

Risk-Prone and Risk-Averse Foraging Strategies Enable Niche Partitioning
by Two Diurnal Orb-Weaving Spider Species

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by

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ABSTRACT

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Niche partitioning is a major component in understanding community ecology and how ecologically similar species coexist. Temporal and spatial partitioning and differences in foraging strategy, including sensitivity to risk (variance), likely contribute to partitioning as well. Here, we approach this partitioning with fine resolution to investigate differences in overall strategy between two species of diurnal, orb-weaving spiders, *Verrucosa arenata* and *Micrathena gracilis* (Araneae: Araneidae), that share similar spatial positioning, temporal foraging window, and prey. Through field observation, we found that *V. arenata* individuals appear to increase spatial and temporal sampling to compensate for an overall risk-prone strategy that depends on the interception and active capture of rare, large prey. Conversely, *M. gracilis* individuals employ a risk-averse strategy relying on passive capture of small but abundant prey consumed alongside the orb. We have thus identified how differing risk-sensitive foraging strategies may contribute to niche partitioning between otherwise similar species.

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DEDICATION

Were it not for the unconditional support of my wife, Lauren Stotsky Long, this thesis would not exist, and I would likely not have been able to continue pursuing my passion for scientific research. Lauren, thank you for your infinite encouragement over the course of my Master's degree and for enabling me to spend so many days in the woods collecting data. During my tenure in the Spider Lab at ETSU, thank you for your patience with me bringing spider specimens into our home rather than removing them like a typical husband would. You are loved and appreciated more than I could fit in a second manuscript of similar length as this, and your tenacity in your own career inspires my pursuit to emulate the same in my own.

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I would also like to dedicate this thesis to the many wonderful department employees essential to the function of our University whose names escape our manuscripts, the countless professors who invested in my academic training during my time at ETSU, and the administrative officials willing to make difficult decisions to protect our community during the COVID-19 pandemic. Godspeed, and go Bucs.

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CHAPTER 1. INTRODUCTION

The Competitive Exclusion Principle

In any given environment, there exists a finite amount of resources, including space, time, and nutrition. Any and all organisms in a given environment are thus in perpetual competition for these limited resources (both within and among species), and if two species have exactly the same needs and thus occupy the same ecological niche in a constant environment, one will eventually outcompete the other (Grinnell 1904). This principle, later formulated as Gause's law of competitive exclusion, was empirically demonstrated through one species of *Paramecium* outcompeting another in a constant environment (Gause et al. 1934; Hardin 1960).

However, given some variation in the environment, either by changing conditions or by increasing complexity, species that compete are allowed to coexist to some degree (Gause et al. 1934). This opportunity to coexist and the competition therein can drive niche partitioning, in which the species evolve to differentiate from one another in order to compete less strongly, allowing more stable coexistence. For example, otherwise similar species of *Anolis* lizards in the same environment are behaviorally differentiated to capture differently-sized prey, while frogs and lizards in the same Amazonian environment appear to partition prey captures both by size and type of prey (Pacala and Roughgarden 1985; Caldwell and Vitt 1999). This extends to spatial partitioning, seen in species of warblers that partition different parts of trees, and temporal partitioning, seen in species of sharks that each have distinct foraging windows around coral reefs (MacArthur 1958; Lear et al. 2021). Furthermore, if species are held below their carrying capacities allowed by nutritional abundance because of another force such as predation, neither may exploit their niche completely enough to begin significantly impacting one another by

competitive exclusion in the overlapping niche. Thus, species with similar ecological positioning can coexist through variance in environmental characteristics and many different mechanisms of niche partitioning.

Optimal and Risk-Sensitive Foraging

The field of optimal foraging theory, first introduced by Charnov 1976a and 1976b, seeks to explain how natural selection optimizes foraging behaviors and has been applied to myriad areas of study beyond the life sciences. Predicated on the assumption that the income from foraging is at least a proxy for individual fitness (usually from additional energetic investment towards increased reproduction), the beginning stages of the theory focused on the long-term rate of energy acquisition, in which organisms should prefer nutritional sources that offer the highest mean intake per unit of time to acquire in order to maximize their fitness (reviewed in Stephens and Krebs 1986). However, organisms in nature are not presented with a perfectly consistent stream of income on a daily basis: they must also balance the variance, or risk, of their foraging strategies. Risk-sensitive foraging received significant attention in the years following the introduction of optimal foraging theory, beginning largely with Caraco et al. 1990, and was found across a broad swath of taxa (reviewed in Kacelnik and Bateson 1996). The fundamental premise of risk-sensitive foraging is that organisms should discriminate between different nutritional sources by both their means and their variances in order to express a preference for whichever source imparts the highest fitness. Further investigation into several sub-areas within risk-sensitive foraging followed through the next decade: energy-budget effects, risk in amount vs. time, and multiplicity of choice (reviewed in Bateson 2002).

Organisms are often classified as energetically budget-positive or budget-negative in a certain environmental context. An energetically budget-positive individual is one that is able to forage for a surplus of nutrition beyond its baseline caloric needs to stay alive (termed the “starvation threshold”); an energetically budget-negative individual cannot. Caraco et al. 1990 demonstrated that in yellow-eyed juncos (*Junco phaeonotus*), daily energy budgets (and the resulting starvation threshold) can be manipulated with environmental temperature changes: by decreasing the temperature, the caloric requirement to survive increases due to required maintenance of internal temperature. If the expected mean reward for a day is above this starvation threshold, such as in normal temperature conditions, then the birds prefer a more consistent food source (3 seeds daily > 0 or 6 seeds with equal probability) and are thus more risk-averse between sources with the same mean (Caraco et al. 1990). However, if the expected mean reward for a day is below this starvation threshold, such as in the lowered temperature conditions, the preference reverses towards the riskier food source (3 seeds daily < 0 or 6 seeds), and the birds become more risk-prone in an attempt to “get lucky” and receive a reward large enough to survive (Caraco et al. 1990). Whether the individuals receive the heightened reward or not is irrelevant: when faced with certain death over time, any chance of survival is better than nothing while they wait for better conditions. Risk-sensitivity has been empirically demonstrated in other models, such as hummingbirds that must risk foraging while perpetually on the brink of starvation (Stephens 1981; Bateson et al. 2002), black-capped chickadees that prefer lower-variance prey while budget-positive (Barkan 1990), and bumble bees that modulate risk appetite depending on not only individual nutritional state but overall colony energy reserves as well (Cartar and Dill 1990). These predictions continue when reproduction is added to further theoretical modeling (McNamara et al. 1991).

Natural populations are often not presented with equivalent mean food sources, however. Their options may be along an intersecting spectrum of mean and variance, and the variance may be applied to several measures: time until reward received or amount of reward. If a constant mean reward can be foraged with either a constant delay or a variable delay, the variable delay will sometimes provide the reward faster in the short-term, increasing the short-term rate above that of the constant delay and becoming the preferred option (Harder and Real 1987; Possingham et al. 1990; Caraco et al. 1992). If the reward amount varies with a constant delay, however, the time needed to consume the food also varies. If more food is obtained and the time to consume it becomes longer, the short-term rate of energy acquisition actually decreases (in other words, the rate of nutritional intake over the time period in which the organism is foraging for the reward) despite the higher long-term rate, making a constant reward with a higher short-term rate the preferred option, as demonstrated in other models as well. Empirical support for this preference has been shown again in yellow-eyed juncos (Caraco et al. 1992) and starlings (Reboreda and Kacelnik 1991; Bateson and Kacelnik 1995). Thus, when foraging reward varies in amount, organisms become risk-averse; when foraging reward varies in time delay, organisms become risk-prone.

Finally, when considering the foraging options available to a given organism, there may be several to choose from, each with different means and variances. In trinary choice experiments, the typical trends predicted by both long-term and short-term rate begin to break down, and further considerations must be made (Hurly and Oseen 1999; Bateson 2002). Some studies suggest an individual learning component or perhaps other factors such as life history or predation risk are at play (Lara et al. 2013; reviewed in Ferrari et al. 2009). Predation risk can

greatly influence foraging strategy and even drive counter-intuitive decision-making (Sih 1992; Kolodny and Stern 2017; reviewed in Lima and Dill 1990; reviewed in Ferrari et al. 2009).

A further iteration of the risk-sensitive model with reproduction was developed by Hurly (2003): the twin-threshold model, which adds a second “reproduction” threshold to the upper end of the reward acquisition rate spectrum. In doing so, organisms that must meet daily caloric requirements (the starvation threshold) as well as save up energy to yoke eggs or feed offspring can be modeled more accurately. In these cases, as in the presented model of hummingbirds, an organism that would otherwise be risk-averse if budget-positive may unexpectedly become more risk-prone if good fortune enables successful reproduction (Bateson et al. 2002; Hurly 2003). Thus, organisms may engage in more risk-prone foraging for a chance to reproduce, even if their strategy allows survival already.

