Oxford, G. S. (1998). Guanine as a colorant in spiders: development, genetics, phylogenetics and ecology. In *Proceedings of the 17th European Colloquium of Arachnology, Edinburgh 1997* (ed. P. A. Selden), 121–131. Manchester: British Arachnological Society.
- Sage, R. (1982). Wet and Dry-weight Estimates of Insects and Spiders Based on Length. *The American Midland Naturalist*, 108(2), 407–411. doi:10.2307/2425505
- Stellwagen, S. D., Opell, B. D., & Clouse, M. E. (2015). The impact of UVB radiation on the glycoprotein glue of orb-weaving spider capture thread. *Journal of Experimental Biology*, 218(17), 2675–2684. doi: 10.1242/jeb.123067
- Uetz G. W., Johnson, A. D., & Schemske, D. W. (1978). Web placement, web structure, and prey capture in orb-weaving spiders. *Bulletin (British Arachnological Society)*, 4(4), 141–148.
- Uetz, G. W. & Hartsock, S. P. (1987). Prey Selection in an Orb-Weaving Spider: *Micrathena Gracilis* (Araneae: Araneidae). *Psyche: A Journal of Entomology*, 94(1-2), 103–116. doi: 10.1155/1987/16298
- Vanderhoff, E. N., Byers, C. J., & Hanna, C. J. (2008). Do the Color and Pattern of *Micrathena gracilis* (Araneae: Araneidae) Attract Prey? Examination of the Prey Attraction

Hypothesis and Crypsis. *Journal of Insect Behavior*, 21(6), 469–475. doi:

10.1007/s10905-008-9142-3

Watts, J. C., Herrig, A., Allen, W. D., & Jones, T. C. (2014). Diel patterns of foraging aggression and antipredator behaviour in the trashline orb-weaving spider, *Cyclosa turbinata*. *Animal Behaviour*, 94, 79–86. doi: 10.1016/j.anbehav.2014.05.020

Watts, J. C., Ross, C. R., & Jones, T. C. (2015). Diel and life-history characteristics of personality: consistency versus flexibility in relation to ecological change. *Animal Behaviour*, 101, 43–49. doi: 10.1016/j.anbehav.2014.12.020

Watts, J. C., Jones, T. C., Herrig, A., Miller, M., & Tenhumberg, B. (2018). Temporal Variation in Predation Risk May Explain Daily Rhythms of Foraging Behavior in an Orb-Weaving Spider. *The American Naturalist*, 191(1), 74–87. doi: 10.1086/694775