Despite the iterative improvements to risk-sensitive foraging models and their linkage back to decisions in natural environments, a unifying theory that accounts for varied experimental evidence has yet to take shape. However, attention has been paid to some groups of organisms that allow us to tease apart the adaptive value of various behavioral decisions and foraging patterns.

Orb-Weaving Spiders as Ecological Models

Orb-weaving spiders have long been used as models to investigate various aspects of behavioral ecology. Spiders are both predators and prey: as predators, they are potentially subject to competitive exclusion and risk-sensitive foraging; as prey, they are potentially subject to the risk of being killed while exposed, and in particular, while foraging.

Risk-sensitive foraging has been directly observed in several spider species. Individual long-jawed orb-weaving spiders (*Tetragnatha elongata*) in prey-dense areas rebuild webs more often in order to take a spatial resample and achieve nutritional intake closer to the overall plentiful mean (a risk-averse strategy), while spiders in prey-sparse areas resorted to not rebuilding to accept variance (the risk-prone strategy) and attempt to intake enough nutrition to successfully reproduce; however, further work proposed that the root cause was conspecific competition for space to construct webs (Gillespie and Caraco 1987; Smallwood 1993). At the population level, prey abundances, and the variances thereof, cause some species to transition between risk-averse and risk-prone strategies: in the orbweaver *Metepeira spinipes*, individuals occupy a variety of prey-sparse and prey-dense habitats with seasonal fluctuations and will forage solitarily when prey is sparse during dry climatic conditions but converge into large colonies with expansive webs when prey is abundant during wet climatic conditions (Uetz 1982). Thus, when prey densities are high, these individuals accept a relative decrease in mean prey intake per individual for a reduction in variance because the mean is high enough, but when the mean is lowered, individuals adopt the high-variance strategy of foraging individually, increasing the likelihood that they will intake enough nutrition to successfully reach reproduction (Uetz 1982). Even *A. studiosus* juveniles demonstrate risk-sensitive foraging by potentially striking off alone from the mother-offspring colony to expose themselves to higher variance while foraging alone if colony prey capture is low (Jones and Parker 2002).

Risk-sensitive foraging depends on organisms being able to determine, usually by some proxy, the profitability of a certain site or strategy. Some orb-weavers appear to be able to discriminate site quality (likely through the proxy of nutritional state after foraging attempts) and will perform the risk-prone behavior of relocation if nutritional intake is low, possibly below

survival threshold, and prolonged hunger promotes these riskier foraging decisions as a last-ditch effort to survive (Hodge 1987b; Leclerc 1991; Bilde et al. 2002; Edwards et al. 2009).

Following periods of scarcity, spiders can readily gain body mass back and may be well-suited to enduring periods of poor intake by recycling web silk and remaining still in the orb during foraging periods (Provencher and Reichert 1991). If disturbed multiple times while foraging, individuals will relocate but remain closer to sites with high capture means (Chmiel et al. 2000).

Even within lucrative areas, in line with the two-threshold model presented by Hurly (2003), risk-prone foraging may still be advantageous even when the mean provides enough to reproduce because it may enable some individuals to produce the same number of offspring earlier, which may decrease the risk of failing to lay eggs before the end of the season in annual species (2003; Bednekoff 1996). Should an individual select a prey-rich site and be well-satiated, it may modulate foraging behaviors and reduce web investment to directly divert additional energy to egg production (Wise 1979; Sherman 1994). By some estimates, larger but rarer captures not only represent a significantly-variable nutritional intake but may be required to push an individual above the reproduction threshold, so even spiders that may not focus on actively captured prey are still incentivized to remain in the web in case large prey appear (Venner and Casas 2005). While some studies have suggested that orb-weaving spiders are food-limited, as artificially increasing prey intake in some species directly results in increased egg production, later investigation noted that even very similar species in a similar habitat suffer very limited negative effects from competition (Wise 1979 and 1981). Thus, there is potential for certain conditions to drive both risk-averse and risk-prone foraging strategies in orb-weaving spiders, and some orb-weaving species may be relatively released from resource limitation and competition.

Predation risk, as mentioned previously, exerts harsh selective pressure on spider populations and may be a major driver of behavioral decisions (reviewed in Lima and Dill 1990). Spiders have been shown to select lower-prey web locations and compromise foraging efficacy to avoid predators (Blamires et al. 2007). A major predator of spider communities is birds, which have been extensively observed taking spider prey and are likely able to pluck spiders out of the capture orb while they forage (reviewed in Gunnarsson 2007). Another major threat is parasitoid wasps, which use spider hosts to feed developing young (Buschini et al. 2010).

In response to this predation risk, spiders have developed an array of antipredator defenses. Some orb-weaving species have evolved intricate web structures called stabilimenta that may help camouflage the spider as it forages or increase visibility of the web to avoid destruction (Opell et al. 2006; Blackledge 1998). Others have evolved abdominal spines that may deter birds due to the difficulty swallowing the spider or wasps due to the difficulty of bringing the body back to the nest for packing into food storage structures (Magalhães and Santos 2012). Warning coloration through guanine deposition, which gives a distinct visual appearance and a foul taste, is also hypothesized to deter predators or aid camouflage and is more common in species that live in more exposed habitats (Anderson 1966; Oxford 1998; Vanderhoff et al. 2008). Guanine coloration may also have a prey attractant function, but evidence varies by species (Vanderhoff et al. 2008; Rao et al. 2014).

Perhaps the most varied evolutionary response to predator and prey abundances is in circadian-regulated behavior patterns. In orb-weaving spiders, being able to anticipate environmental conditions beforehand is particularly important because of the delay between web construction to prey capture and the harsh selective pressure of predation on ill-timed activity. Recently, orb-weaving spiders have shown unusually high variation in endogenous circadian

period length, and many species show cyclical fluctuations in antipredator behavior, boldness towards disturbances, and aggression towards prey (Moore et al. 2016; Watts et al. 2014; Watts et al. 2015; Jones et al. 2011). A previous model predicted that predation risk, energetic state, and prey availability all intersect such that behavior should fluctuate to accommodate for regular environmental changes (Watts et al. 2018). While individuals become more active to forage for prey, perhaps equally important are periods of inactivity undergone to avoid interactions with predators (reviewed in Lima and Dill 1990), and both of these components are the manifestations of an individual's chronotype, which is the periodicity of the endogenous clock that allows organisms to schedule behaviors. For example, a human with a chronotype that has a period of exactly 24 hours will become more alert in the morning and drowsy in the evening at the same point in each daily cycle. In orb-weaving spiders, chronotype may allow an individual to precisely schedule web construction so that it is ready to forage on just as prey becomes available while also scheduling web takedown so that the spider retreats just as prey ceases or predators become likely to appear. Thus, individual chronotype allows the endogenous clock to offer adaptive value by increasing behavioral efficiency, resulting in higher fitness.

With such varied adaptations and habitats, spider communities have been of particular interest for unraveling the complexity of niche partitioning. More recently, heightened attention has been paid to how ecologically similar species in similar habitats partition resources in order to coexist. Minor differences in microhabitat (different parts of the same plants) and mesohabitat (same plants in different environments) allow ecologically similar species to coexist (Villanueva-Bonilla et al. 2019). In addition to differences in habitat, there is extensive diversity in web structure and location between and within species (Uetz et al. 1978; Chacón and Eberhard 1980). Recent study has found that some web characteristics influence prey captures: larger,

higher orbs capture more large insects, but density of capture threads does not influence the characteristics of captures (Xavier et al. 2021). Even if web structure or position is similar between species, differences in the individual spiders themselves, such as mean body size, can lead to partitioning of prey by size (Richardson and Hanks 2009).

With a broad understanding of the factors that influence foraging strategy, we are prepared to take a more nuanced look at the intersection of risk-sensitive foraging and niche partitioning in a local spider community. Two species, *Verrucosa arenata* and *Micrathena gracilis* (Araneae: Araneidae), appear to occupy the same temporal and foraging niche within a similar habitat, leading to the question: can risk-sensitive foraging explain differences in foraging strategy that allow these species to coexist?

CHAPTER 2. METHODS

Study Species

The spider species, *Verrucosa arenata* and *Micrathena gracilis* (Araneae: Araneidae), are diurnal, orb-weaving spiders commonly found in the patchy, shaded understory of deciduous forest environments throughout most of the Americas (Walckenaer 1841; McCook 1888; Levi 1978; Hodge 1987a; Lise et al. 2015). They overlap in body length, with mature female *V. arenata* generally measuring between 7 to 14 mm (Rao et al. 2011) and mature female *M. gracilis* generally measuring between 4 to 10 mm (McCravy and Hessler 2012). These species construct their spatially-isolated orbs between vegetative scaffolding in the morning, forage on flying insect prey throughout the day, and may consume the orb before retreating in the evening (Biere and Uetz 1981; Francini and Dalla-Pria 2015). Their captures consist largely of Dipteran, and to a lesser extent, Hymenopteran, Homopteran, and Coleopteran insect prey, and individuals will ignore smaller prey items that passively collect in the orb while actively capturing larger prey by handling and envenomating (Uetz and Hartsock 1987; Rao et al. 2011). Both species are sexually dimorphic with the larger females leading the typical orb-weaver lifestyle that most casual observers recognize (Bukowski and Christenson 1997; Magalhães and Santos 2012).

Despite their similar temporal and foraging niche in a similar habitat, a few key differences easily distinguish the two species. The first and most apparent in natural observation is web structure: *V. arenata* orbs are relatively large (roughly 20-60 cm) and down-biased with a relatively sparse capture spiral, while *M. gracilis* orbs are smaller (roughly 10-30 cm) and symmetrical with a more condensed capture spiral (Uetz and Hartsock 1987; Francini and Dalla-Pria 2015). Mature females are also different in physical appearance: *V. arenata* are

mostly amber-colored with a distinct white or yellow triangle pattern on the dorsal side of the abdomen and lack heavy sclerotization or spines, while *M. gracilis* are mostly black with black-and-white abdomens and 6 distinct abdominal spines (Vanderhoff et al. 2008; Magalhães and Santos 2012). Behaviorally, *V. arenata* appear capable of capturing larger prey through “reeling” behavior, a larger web size, and facing upwards while foraging, whereas *M. gracilis* tend to lose larger prey items (Uetz and Hartsock 1987; Ceballos et al. 2005; Rao et al. 2011; Rao et al. 2019).

Spider Field Observations

To observe spiders in the field, mature *Micrathena gracilis* and *Verrucosa arenata* females were followed from roughly 0630 to roughly 2300 in a heavily-forested city park in Washington Co., TN over 8 separate observation days from August to October 2021, with a maximum of 20 individuals per species per observation day. Individuals were located as early as possible, marked by staking a numbered flag directly beneath the spider’s location to avoid disturbance, and revisited for observation no later than roughly one hour since previous observation. Individuals were continually marked upon identification until the maximum of 20 per species was reached. If an individual could not be located upon revisit, it was noted as missing, and if the individual could not be located upon a second revisit, the flag was collected and placed under a new individual to continue data collection. Before dawn and after dusk, care was taken to limit artificial light exposure by using a red LED headlamp when pointing towards spiders under observation.

Time of observation, whether the orb remained up, behavioral state of the individual, prey lengths, and whether prey items were ignored or actively consumed were noted with each

revisit to the spider. Sketches were made of each orb to label approximate prey positions and limit possible recounting of prey items upon subsequent visits.

Data Validation

As with most field studies, unexpected occurrences during data collection can confound trends representative of the typical state. Data collected must be filtered properly to reduce noise and make sound conclusions. Depending on the analysis at hand, different levels of filtering must be applied to ensure that the resulting datasets are robust and representative of natural occurrences.

For orb-weaving spiders, foraging period—the opportunity to capture prey for nutritional intake—truly begins once the capture spiral is constructed. Thus, to understand what comprises a typical foraging period, the timing of capture spiral construction must be measured. However, when these species of orb-weaving spiders experience web damage that interrupts foraging during the day, they may decide to rebuild the orb, causing ambiguous instances of capture spiral rebuilding which cannot be distinguished from the initial construction without tracking specific individuals by marking. To better understand when these species begin to forage, a distribution of the timing of capture spiral construction was created. We excluded capture spiral observations with a known cause for delay of capture spiral construction (such as the observer breaking framing threads before the spider could begin the capture spiral) and with a known or reasonably assumed cause for a rebuild (such as the observer or weather conditions destroying the web, resulting in a new capture spiral soon after). Thus, with these filters applied, we are left with a distribution of capture spiral construction by individuals of each species with a minimized influence of “random” events that affect initiation of foraging. Using the curve of the

distribution, we can better make decisions about what observations should be included in other analyses as representative of the uninterrupted, natural timing of foraging.

To measure foraging activity with a resolution finer than being broadly “diurnal,” we sought to create a distribution of foraging duration for each species to understand how they temporally sample the environment for prey. With a known distribution of capture spiral construction, we assigned a cutoff for the initiation of foraging behavior: for *V. arenata*, this was 1000, and for *M. gracilis*, this was 1400. Even if capture spiral construction was not observed for a given individual, as long as it was observed foraging before the cutoff, it is reasonable to assume that the individual likely constructed the web around the mean capture spiral construction time and is thus representative of undisturbed foraging period. Any first observations of foraging and capture spiral creation beyond the cutoff for typical orb construction were excluded. Thus, only foraging periods that began within the filtered distribution of capture spiral construction were included. However, any natural interruptions that force individuals to cease foraging are a valid and naturally-occurring risk that these species experience. Thus, only anthropogenic foraging interruptions force exclusion of the orb duration from the foraging duration dataset. A small proportion of individuals continued to forage until final observation around 2100 despite most retreating or taking down the orb, so we also include these observations as representative of the end of a productive foraging period. Based on the distribution of prey availability throughout the day ramping down into the evening, we assume any foraging beyond this point is minimally productive.

With an understanding of the typical foraging duration for each species, we considered nutritional intake during these periods. Both species can decide to actively capture or ignore prey items that hit the capture spiral, and if the orb is consumed at the end of the foraging period,

ignored prey can still be collected (Uetz and Hartsock 1987; Rao et al. 2011). Prey that disappeared from the web before the end of the foraging period were excluded. Additionally, both species take a non-trivial amount of time to consume actively captured prey, with each additional millimeter in body length adding additional time needed to completely consume the prey. Prey items that were actively consumed often took at least an hour, and because observation revisits were no more than roughly an hour apart, we assume that any actively captured prey would have been observed before the spider finished feeding and discarded the remaining waste. Using a previously established linear regression model to estimate wet and dry biomass for Dipteran prey, the net absorbable biomass (as spiders liquify the wet internal contents and discard the dry exoskeleton) offered by each prey item could be summed to an ignored and eaten biomass total per foraging period (Sage 1982). With the same cutoffs for initiation of foraging duration, we filtered observations for orbs that represent a typical day of nutritional income, split by eaten and ignored by the individual spider.

Using the same biomass estimation technique, we also considered the distribution of biomass intake per time block for each species. All prey items, regardless of whether the spider was observed before the cutoff, were included as long as there was a previous observation in which the prey item was not present to accurately bin the timing of prey arrival. For example, a spider that began to be observed at 1500 could not have its ignored prey collected in the orb thus far included, because there is no way to know when that prey appeared; however, the spider's captures from then onward can be included because of the presence of a previous observation confirms that the new prey arrived during the preceding time period between observations. To account for differences in the number of webs available, we then scaled these biomass totals by

the number of webs under observation during a given period. Thus, we produced a distribution of biomass captured (both eaten and ignored) per time block per orb for both species.

CHAPTER 3. RESULTS

Distribution of First Capture Spiral Construction Observations

The time (h) of all capture spiral observations for each species without a known cause of delay or rebuild were compared (*V. arenata*: $n = 60$; *M. gracilis*: $n = 60$). We conducted a t-test assuming unequal sample variances, and there was a significant difference in mean first capture spiral observation time between the species with *V. arenata* building earlier than *M. gracilis* ($VA: 7.64 \pm 0.82 \text{ h} < MG: 10.79 \pm 1.84 \text{ h}$, $t = -12.01$, $df = 81.46$, $p < 0.001$). From an F-test, there was a significant difference in variance of capture spiral observation time, with *M. gracilis* showing higher variance than *V. arenata* ($VA: 0.68 \text{ h} < MG: 3.45 \text{ h}$, $F = 5.06$, $df = 59, 59$, $p < 0.001$). Observations were binned to the end of the half-hour in which they were contained and converted to proportion of observations per species on each axis to normalize the columns in Figure 1.

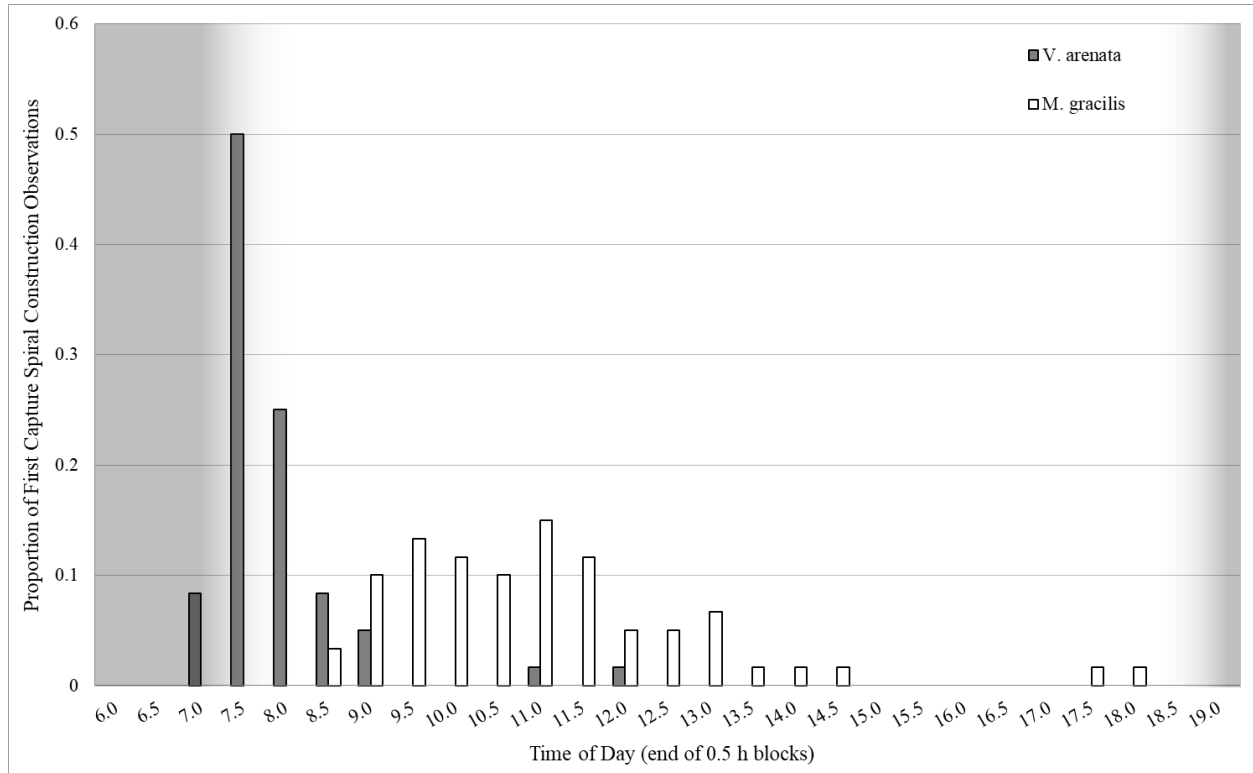


Figure 1. First capture spiral construction observations. Distribution of first observations of capture spiral construction are binned by the end of the half-hour time block with respect to time of day and normalized to proportion of observations per species. Sunrise and sunset from the observation period closest to the middle of our study season are shown with shading. *V. arenata* observations are represented by shaded bars; *M. gracilis*, by white. We observed a rapid ramp in frequency of this behavior in *V. arenata* and a more gradual increase in *M. gracilis*.

Distribution of Foraging Duration

Foraging duration (h), from capture spiral construction or pre-cutoff foraging until retreat or final foraging observation, was compared. This comparison excluded *V. arenata* that were first observed building a capture spiral or foraging after 1000 and *M. gracilis* after 1400 as well as orbs that experienced human-caused disruption (*V. arenata*: n = 111; *M. gracilis*: n = 79). We

conducted a t-test assuming unequal sample variances, and there was a significant difference in mean foraging duration, with *V. arenata* foraging longer than *M. gracilis* (*VA*: 9.72 ± 4.19 h < *MG*: 8.64 ± 2.86 h, $t = 2.1$, $df = 187.74$, $p = 0.037161$). From an F-test, there was a significant difference in variance, with *V. arenata* showing higher variance than *M. gracilis* (*VA*: 17.73 h > *MG*: 8.29 h, $F = 2.15$, $df = 110, 78$, $p = 0.000217$).

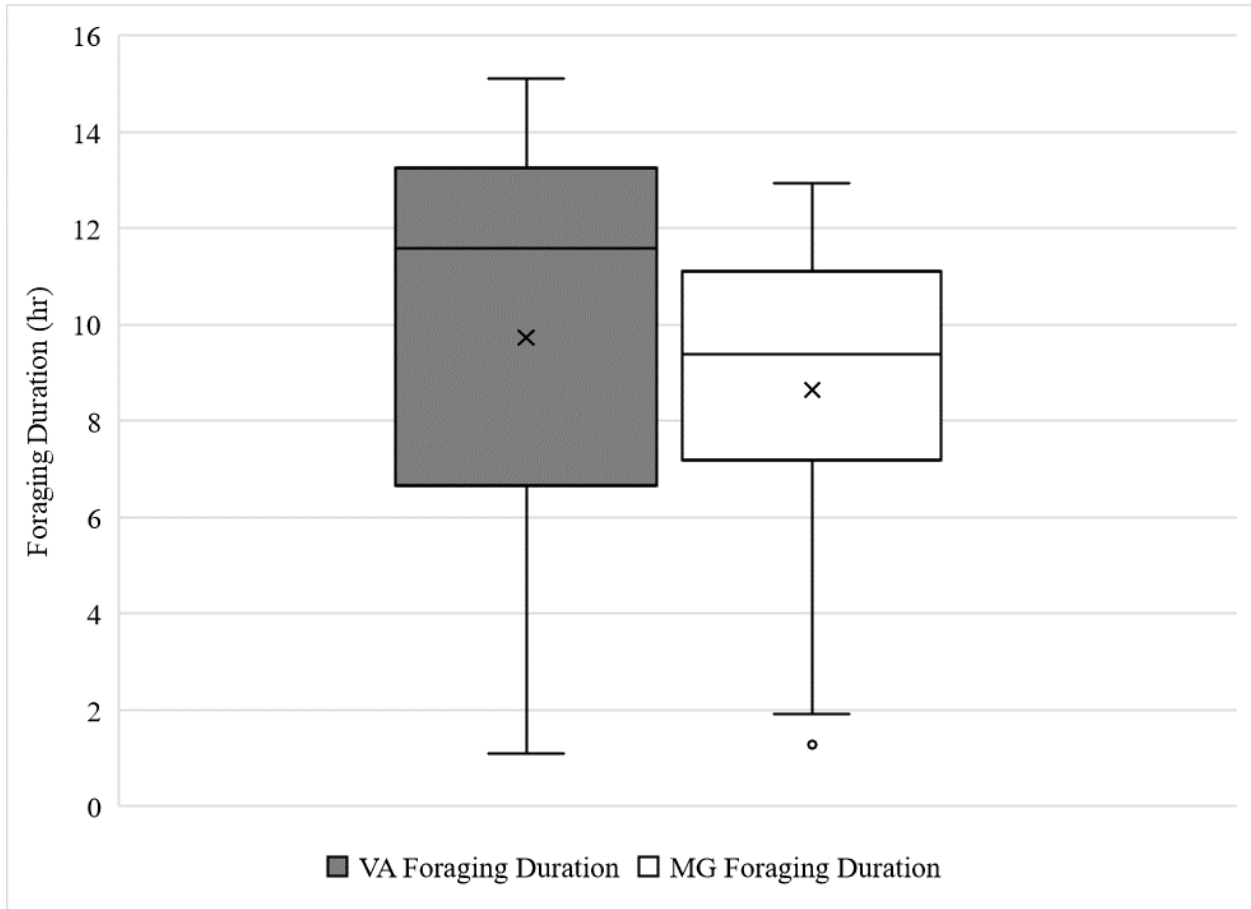


Figure 2. Foraging duration. Distribution of foraging duration (h), irrespective of time of day, in individuals that began foraging before each species cutoff. *V. arenata* are represented by the shaded plot; *M. gracilis*, by white. One *M. gracilis* outlier is included. We see a higher mean foraging duration (notated with a central “x”) in *V. arenata*, imparted by earlier initiation and later conclusion, but increased variance due to higher chance of interruption by web damage.

Interruptions to Foraging Period

Fate of all orbs under observation was recorded (*V. arenata*: n = 170; *M. gracilis*: n = 87). Extensive damage to the orb that resulted in the individual no longer foraging in the center of the orb was noted as an interruption to foraging. Additionally, when webs were missing upon revisit outside of the typical period in which these species either consume the orb or decide to retreat (generally later in the evening, beginning around 1900), this was assumed to be web destruction that caused an interruption to foraging. Only interruptions of anthropogenic nature are excluded. In a Fisher's Exact Test, species significantly predicted orb fate, with *V. arenata* experiencing more interruptions to foraging than *M. gracilis* (*VA*: 40.36% > *MG*: 21.98%, n = 257, df = 1, p = 0.0037). Thus, the propensity of the orbs of each species to be damaged enough to interrupt foraging is presented in Figure 3.

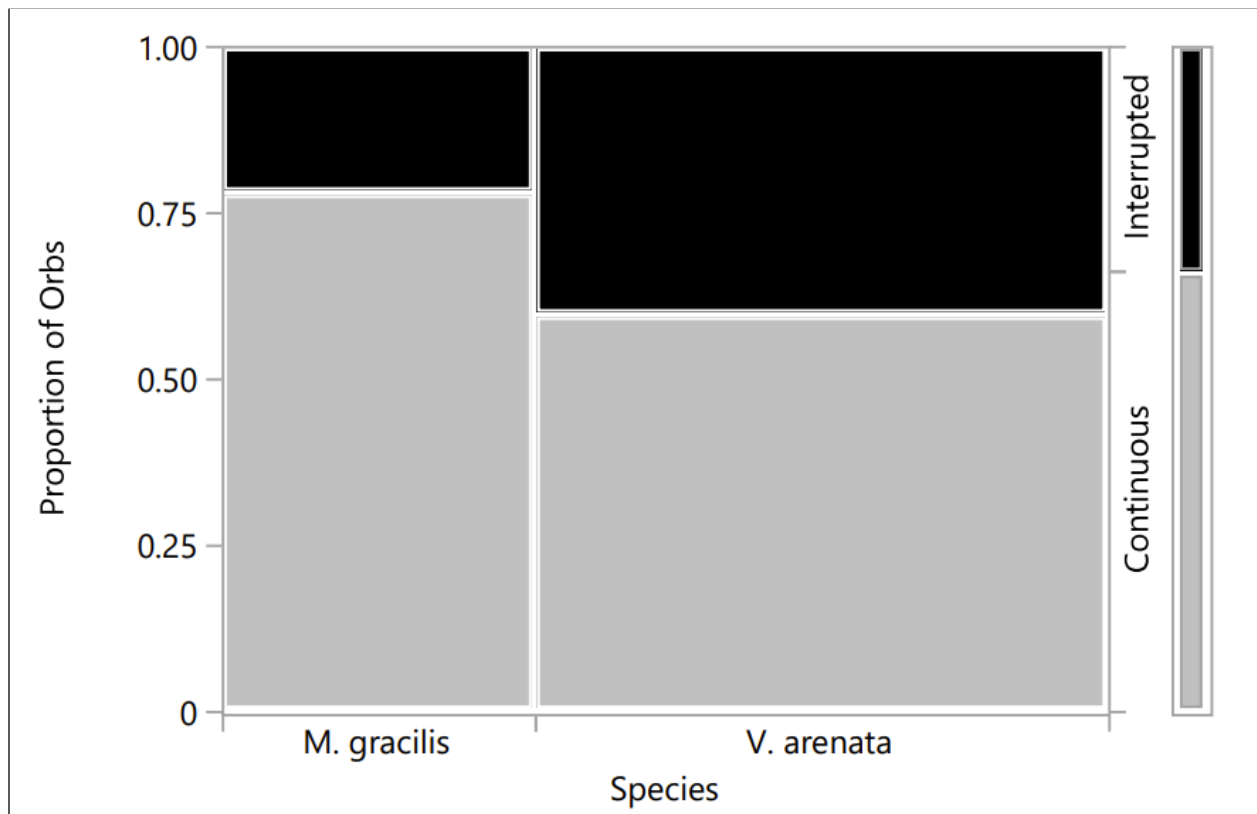


Figure 3. Foraging interruptions. Proportion of orbs naturally damaged enough to interrupt foraging of each species, with continuous (uninterrupted) webs in light gray and interrupted webs in black. *M. gracilis* is represented by the left column; *V. arenata*, by the right.

Distribution of Biomass Totals

Net biomass totals (g), defined as the difference in wet and dry biomass calculated using Diptera linear regression (Sage 1982) and split by eaten and ignored, for individuals constructing capture spirals or foraging before each species cutoff were compared (*V. arenata*: n = 111; *M. gracilis*: n = 79).

We conducted a t-test assuming unequal sample variances on ignored biomass totals, and there was not a significant difference in mean ignored biomass per individual (*VA*: 1.7845 ± 1.7141 mg = *MG*: 1.5666 ± 1.1629 mg, $t = 1.04$, $df = 187.62$, $p = 0.298038$). From an F-test, there was a significant difference in variance, with *V. arenata* showing higher variance than *M. gracilis* (*VA*: 2.9382 mg > *MG*: 1.3523 mg, $F = 2.18$, $df = 110, 78$, $p = 0.000172$).

We conducted a t-test assuming unequal sample variances on eaten biomass totals, and there was a significant difference in mean eaten biomass per individual (*VA*: 1.4754 ± 4.2984 g > *MG*: 0.2771 ± 0.5330 g, $t = 2.91$, $df = 114.73$, $p = 0.004393$). From an F-test, there was a significant difference in variance, with *V. arenata* showing higher variance than *M. gracilis* (*VA*: 18.4760 mg > *MG*: 0.2840 mg, $F = 65.29$, $df = 110, 78$, $p = 0.000172$).

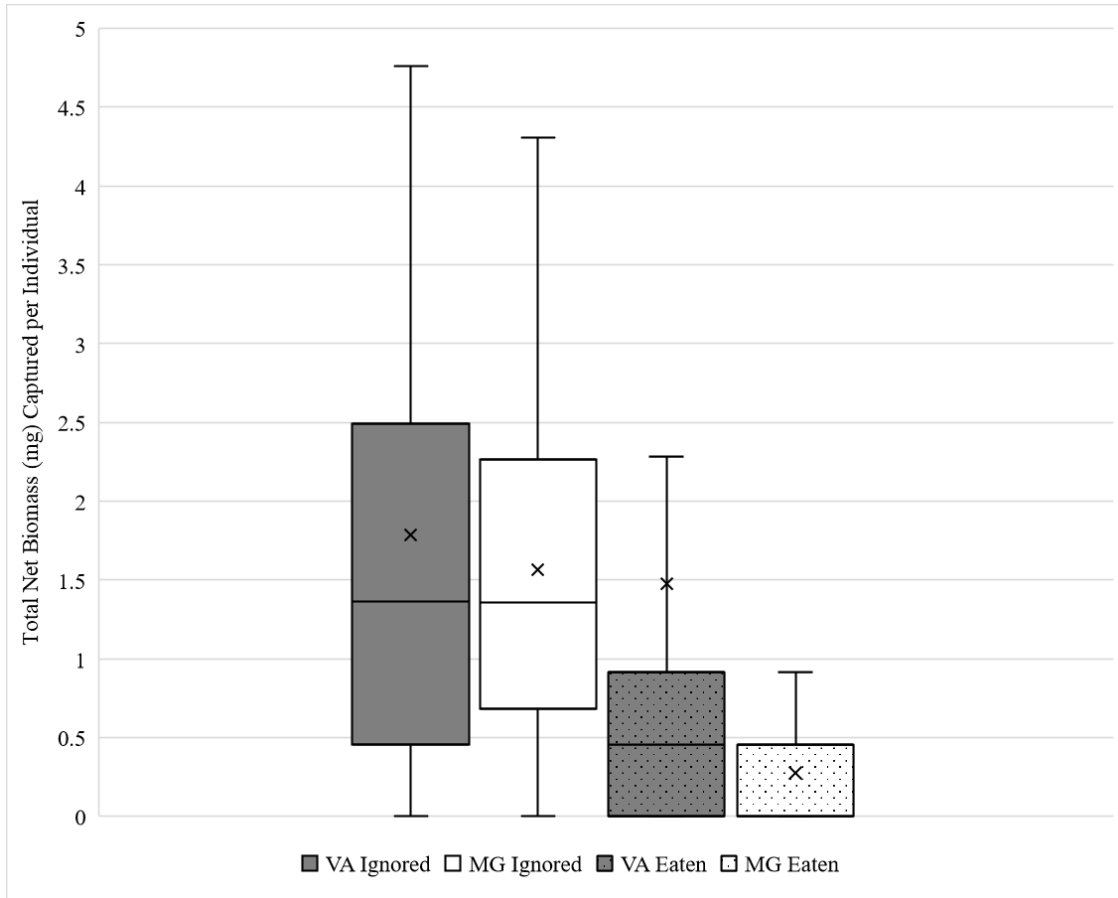


Figure 4. Biomass totals. Distribution of total net biomass totals (g) per individual that began foraging before species cutoffs, split by eaten (solid, on the left) and ignored (dotted, on the right). *V. arenata* is represented with shaded plots; *M. gracilis*, by white. Outliers are hidden for legibility of the figure but are included in the dataset, as rare but valuable captures, especially by *V. arenata*, contribute significant biomass and are equally valid observations. *V. arenata* have similar passive captures and higher actively consumed captures than *M. gracilis* but experience higher variance in both.

Distribution of Biomass per Time Bin

To visualize the distribution of prey captures for each species over the foraging period, a total number of webs in which the spider was foraging were observed during each time block.

This total of observed webs allowed us to normalize the average prey captured and account for the increase in webs under observation during the day. For each web, net biomass totals (in mg, split by eaten and ignored) were totaled during each time block, then divided by the number of unique webs observed during the hour. The means of net biomass per web per time block for each species, split by eaten and ignored, produced Figures 5 and 6.

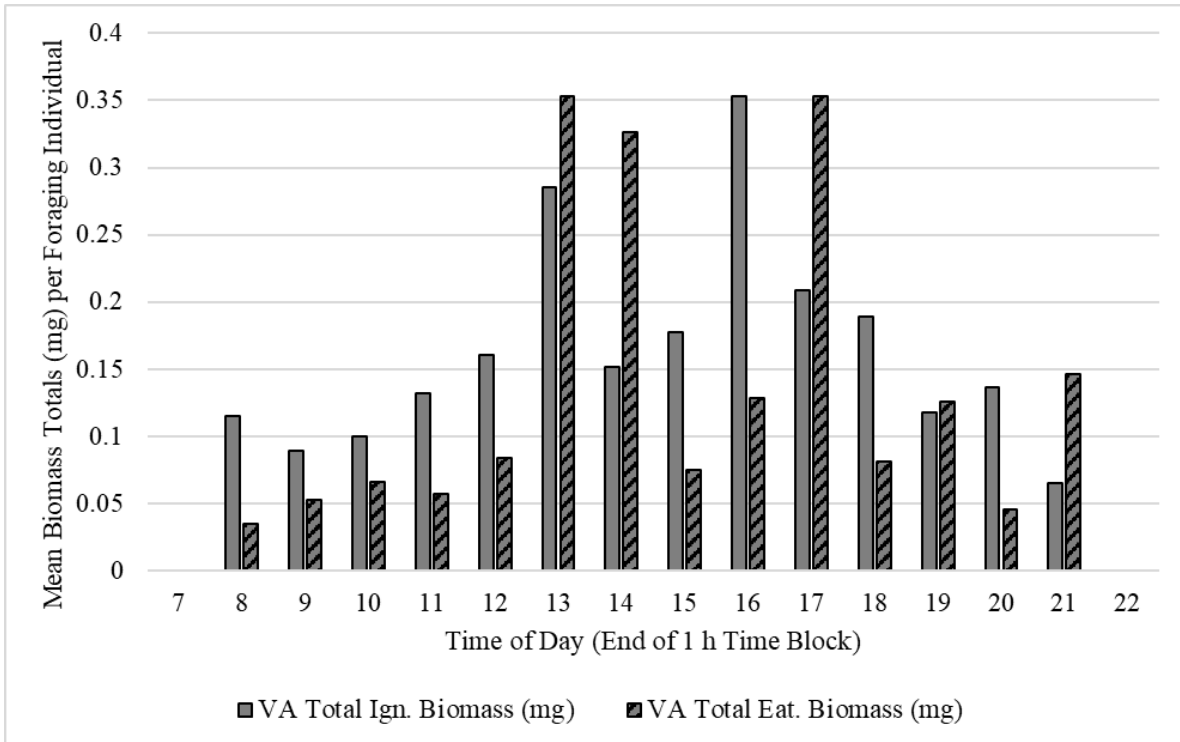


Figure 5. Temporal mean biomass per *V. arenata*. Mean net biomass totals (mg), split by ignored (solid) and eaten (lined), per individual foraging per time block for *V. arenata*. We see successful captures by *V. arenata* once they begin building webs around 800, with a peak near the middle of the foraging period, around 1500. Eaten biomass, especially during the afternoon (1300-1700), rivals passive prey capture.

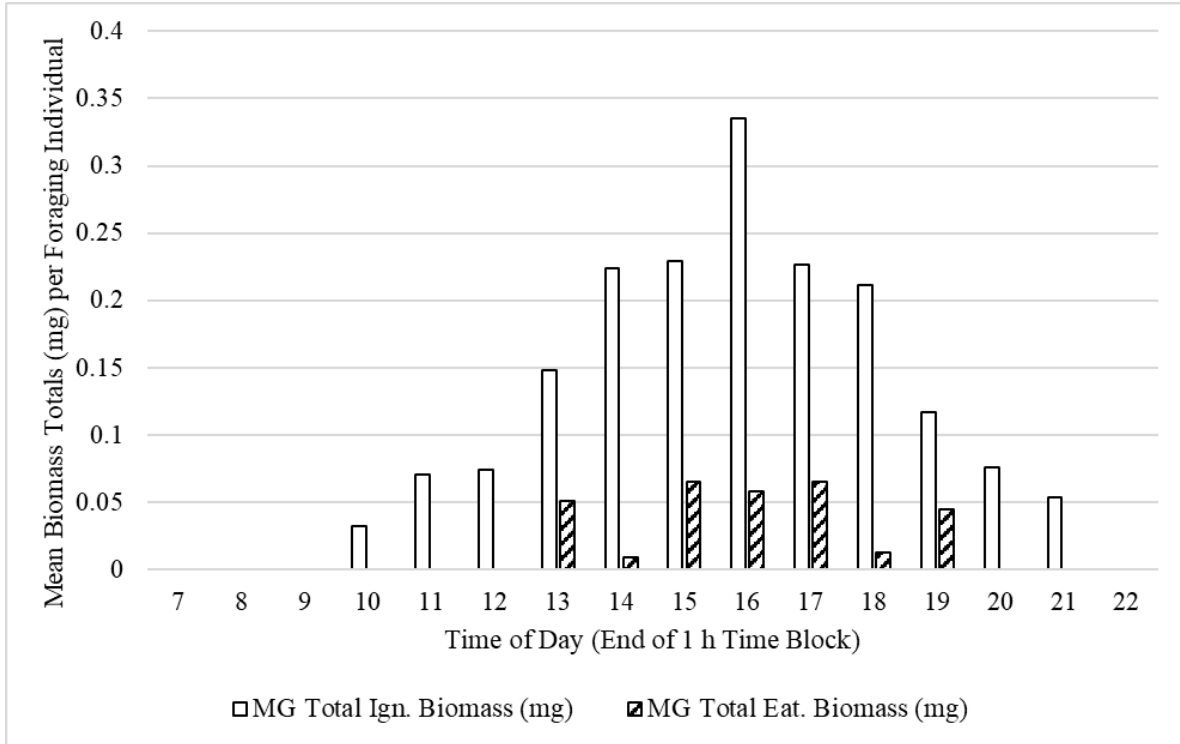


Figure 6. Temporal mean biomass per *M. gracilis*. Mean net biomass totals (mg), split by ignored (solid) and eaten (lined), per individual foraging per time block for *M. gracilis*. We see a gradual ramp upwards during midday and early afternoon and downwards during the evening in passively collected prey with a peak around 1600, with relatively little prey actively captured per foraging individual.

Spider Decision by Prey Length

To understand how each species typically responds when prey of a certain size class is intercepted, prey lengths and the resulting decision to attack or ignore were plotted out of a maximum percentage of all prey items of that class, producing Figures 7 and 8.

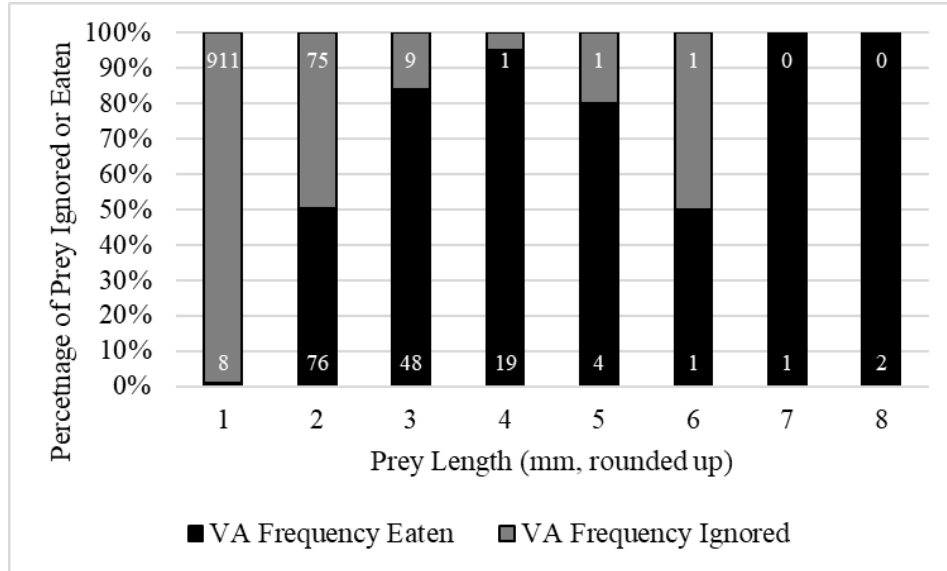


Figure 7. *V. arenata* prey by length. Prey lengths (mm, rounded up), split percentage-wise out of 100% by eaten (black) and ignored (dark gray), captured by *V. arenata*. Number of prey items of each size class and decision are noted on the ends of each column in white, with ignored frequencies at the top and eaten frequencies at the bottom. Very small prey (<2 mm) are largely ignored, while the majority of prey above 3 mm in length are actively attacked and consumed. Larger prey (>4 mm) are rare but accessible. Large prey items that were ignored were typically intercepted while the spider was still feeding on a previous prey item.

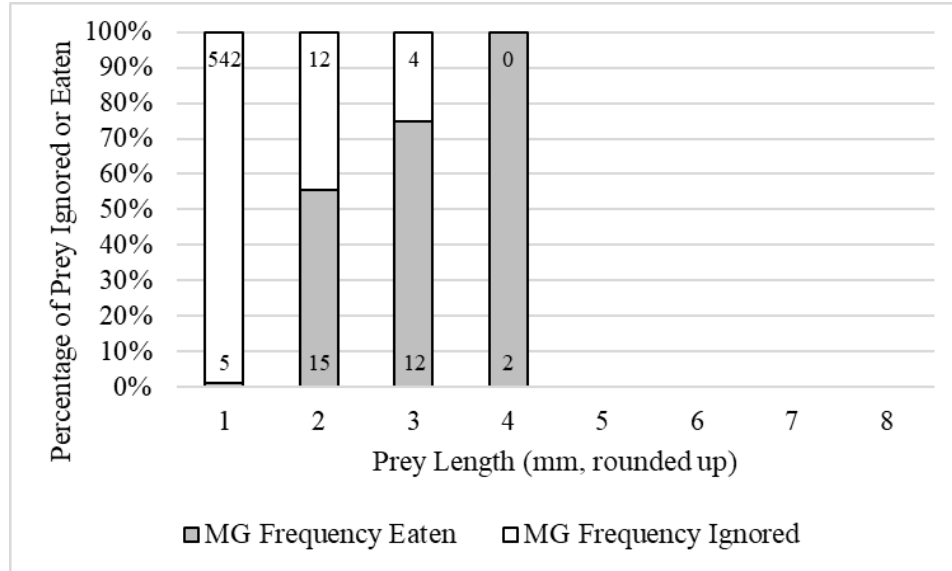


Figure 8. *M. gracilis* prey by length. Prey lengths (mm, rounded up), split percentage-wise out of 100% by eaten (light gray) and ignored (white), captured by *M. gracilis*. Number of prey items of each size class and decision are noted on the ends of each column in black, with ignored frequencies at the top and eaten frequencies at the bottom. Similar to *V. arenata*, smaller prey are ignored, while prey >2 mm are typically attacked. However, no observations were made of successful capture of >4 mm prey.

CHAPTER 4. DISCUSSION

Foraging Strategy Differences

Differences in the web characteristics and behaviors that natural selection can modulate in orb-weaving spiders have only just begun to be untangled (Xavier et al. 2021). From field observation and the literature on these two species, four main differences in foraging strategy need to be isolated to explain our observations: capture spiral density, total orb area, particular foraging behaviors, and species temporal foraging window.

Capture spiral density, or the total length of adhesive threads per given area, has been previously shown to not affect size and mass of intercepted insects, and we thus do not ascribe differences in capture characteristics to spiral density alone (Xavier et al. 2021). Capture spiral density could, however, influence the *frequencies* of interceptions within certain size classes. If larger prey are favored, capture thread density can be decreased without compromising orb efficacy per area (Sandoval 1994; Xavier et al. 2021). *V. arenata* appears to adopt this sparse-spiral strategy. Alternatively, if smaller prey is favored, increasing capture spiral density may increase the frequency of small prey captures by increasing the likelihood of direct contact with multiple capture spiral threads without intervention from the spider, which is the strategy *M. gracilis* appears to use. Smaller prey captures should correlate directly with total capture thread length so long as the thread is capable of retaining this smaller, weaker prey without intervention, and we believe this to be the explanation for there being no significant difference in mean total ignored biomass captured by both species. By measuring the actual length and estimating energetic investment in natural capture spirals of each species, perhaps some difference in spiral thread length capable of passively capturing small insects or volumes of different silk types can

be teased apart between the two, but we suspect the total thread length is similar. Without increasing its overall orb area, we believe the increased capture spiral density allows *M. gracilis* to increase its spatial sampling on a 1-dimensional scale, which may be an important measure for capturing small, weak prey that can be consumed along with the orb at the end of the day. Perhaps there is some selective factor or physiological constraint preventing *M. gracilis* from expanding its orb beyond this typical range, such as increasing the chance that very large prey hit the web and destroy it, and increasing capture thread density allows either a reduction in variance or increase in mean of prey collected. By limiting investment in the framing and radial strands needed to support a larger orb, perhaps additional investment can be made into more capture spiral silk if only a limited volume of silk can be stored before constructing the web. It has also been shown that increased capture thread density might aid in capturing large prey items that become ensnared in multiple capture lines (Blackledge and Eliason 2007). However, because these larger prey captures were rarely observed in *M. gracilis* during our study, the increased capture thread density observed in this species likely serves a different function than large prey retention. Large prey scarcity in our study may be an artifact of limited sampling or differences in study environment, as a previous study observed *M. gracilis* capturing larger prey (Uetz and Hartsock 1987). If *M. gracilis* intercept fewer large prey items, this species comparison may demonstrate the architectural tradeoffs between retention and interception proposed by other studies (Chacón and Eberhard 1980; Blackledge and Eliason 2007). Smaller orbs make large prey interception less likely for *M. gracilis*, but should interception occur, retention may be more likely.

Total orb area can be considered as the measure of the area offered by the full capture spiral as if it were a cohesive surface upon which prey items strike. If an insect is not small or

agile enough to slip between the individual strands in the capture spiral without contact, the entire surface area should be considered a valid capture area for larger prey that cannot do so. Here, there is another distinct difference between our two comparison species, with most *V. arenata* orbs being much larger in diameter (30-60 cm) than most *M. gracilis* orbs (10-30 cm). Because *V. arenata* capture thread density is much lower, individuals can increase total area covered per unit of silk, which is predicted to increase large insect interceptions with roughly the same energetic investment (Herberstein and Elgar 1994; Xavier et al. 2021). It appears *V. arenata* are increasing their sampling on a 2-dimensional scale, which is predicted to increase interception of larger prey items. These prey items are the major contributors to the significantly higher total biomass that *V. arenata* actively consume. By increasing this 2-dimensional sampling, perhaps *V. arenata* are able to lower the variance experienced while targeting larger prey items, allowing them to forgo needing to consume the orb and collect smaller prey. *V. arenata* orbs are also bottom-top asymmetrical, which may balance the time it takes for a spider to reach prey in any direction from the central hub (Rao et al. 2011), whereas the symmetry of *M. gracilis* orbs may imply deprioritization of their ability to attack prey that is intercepted in areas of the orb that take the spider longer to reach (Biere and Uetz 1981). While no preference is shown for the angle of the orb surface rotated along a central vertical axis in *V. arenata* (Francini and Dalla-Pria 2015), which might be explained by another study that found that prey movement in this environment is largely non-directional (Biere and Uetz 1981), the consistently upright angle along a central horizontal axis (perpendicular to the ground) may encourage interception of larger, horizontally-traveling prey that cover more distance. *M. gracilis* individuals may be somewhat released from this strictly-upright orb orientation if they favor smaller, swarming prey

that travel both vertically and horizontally and that move mostly with respect to other conspecific individuals in the swarm rather than with respect to covering distance in the environment.

Once insects strike the web, individual behavior remains one of the final deciding factors whether prey items will become food or a lost opportunity. *M. gracilis* were previously found to ignore smaller prey (<3 mm in length) while actively attacking larger prey (4-8 mm), but larger prey than this typically escape from the web (Uetz and Hartsock 1987). In our study, however, *M. gracilis* captured significantly fewer larger prey items, and no observations were made of *M. gracilis* capturing >4 mm prey at all. Perhaps differences in habitat, season, or sample size can explain this distinct lack of large prey captures, but it may also indicate that these prey items are so rare for *M. gracilis* because of their smaller orb area that they may not present much selective pressure for successful capture. The average length of actively consumed items was significantly higher for *V. arenata* than *M. gracilis*. Despite *V. arenata* capture thread density being lower, individuals demonstrate “reeling” behavior in which they pull radial strands inward while running towards prey, which likely serves to further ensnare prey among multiple capture threads before the spider handles the prey and risks counter-attack while envenomating (Rao et al. 2019). Unlike other orb-weaving spiders, *V. arenata* individuals uniquely orient abdomen-down in the capture spiral, likely to face towards the upper portion of the web where the larger prey that fly higher are more common (Rao et al. 2011). As an example of this larger prey, *V. arenata* were observed capturing large Hymenopteran prey, such as *Vespula spp.* (yellow jacket wasps), which are potentially dangerous prey items that would likely escape from *M. gracilis* orbs or kill the spider in retaliation (Uetz and Hartsock 1987; Ceballos et al. 2005; Long, *pers. obs.*). Thus, behaviorally, *V. arenata* appear to be better primed for successfully subduing larger prey items than *M. gracilis*, whose behavioral distinction is reliably consuming the orb at the end of the

foraging period each evening. *V. arenata* individuals appear more capable of securing nutritional income from larger but rarer prey, while *M. gracilis* individuals appear to occasionally capture medium prey while consistently collecting passive prey by consuming the orb.

Temporal distributions of prey and predators are of increasing interest in recent studies (Schwartz et al. 2017), and the resulting ecological interactions are often dictated by the chronotype of the species in question. *M. gracilis* individuals begin their foraging period significantly later in the morning than do *V. arenata* individuals; thus, on a daily scale, they sample a narrower temporal window. However, they experience web destruction significantly less than *V. arenata*, which may be another advantage of a smaller web, perhaps from not intercepting as many larger insects that highly damage the web or not absorbing as much force from gusts of wind blowing perpendicular to the orb. This may indicate that on a seasonal scale, their temporal sampling period is much more consistent, with more mid-range days than highly profitable or highly indebting. Our field observations were not able to account for the propensity of each species to rebuild the web following foraging disruption without tagging spiders at an individual level, so perhaps the higher web disruption experienced by *V. arenata* is negated by a willingness to rebuild the capture spiral throughout the day. The opportunity cost of the time taken to rebuild might be lower in *V. arenata* individuals, as several were observed completing a capture spiral in less than 30 minutes, while *M. gracilis* seem to take roughly an hour (Long, *pers. obs.*). Thus, by extending the foraging window both earlier and later than *M. gracilis*, *V. arenata* appears to increase temporal sampling within the general diurnal activity pattern. *M. gracilis* has been shown to capture largely Dipteran and Hymenopteran prey (Uetz and Hartsock 1987), which likely comprise a majority of this diurnally available prey for both species.

One major missing component from our study is observations of predation, as well as observations overnight in general. While *M. gracilis* individuals reliably consume their orbs in the evening, a high proportion of *V. arenata* individuals simply abandoned the orb to retreat to the edge of framing strands or a nearby branch; however, upon beginning the observation periods in the morning, no *V. arenata* webs were noted as already present. If *V. arenata* individuals needed the passive income of ignored prey to survive, we would predict that they should immediately consume the orb and not risk it being lost overnight, and they consistently do not. Do *V. arenata* leave the web up overnight to continue sampling without remaining in the orb and consume it before dawn, or do they ignore the orbs which are simply lost before morning? Relinquishing foraging overnight despite targeting larger prey contradicts a previous study that found that larger insects, which would need to be handled and subdued, are more common in nocturnal foraging periods, but perhaps this is environment-dependent (Xavier et al. 2021). Are they capable of coming down from the retreat in order to capture prey if vibrations are detected?

We suspect that increased risk of predation may drive selection against the foraging period extending into the night, but a small proportion of *V. arenata* individuals continued to forage after the final observation around 2300; perhaps individual hunger state pushes some individuals to take the risk of foraging at night if they have had little success during the day (or compounded failures over several unfortunate days). Further study in which individual nutritional state and foraging cessation are compared while observers are extremely careful not to expose individuals to perhaps any artificial light should be done. We also suspect that predation during the day, when visual cues are strongest, is the explanation for the anti-predator defenses (guanine deposition in both, and abdominal spines in *M. gracilis*), but guanine coloration in *V. arenata* has been shown have a prey attractant function (Rao et al. 2014). Thus,

perhaps coloration serves a very different function in each species: in *V. arenata*, it attracts prey to encourage a sequence of highly profitable days before a rare predation event occurs, while in *M. gracilis*, it dissuades predators from disrupting foraging so individuals can continue taking consistent temporal samples with reliable prey intake.

A Synthesis of Risk-Sensitivity, Foraging Strategy, and Community Ecology

Daily life in the deciduous forest ecosystem offers a limited amount of temporal, spatial, and nutritional resources for these species to exploit. Within a given temporal foraging period, and a given spatial sample of the orb, these two spider species must capture the nutritional intake needed to survive and reproduce.

M. gracilis individuals appear to collect small, abundant insects that can be passively captured and consumed with the orb and thus have increased the capture thread density to raise thread length for a given area while remaining present if medium prey items that must be actively captured are intercepted. By employing anti-predator defenses to reduce predation risk during the day and potentially dissuade predators before an attack occurs, they may be able to forage consistently and reach the reproduction threshold over the course of a season through a risk-averse strategy. They experience less variance in passive and active prey captures as well as fewer foraging interruptions, but mean total biomass intake is lowered because of the focus on smaller prey. Thus, the foraging strategy of *M. gracilis* can be summarized as risk-averse, focused on reducing variance because mean daily intake is above the survival threshold and, on a broader scale, mean seasonal intake is above the reproduction threshold.

V. arenata individuals appear to focus on large, rarer insects that must be actively captured using unique behavioral adaptations, such as reversed orientation and reeling, and

appear to forego prey collected passively in the capture spiral. Their coloration may increase prey interceptions, but they may be forced to accept the risk of rare predation events during the day without spines or stabilimenta. Larger capture spirals, a longer potential foraging period, and behavioral adaptations increase sampling to compensate somewhat for variance in prey interceptions and minimize prey escape, but the overall strategy causes them to experience more variation in active and passive prey captures as well as more foraging interruptions. In our study, the *V. arenata* population as a whole experienced a higher mean biomass intake, but this is distributed unevenly amongst individuals by increased variance. Thus, the foraging strategy of *V. arenata* can be summarized as risk-prone, focused on targeting more valuable insects and accepting variance so that some members of the population might quickly reach the reproduction threshold before predation or starvation occurs.

These distinct foraging strategies appear to allow these species to coexist in the same habitat. While they sample out of the same diurnal flying insect prey, there may not be harsh interspecific competition, similar to other orb-weaving spiders in previous studies (Wise 1979 and 1981). Smaller insects appear abundant enough to sustain the *M. gracilis* population through passive orb consumption, and some *M. gracilis* individuals are fortunate enough to capture a few medium prey items. *V. arenata*, however, forgo smaller prey and consistently capture medium-sized insects, while some *V. arenata* individuals are fortunate enough to capture a few large prey items. While smaller prey ensnared in *V. arenata* orbs are removed from the total available prey for *M. gracilis*, the relative abundance of these smaller insects implies little harm to either species from competition in the current state of this ecological community. Food limitation and its impact on population growth deserves further investigation. If both species are food-limited for egg production, but not because of direct competition, then perhaps the

limitations are on how efficiently each species can collect desired prey. If both species are not food-limited, however, predation or other physiological constraints on population growth (such as suitable habitat, predation risk, abdomen size limiting the number of eggs produced, or nutritional restrictions other than purely biomass) likely determine carrying capacity in these populations.

If released from direct competition, other consequences of risk-sensitive foraging may drive specialization between these two species. If *V. arenata* webs were to become denser, they might collect more small prey, but physiological restrictions on web size (silk volume, time investment, additional metabolic cost of construction) would likely reduce spatial sampling and force a tradeoff for capturing less large prey. Similarly, if *M. gracilis* webs were to expand under the same physiological restrictions to perhaps capture more large prey, lowered capture thread density would likely increase variance in passively captured prey while individuals struggle to successfully subdue larger prey because of a lack of behavioral adaptations in handling. As the community exists presently, small flying prey might pass through more sparse *V. arenata* webs and end up in nearby *M. gracilis* webs; similarly, larger prey that escape or miss smaller *M. gracilis* webs might continue on to be captured in *V. arenata* webs, explaining why these spiders can be observed in very close proximity to one another, even using the same plants for attachment points.

These distinct strategies also imply annual fluctuations in population size of each species depending on the preceding year. If one year has an abundance of flying insects that make foraging particularly profitable, *V. arenata* will likely have abundant offspring that will hatch the following year, while *M. gracilis* may experience limited growth. However, if a year is

particularly sparse on prey, *V. arenata* populations may experience a crash, while *M. gracilis* populations remain lowered but more stable.

If selection for foraging period is not harshly regulated, either species could potentially extend the foraging period into the night (as we observed in a small proportion of individuals, perhaps because of nutritional state), but there appears to be some tradeoff component left undescribed here. If there is very little prey and thus very little potential gain from foraging overnight, we would predict that retreat is more beneficial than risking web damage, for example. If there is substantial prey overnight, we would predict that some other selective force on foraging period is the driver of diurnal activity, such as increased risk of predation at night or perhaps even a physiological cost of extending the maximum foraging period.

Final Conclusions

With this study, we have identified different approaches to risk-sensitive foraging between species which could contribute to niche partitioning within the temporal and foraging niche and in the same habitat. We believe that partitioning along certain prey sizes allows these two species to coexist, and in turn, each has further specialized to adapt to the resulting variance from each strategy. Investigating niche partitioning through the lens of risk-sensitive foraging might answer further questions about how similar species coexist even once maximum spatial and temporal partitioning seems to have been reached. We also provide finer resolution on the temporal distributions of behaviors and prey captures for well-described species.

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